Orientation discrimination across the visual field: matching perceived contrast near threshold

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Abstract

Performance can often be made equal across the visual field by scaling peripherally presented stimuli according to $F = 1 + E/E_2$ where E_2 is the eccentricity at which stimulus size must double to maintain foveal performance levels. Previous studies suggest that E_2 for orientation discrimination is in the range of 1.5°–2° when stimuli are presented at contrasts well above detection threshold. Recent psychophysical and physiological evidence suggests spatial reorganization of receptive fields at near-threshold contrasts. Such contrast-dependent changes in receptive field structure might alter the amount of size scaling necessary to equate task performance across the visual field. To examine this question we measured orientation discrimination thresholds for a range of stimulus sizes and eccentricities (0°–15°). We used the same procedure previously employed except that stimuli were presented at near-threshold contrasts. We controlled for the effects of perceptual contrast on thresholds through a matching procedure. A standard line of 3° in length presented at fixation was set to 2 just noticeable differences above detection threshold. The perceived contrast of all other stimuli was adjusted by the subject to match this one. Orientation discrimination thresholds were then obtained at these matching contrasts for all stimulus sizes and eccentricities. E_2 values of 3.42° and 3.50° were recovered for two subjects; these values were about a factor of two larger than E_2 values previously found for this task when stimuli were presented at higher physical contrasts.
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1. Introduction

Performance on many spatial vision tasks depends on visual field location and tends to decline with increasing retinal eccentricity. Thresholds can often be made equal, however, when stimuli are scaled in all spatial dimensions according to

$$F = 1 + E/E_2 \qquad (1)$$

where E_2 indicates the eccentricity (E) in degrees at which stimulus size must double to maintain equivalent-to-foveal performance levels (Levi, Klein, & Aitse-baomo, 1984, 1985). The smaller the value of E_2 the faster stimulus size must increase in the periphery in order for thresholds to remain constant. The magnitude of E_2 is often thought to reflect eccentricity-dependent changes in the spatial scale of the mechanisms required to perform the task at hand. It was therefore hoped that this psychophysically-derived measure would reveal something about the neural mechanisms that subserve performance on different tasks (Toet & Levi, 1992). Ideally, tasks could be classified according their E_2 value.

There is at least some evidence that E_2 can indeed provide information about the functional organization of the visual system. Mäkelä, Whitaker, and Rovamo (1993) suggested that tasks such as curvature detection, vernier acuity and orientation discrimination probably rely on similar cortical mechanisms (i.e., orientation

selective mechanisms) and pointed out that these tasks often elicit E_2 values within a reasonably similar range when tested using similar spatial scaling methods; viz., curvature detection, $E_2 = 1.42°–2.27°$ (Whitaker, Latham, Mäkelä, & Rovamo, 1993); vernier acuity, $E_2 = 1.06°–1.96°$ (Whitaker, Rovamo, MacVeigh, & Mäkelä, 1992); orientation discrimination, $E_2 = 1.95°$ (Mäkelä et al., 1993) and $E_2 = 1.29°–1.83°$ (Sally & Gurnsey, 2003). These E_2 values are generally smaller than those obtained for grating detection tasks in which values of 2.5° or more are often recovered; these latter tasks are assumed to be limited by retinal mechanisms (e.g., Levi et al., 1985; Wilson, Levi, Maffei, Rovamo, & DeValois, 1990). Experiments that have derived E_2 estimates from the relative decline in performance for stimuli of a fixed size—rather than through size scaling methods—also find that E_2 values for position acuity tasks, such as vernier acuity, tend to be much smaller than those recovered for grating detection and resolution tasks (e.g., $E_2 \approx 0.77°$, Levi et al., 1985; $E_2 = 0.8° \pm 0.2°$, Beard, Levi, & Klein, 1997).

It is apparent from the brief review above that E_2 values, even for the same task (e.g., vernier acuity), can vary widely from laboratory to laboratory (see Table 2, Beard et al., 1997). Also, E_2 values can also vary greatly across tasks (from less than 1° to greater than 10°, Whitaker, Mäkelä, Rovamo, & Latham, 1992). Beard et al. pointed out that some of this variability may reflect differences in testing methodology as well as experimental confounds such as the involvement of different visual mechanisms across testing conditions. Variations in perceptual contrast across stimulus sizes and eccentricities may also confound experimental findings.

Melmoth, Kukkonen, Mäkelä, and Rovamo (2000b) and Mäkelä, Näsänen, Rovamo, and Melmoth (2001) have suggested that the 100-fold range of E_2 values reported in the literature may reflect—at least in part—the use of experimental procedures that do not explicitly consider eccentricity-dependent limitations associated with stimulus contrast. They argued that contrast may need to be scaled with eccentricity in much the same way that size must be scaled, in order to capture all eccentricity-dependent variability in the data. Melmoth et al. (2000b) and Mäkelä et al. (2001) measured contrast sensitivities for target identification or detection as a function of image size at various eccentricities in the visual field. An E_2 for size (E_{2Size}) and an E_2 for contrast ($E_{2Contrast}$) were determined by computing the amount of horizontal shift (size scaling) and vertical shift (contrast scaling) required to superimpose contrast thresholds obtained at all sizes and eccentricities. Mäkelä et al. (2001) obtained values for E_{2Size} of 1.43° and 1.87° for two subjects in a face discrimination task when *size scaling* alone was used to scale the data. The values were *larger* ($E_{2Size} = 2.73°$ and 3.19°) and more eccentric-

ity-dependent variance was explained, when both size and contrast scaling was performed.

Sally and Gurnsey (2003) also concluded that controlling perceptual contrast is critical when calculating E_2 values, but arrived at this conclusion from a different perspective. We determined E_{2Size} for orientation discrimination using stimuli of much higher physical contrasts and included in our calculations of E_{2Size} only orientation thresholds that remained at an asymptotic level over a range of stimulus contrasts (Sally & Gurnsey, 2003). The values of E_{2Size} recovered in this way tended to be somewhat *smaller* ($E_{2Size} = 1.29°–1.83°$) than those that we obtained using identical stimuli but without the requirement that thresholds reach an asymptotic level with respect to variations in contrast ($E_{2Size} = 2.08°–3.25°$). Therefore, our results as well as and those of Mäkelä et al. (2001) indicate that estimates of E_{2Size} may be erroneous when the contrast dimension is not taken into account. These findings also suggested to us that E_{2Size} may depend on the contrast level at which discrimination performance is evaluated; viz., E_{2Size} may be small when stimulus contrast is sufficiently high and large when stimuli contrast is close to threshold.

On the other hand, orientation discrimination and face discrimination may rely upon quite different processes. Therefore, to assess the suggestion that E_{2Size} is relatively larger for low-contrast stimuli, it would be best to compare the effect of contrast within a single task. With this in mind, Sally, Gurnsey, and Poirier (2002) determined E_{2Size} for orientation discrimination using a broadband stimulus identical to that used by Sally and Gurnsey (2003) using two methods (Melmoth, Kukkonen, Mäkelä, & Rovamo, 2000a, 2000b; see also Strasburger, Harvey, & Rentschler, 1991 and Poirier & Gurnsey, 2002) that control for contrast at near-threshold levels. The subject's task was to discriminate between a vertical line and one oriented 1.5° from vertical. We found that both procedures yielded comparable size-scaling estimates (E_{2Size}) that averaged 5.44° (range 3.71°–6.36°). These values are far larger than those recovered in our study using stimulus contrasts well above detection threshold in which an average E_{2Size} of 1.51° equated orientation discrimination performance across eccentricities (Sally & Gurnsey, 2003). We also found that the average $E_{2Contrast}$ was very large, indicating that very little or no contrast scaling was required to capture all eccentricity-dependent variation in the data.

Taken together, the results of Sally and Gurnsey (2003) and Sally et al. (2002) suggest that small values of E_{2Size} are recovered at contrasts well above threshold and large values of E_{2Size} are recovered at contrasts close to detection threshold. However, the conditions of the two experiments were quite different so it would be useful to replicate most of the conditions of Sally and Gurnsey (2003) using stimuli that are equated for per-

ceptual contrast at near threshold levels. This is the objective of the present research.

To achieve this we selected a 3° line presented at fixation to serve as a reference stimulus. The reference was then set to a contrast level 2 just noticeable differences (JNDs) above detection threshold and the perceived contrast of all other stimuli at all eccentricities was adjusted by the observer to match that of the standard. Once the perceived contrast of all line stimuli was equated we determined orientation discrimination thresholds for all line sizes at all eccentricities. The amount by which peripheral curves had to be shifted laterally to superimpose all data determined the $E_{2\text{Size}}$ for orientation discrimination.

2. Method

2.1. Subjects

Two subjects, SM and one of the authors (SS), participated in all phases of the experiment. Both subjects were moderate myopes and wore their distance correction during testing. Viewing was monocular with the dominant eye (left for both subjects) and stimuli were presented to the temporal retina.

2.2. Apparatus

Stimulus images were generated using a Power Mac G4 computer and presented on a 21 in. Sony Trinitron CRT colour monitor having a pixel resolution of 1600×1200. Pixel width was 0.233 mm and the frame refresh rate was 85 Hz. Background luminance of displays was 13.0 cd/m^2. Luminance resolution was increased by combining color channels with a video summation device (Pelli & Zhang, 1991) which allows contrast resolution of up to 12-bit accuracy. Software available in the VideoToolbox (Pelli, 1997) was used to calibrate the device, and correct for display non-linearities. Absolute luminance levels were determined with a Minolta CS-100 photometer.

2.3. Stimuli

Stimuli were created and the experiments were run in the MATLAB (Mathworks Ltd.) programming environment using routines provided in the Psychtoolbox (Brainard, 1997) that permit access to the routines in VideoToolbox (Pelli, 1997). Stimuli were broadband line patterns having Gaussian cross-sections (with a spread of σ_G) along their minor axes. The nominal line width ($\pm 2\sigma_G$) was 11% of its length. These stimuli were identical to those we used previously in orientation discrimination tasks by Sally and Gurnsey (2003) and Sally

et al., 2002 and similar to stimuli used by Mäkelä et al. (1993).

2.4. Procedure

The following details were common to all tasks. Thresholds measurements were obtained using either an adaptive procedure (QUEST, Watson & Pelli, 1983; Pelli, 1987) which assumes an underlying Weibull function or by the method of adjustment. Tasks using the adaptive procedure were two-interval forced-choice (2IFC) and the 82% correct detection level was taken as threshold. Auditory feedback was provided after each response. Threshold estimates resulted from approximately 60–65 trials. Details concerning the method of adjustment are provided below. For all tasks, the final threshold represents the mean of three estimates. To avoid fatigue the data were collected in a large number of sessions lasting approximately 25 min each. All testing was conducted in a dimly lit room. The subjects received extensive practice with all tasks before data collection began.

2.4.1. Selecting the contrast level of reference stimulus

The reference was a 3° vertical line stimulus identical to that used in the orientation discrimination task (see below) and within the range of stimulus sizes that were tested (0.1875°–12°). The stimulus was presented at fixation and preceded by a fixation dot (6 pixels in diameter). The QUEST procedure was used to determine contrast detection threshold for the reference stimulus. Each stimulus interval was 200 ms in duration with an inter stimulus interval (ISI) of 300 ms. Each interval was signaled by an auditory tone as well as a square frame (2 pixel line width at 17.25 cd/m^2, 5.8° in diameter) centred at the location of the test stimulus. A frame was only provided for this part of the experiment and was required because of the brief duration of test and inter-stimulus intervals. The subject's task was to indicate, via the mouse, the interval in which the stimulus had appeared.

A similar 2IFC adaptive procedure was used to determine contrast increment thresholds (JNDs) for the reference stimulus. Stimulus interval and ISI duration were as indicated above. A trial consisted of the sequential presentation of the two, 3° vertical line stimuli. One interval contained the stimulus set to a fixed predetermined level of contrast (contrast threshold or 1 JND above threshold) and the contrast of the test stimulus in the other interval was varied. The subject's task was to indicate the interval containing the stimulus with the highest contrast.

2.4.2. Matching perceived contrast/Measuring contrast detection thresholds

The 3° reference line was set to 2 JNDs above detection threshold for each subject. This provided a

standard to which the perceptual contrasts of all other lines (of all sizes and eccentricities) were matched using the method of adjustment. The reference and test stimulus were presented simultaneously for 500 ms at all eccentricities except fixation. (The 500 ms presentation duration was found to produce less variable matches than the 200 ms presentation duration.) For foveal presentations, the reference and test stimuli were presented sequentially with an inter-stimulus interval of 600 ms. Subjects matched the perceived contrast of the test stimulus with that of the reference by pressing the up and down arrow keys on the computer keypad. While the arrow keys were depressed no stimulus appeared. When the arrow keys were released the stimulus immediately reappeared on the screen for 500 ms. The subject repeated the adjustment process until satisfied with the match (usually about 10–20 presentations were required). The subject then terminated the trial using a key on the keyboard.

Stimulus sizes were manipulated by varying viewing distance and/or changing the size of the stimulus on the display. Stimulus sizes ranged from 0.1875° to 12° in logarithmic steps. Stimuli from 3° to 12° were viewed from 50 cm. The largest stimulus size was created by changing pixel resolution to 800×600 and doubling the spatial extent of the image (in pixels) horizontally and vertically; i.e., this quadrupled the number of pixels per stimulus. Stimuli smaller than 3° (1.5°, 0.75°, 0.375° and 0.1875°) were viewed from successively greater distances. The smallest stimuli were viewed from a distance of 375 cm and pixel number was reduced (line length changed from 112 to 53 pixels). All eccentricities were tested at one stimulus size before moving to the next size. The order in which stimulus sizes and eccentricities were tested was random.

The adjustment procedure described above was modified to obtain contrast detection thresholds for all of the viewing conditions. The test stimulus was presented in a single interval of 200 ms signaled by the presence of a tone. A fixation dot was provided for all eccentricities except the fovea. The subject's task was to adjust the contrast of the test stimulus using up and down arrow keys until the presence of contrast could be just detected. As in the contrast matching task, the stimulus did not appear on the screen while arrow keys were depressed. The adjustment process was terminated once the subject was satisfied with the contrast level selected (usually about 8–12 stimulus presentations).

2.4.3. Orientation discrimination experiment

The task was designed to be similar in all respects except stimulus contrast to the orientation discrimination experiment previously reported by Sally and Gurnsey (2003). The contrasts of the test stimuli were set to the level determined from the matching procedure. Orientation thresholds were measured over a range of sizes at

0°, 2.5°, 5°, 10° and 15° in the right visual field (temporal retina). The viewing sizes/distances were as indicated for the contrast matching task. A fixation dot (6 pixels in diameter) was present for all eccentricities except at fixation. All eccentricities were tested at one stimulus size before moving to next size. The order in which stimulus sizes were tested was random. The horizontal stimulus location was jittered by 5% of the stimulus size from trial to trial so that absolute stimulus location could not provide an orientation cue.

A trial consisted of the sequential presentation of two line stimuli. Each pattern was presented for 200 ms separated by an inter-stimulus interval of 300 ms. One of the lines was vertical and the other was tilted counterclockwise. The subject's task was to report via the mouse which interval contained the tilted stimulus.

3. Results

3.1. Contrast matching and contrast detection thresholds

Fig. 1 shows contrast matching (top graphs) and contrast detection thresholds (bottom graphs) plotted
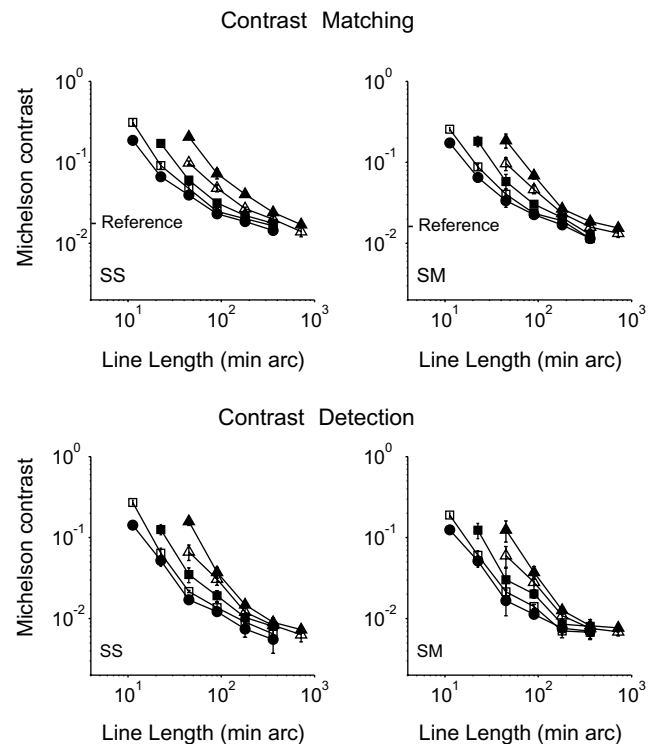

Fig. 1. Michelson contrast thresholds at each eccentricity plotted as a function of line length for contrast matching (top graphs) and contrast detection (bottom graphs) for subjects SS and SM. Standard errors are shown for each point. The contrast level of the reference stimulus is indicated. Eccentricities from zero to fifteen degrees: 0° (filled circles), 2.5° (unfilled squares), 5° (filled squares), 10° (unfilled up-arrows), 15° (filled up-arrows).

against line length for each of the five eccentricities. At each eccentricity thresholds show an initial rapid decline followed by a more gradual change, and finally reach a plateau at very long line lengths. Also, for both tasks, average minimal values (i.e., thresholds or matching contrasts) are essentially identical at all eccentricities. Because of this we did not use a double scaling procedure (e.g., Melmoth et al., 2000a, 2000b; Poirier & Gurnsey, 2002) to fit the data (see below). In other words, only size scaling was used in the fits. Therefore, all E_2 values reported are those for size-scaling and E_2 should be read as $E_{2\text{Size}}$.

We assumed the relationship between line length and contrast threshold would be well described at all eccentricities by the function

$$C = C_{\min}(1 + L_{\text{crit}}/x)^n \qquad (2)$$

adapted from Mäkelä et al. (1993), where C is the contrast threshold, $C_{\min}$ refers to the minimum contrast threshold, L_{crit} refers to the critical line length marking the transition between the decreasing and constant parts of Eq. (2), n determines the slope of the line and x refers to scaled line length. (We also assumed that this function would well describe the contrast matching data.) According to linear scaling theory, thresholds at all eccentricities should fall onto a single curve when line length is scaled (divided by) by an appropriate constant; i.e., $F = 1 + E/E_2$. For each subject, the entire data set was fit by finding parameters for $C_{\min}$, L_{crit}, n, and E_2 that minimize the deviation of the data from the parametric curve. Our measure of deviation was the RMS error defined as

$$e_{\text{rms}} = \sqrt{\frac{1}{n}\sum_{i}^{n}(\log Y_{i(\text{est})} - \log Y_i)^2} \qquad (3)$$

where n is the number of data points, Y_i is a measured data point and $Y_{i(\text{est})}$ is the value predicted by the parametric function. We express the goodness of the fit as $G = 1 - e_{\text{rms}}$ (Melmoth et al., 2000a, 2000b). The data were fit using the error minimization routine provided in MATLAB (Mathworks Ltd.); this routine (f_{mins}) uses the Nelder–Mead simplex (direct search) method. Numerical solutions found in this way may represent local rather than global minima. Therefore, we ran the minimization routine twenty times for each fit, each starting from a different randomly chosen initial condition, and we report the best fits obtained in this way.

Scaled line length data for the contrast detection and contrast matching tasks are shown in Fig. 2. Best-fitting functions are indicated as solid curves. Goodness of fits values ranged from $G = 0.94$ to 0.96 and were similar across the two tasks and subjects. Values for $C_{\min}$, L_{crit}, and n for the contrast detection task were 0.005, 26.28 and 2.74 for SS and 0.005, 29.52 and 2.47 for SM, respectively. The corresponding values of these parame-
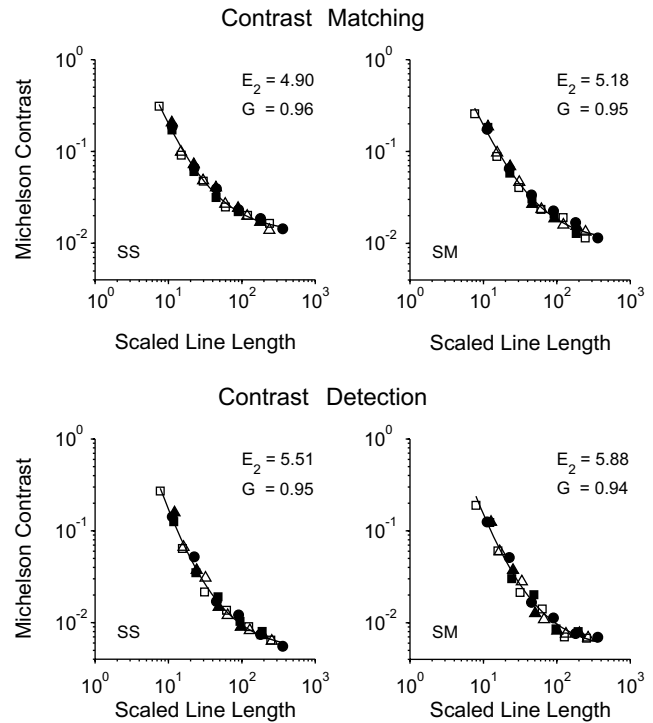

Fig. 2. Scaled line length data for the contrast matching (top graphs) and contrast detection (bottom graphs) tasks. Scaled line length equals the actual line length (in minutes of visual angle) divided by F, where $F = 1 + E/E_2$. Goodness of fit (G) is indicated.

ters for the contrast matching task were 0.013, 24.04 and 2.23 for SS and 0.013, 35.89 and 1.93 for SM, respectively. The average E_2 for the contrast detection task was 5.7° (5.51° and 5.88° for SS and SM, respectively) and 5.04° (4.90° and 5.18° for SS and SM, respectively) for the contrast matching task. E_2 values were therefore in the same range for both tasks and on average only 13% larger for contrast matching. The similarity of E_2 values for contrast matching and contrast detection is not unexpected; it is likely that comparable low-level mechanisms subserve performance on both tasks.

3.2. Orientation discrimination thresholds

Orientation discrimination versus line length functions (see Fig. 3, top panels) have the same general form at all eccentricities. Thresholds show an initial steep decline, followed by a more gradual decrease with increasing line length and appear to approach a plateau at very long line lengths. The average minimum thresholds were 1.32° and 1.29° for subjects SS and SM, respectively. At high contrasts these subjects achieved minimal orientation thresholds of 0.56° and 0.55° for SS and SM, respectively, for the same stimuli (Sally & Gurnsey, 2003).

We fit the orientation threshold versus line length data using Eq. (4)

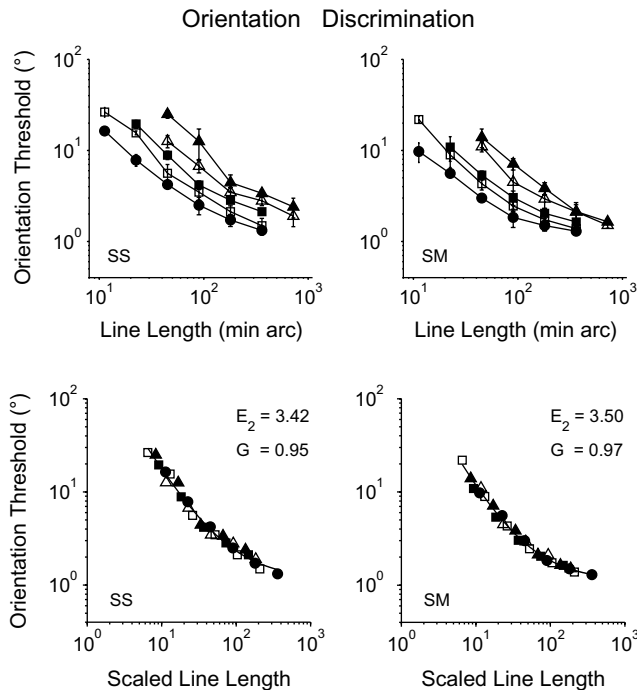$$\Delta\theta = \theta_{\min}(1 + L_{\text{crit}}/x)^n \qquad (4)$$

Fig. 3. Orientation discrimination thresholds (°) at each eccentricity plotted against line length (top graphs) for subjects SS and SM. Standard errors are shown for each point. Scaled line length data (bottom graphs). Symbols refer to eccentricities as in Fig. 1. Goodness of fit (G) as indicated.

where $\Delta\theta$ indicates orientation threshold, θ_{min}, the smallest discriminable orientation difference; L_{crit}, x and n have the same interpretation as in Eq. (3). Details of fitting procedure were as described above for the contrast detection and contrast matching tasks. Scaled line length data for two subjects are shown in Fig. 3 (bottom graphs). Goodness of fits values were $G = 0.95$ and 0.97 for subjects SS and SM, respectively. These values compare favourably with those obtained previously at high contrasts ($G = 0.95$ for SS and SM). Thus, a substantial amount of eccentricity-dependent variability was removed from the data using a single scaling function. Values for θ_{min}, L_{crit}, and n were 1.16, 69.55 and 1.34 for SS and 1.11, 40.95 and 1.45 for SM, respectively. The average E_2 recovered for this task was 3.46° (3.42° and 3.50° for SS and SM, respectively). These values are considerably larger than those obtained using an identical stimulus at high contrasts (Sally & Gurnsey, 2003). We previously reported an average E_2 for this task of 1.51°; the average was taken across two subjects (SS and SM) and two types of stimuli (broadband and narrowband). The average E_2 value for the broadband stimulus (identical to that used here except for contrast) was 1.38°. Therefore, the present results indicate that E_2 increases by a factor of 2.51 (i.e., 3.46/1.38) at near threshold contrasts. The E_2 values for orientation discrimination in the present experiment are also substan-

tially larger than those obtained by Mäkelä et al. (1993) using a similar stimulus at contrasts well above detection threshold. The authors reported an average E_2 of 1.95° for this task. (We derived E_2 estimates of 1.77°–1.85° for their data using our present fitting procedure.) We can therefore conclude that E_2 values for orientation discrimination are significantly larger when stimuli are presented at near-threshold levels of contrast.

3.3. Matching perceived contrast at high levels of physical stimulus contrast

It might be argued that our conclusion rests upon a comparison of the present data with other studies that have used slightly different methodologies. In the study of Sally and Gurnsey (2003, Experiment 3) we measured orientation thresholds over a range of stimulus contrasts. We included in the calculation of E_2 only those thresholds that had reached an asymptotic level. We did not, however, match perceived contrast to a reference stimulus as in the present study. Although this is true, there are two straightforward responses.

First, consider that if the physical contrasts of all stimuli in the ensemble used by Sally and Gurnsey were increased so that their perceived contrasts matched the highest perceived contrast in the ensemble, then orientation thresholds would not change. The *criterion* for the inclusion of thresholds in the E_2 calculation was that they did not change with increases in contrast.

Second, it *is* fair to ask about the possible variation in perceived contrast across viewing conditions for contrasts at which asymptotic levels of performance had been achieved. To assess this question we chose a 3° line presented at the furthest eccentricity (15°) as a reference stimulus. The Michelson contrast of the reference stimulus was 0.383, which was 75% of maximal available contrast. Subjects SS and SM matched the perceived contrast of all other stimuli [1] to the reference using the same adjustment procedure used for low-contrast stimuli. The initial contrast of the matching stimulus was randomized over a range of Michelson contrasts from 0.153 to 0.485.

Fig. 4 shows contrast matches plotted against line length for each of the five eccentricities. Perceived (matching) contrast is clearly independent of line length and eccentricity (cf., Fig. 1). These data are in agreement with Cannon's (1985) demonstration that at Michelson contrasts of 0.33 and above the perceived contrast of sine wave gratings did not depend on spatial frequency or area. Furthermore, Cannon (1985) showed that at high contrasts perceived contrast showed essentially no change with eccentricity (to 40°), even though there

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[1] Stimuli smaller than 45′ were presented in the high contrast study at 0° and 2.5° but could not be tested because stimulus separation exceeded screen dimensions.
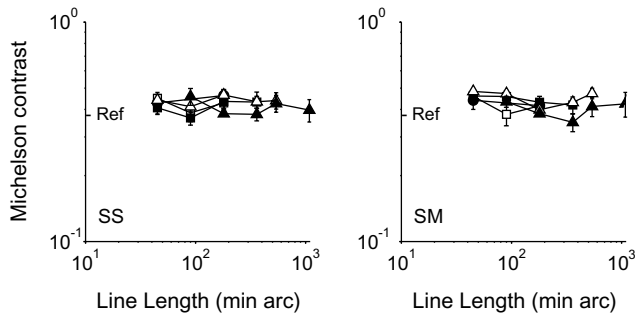
Fig. 4. Michelson contrasts at each eccentricity plotted as a function of line length for contrasts matching at high contrasts used in Sally and Gurnsey (2003) for subjects SS and SM. Standard errors are shown for each point. The contrast level of the reference stimulus (Ref) is indicated. Symbols refer to eccentricities as in Fig. 1.

was an approximately 10-fold variation in thresholds. These results are also consistent with those of Georgeson and Sullivan (1975) who had subjects adjust the contrast of test stimuli to match the perceived contrast of a standard, 5 cpd grating of fixed contrast. At contrasts of 0.3 and above the contrast of the test stimulus was the same as the contrast of the standard grating.

We conclude that perceived contrast of stimuli used in our high contrast experiment were approximately equated. In other words, if Sally and Gurnsey (2003) had employed a contrast matching procedure prior to the measurement of orientation discrimination thresholds, their conclusions would have remained the same. The average E_2 at near-threshold contrasts (3.46°) is 2.51 times greater than the average E_2 recovered using the same broadband stimuli at asymptotically high contrasts (1.38°). When submitted to a one tailed, paired t-test this difference is statistically significant [$t(1) = -37.9$, $p = 0.008$]. This represents an extremely large effect size; Hedges's (1982) $g = 20.23$. In our view, the present data in conjunction with those of Sally and Gurnsey (2003) make a convincing argument for the contrast dependence of peripheral spatial scaling factors.

4. General discussion

In the present study the average size-scaling E_2 for orientation discrimination at low matched contrasts was 251% larger than those we obtained previously at high asymptotic contrasts using otherwise identical stimuli, subjects and orientation threshold measuring procedures (Sally & Gurnsey, 2003). Thus, the contrast level at which stimuli are presented is a critical determinant of spatial E_2.

These results are generally consistent with those of Sally et al. (2002) who reported size-scaling E_2 values for orientation discrimination ranging from 3.71° to 6.86° with an average of 5.44°. This value is larger than our present size-scaling estimate of 3.46°, perhaps be-

cause there were methodological differences between the two studies; i.e., orientation discrimination thresholds were measured in the present study and a fixed orientation difference was used in Sally et al. (2002). Most importantly, however, both studies found that large size-scaling E_2 values for orientation discrimination are required for stimuli with contrasts close to detection threshold. These findings agree with the results of other spatial scaling studies conducted at near-threshold contrasts. For example, size-scaling E_2 values of 2.73° and 3.19° for two subjects have been reported for face discrimination (Mäkelä et al., 2001) and E_2 values of 3.60° and 6.38° have been obtained for detection of phase-distortions in bandpass filtered faces and polar grating stimuli (Melmoth et al., 2000a).

In addition to the size-scaling estimates for orientation discrimination, we determined the size-scaling E_2 values required to equate for perceived contrast as well as contrast detection across eccentricities. Results were very similar for the two cases; 5.7° and 5.04° for the contrast matching and detection tasks, respectively. The similarity of these E_2 values is presumably because stimulus contrasts for the matching and detection tasks were at reasonably similar levels; viz., two JNDs above detection threshold and detection threshold, respectively. It is possible that these E_2 values reflect a reliance on similar mechanisms to solve both contrast matching and detection tasks.

To our knowledge no other studies have determined size-scaling E_2 values associated with contrast (detection and matching) using a broadband stimulus. Tasks that assess the detection of stimulus contrast generally employ narrowband stimuli. In an early study, Rovamo and Virsu (1979) measured contrast sensitivity across the visual field and showed that performance could be made approximately equal at all eccentricities when stimuli were scaled in proportion to local ganglion cell spacing, which corresponds to an E_2 of about 3°. Thibos, Cheney, and Walsh (1987a, 1987b) pointed out the the importance of distinguishing between resolution limits (i.e., limits on the ability to perceive a stimulus veridically) and detection limits (i.e., the limits on the ability to correctly report the presence of a stimulus). Thibos et al. (1987a, 1987b) and Anderson, Zlatkova, and Demirel (2002) provided further evidence that resolution of achromatic and chromatic sine wave gratings is limited by the density of beta (midget) retinal ganglion cells. Thibos et al. (1987b) and Anderson et al. (2002) also showed that in the periphery gratings may be detected at frequencies beyond the resolution limit. In this case the stimuli are perceived non-veridically because they arise from aliasing. Thibos et al. (1987b) report that "At a given eccentricity, the very finest pattern which produces aliasing has a spatial period which approaches the smallest anatomical dimension: the diameter of a single photoreceptor." (p. 2193, data from Polyak, 1941).

Our analysis of these limited data (Fig. 3, Thibos et al., 1987a) suggests that eccentricity-dependent changes in cone size are associated with E_2 values of 10° or more. Taken together, this evidence suggests that large E_2 values for contrast detection and stimulus resolution are often associated with retinal mechanisms. It is therefore reasonable to assume that our size-scaling E_2 values for contrast detection and matching of about 5°–6° reflect subcortical limitations, but we cannot rule out the possibility that these E_2 values are associated with contrast-dependent limitations associated with cortical mechanisms.

Sally et al. (2002) recovered *contrast-scaling* E_2 values that averaged 85.5°, which might seem inconsistent with the *size-scaling* E_2 values recovered for the contrast detection or matching tasks in the present experiment. Of course, there is no inconsistency. The size-scaling E_2 values for contrast in the present study reflect the *horizontal shifts* required to equate perceived contrast and contrast detection across eccentricities. The contrast-scaling E_2 values reported in Sally et al. reflect the *vertical shifts* required to equate contrast at identification threshold at each eccentricity. Sally et al. found that little or no contrast scaling was required because all contrast sensitivity functions reached approximately the same asymptotic level at sufficiently long line lengths. Similarly, in the present experiment the lowest contrast thresholds or matching contrasts were essentially identical at all eccentricities. Thus, size scaling was required to equate contrast detection and perceived contrast across the visual field, but contrast scaling was not.

We note that contrast detection thresholds show a more rapid rise with reductions in stimulus size than do thresholds for contrast matching (see Fig. 2). This means that perceived contrast did not change as dramatically as detection thresholds over the same range of line lengths. Thus, there was not a multiplicative relationship between contrast detection threshold and level of perceived stimulus contrast (Gurnsey, Sally, & Ball, 2002). This is a significant point because a common procedure to equate for stimulus 'visibility' is to present stimuli at a fixed multiple above detection threshold across viewing conditions. To determine if there is a systematic relationship between contrast threshold and perceived contrast, we examined these measures as a function of line length and eccentricity. The pattern of results was consistent across eccentricities and similar for the two subjects. At each eccentricity, the contrast value obtained through contrast matching represented the highest multiple of contrast threshold at the longest stimulus sizes and the smallest multiple at the smallest stimulus sizes. The perceived contrast value was an average of 2.14 multiples of detection threshold for the two largest sizes at each eccentricity and decreased to 1.53 for the two smallest sizes. This means that if we had set all stimuli to the same multiple of contrast threshold

(e.g., 2.14 times threshold), the smallest stimuli at every eccentricity would have had higher physical contrast than that determined in the matching procedure.

The primary aim of this study was to determine whether size-scaling E_2 values for orientation discrimination at near-threshold contrasts are larger than those obtained at stimulus contrasts well above detection threshold. We have shown that this is clearly the case and suggest one possible explanation. E_2 values for orientation discrimination likely reflect eccentricity-dependent changes in the local spatial scale of orientation-selective mechanisms. In other words, stimulus size must increase with eccentricity to maintain equivalent-to-foveal levels of performance because of a concomitant change in the size of orientation-selective filters or receptive fields at visual cortex. Interestingly, recent physiological studies in the macaque have shown that neuronal receptive fields in V1 may be 2- to 4-fold larger at low than high contrasts when measured with the same optimal stimuli (Kapadia, Westheimer, & Gilbert, 1999; Sceniak, Ringach, Hawken, & Shapley, 1999; see Mareschal, Henrie, & Shapley, 2002, for related psychophysical evidence). If changes in receptive fields at low-contrasts are relatively greater at the fovea than periphery, then less spatial scaling (i.e., larger E_2 values) would be required to equate orientation discrimination performance. This possibility remains to be evaluated in physiological studies, however, a recent report by Mareschal and Shapley (2004) appears to be consistent with this idea.

Mareschal and Shapley (2004) measured orientation discrimination thresholds as a function of stimulus contrast and stimulus area at fixation and at 5° eccentricity. At both locations orientation thresholds were essentially independent of stimulus area when contrast was high, but increased with decreases in contrast and area. From the limited data available (see Mareschal & Shapley, 2004, Figs. 1 and 5) it appears that the relative increase in orientation thresholds is greater at fixation than in the periphery over a comparable range of contrasts and areas. For low-contrasts there seems to be a relatively greater increase in orientation threshold with decreases in stimulus area at the fovea than in the periphery. This is consistent with a larger relative change in mechanism area at the fovea than in the periphery as contrast is reduced. We emphasize, however, that this conclusion is based on very limited data. Therefore, the idea that foveal mechanisms show a greater range of contrast-dependent size changes than do peripheral mechanisms awaits more thorough examination.

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