Flicker-Defined Form Stimuli are Minimally Affected by Centre-Surround Lateral Contrast Interactions

Jonathan Denniss, PhD[1,2,3] and Allison M. McKendrick, PhD[1]

[1]Department of Optometry & Vision Sciences, The University of Melbourne, Australia

[2]Computing & Information Systems, The University of Melbourne, Australia

[3]Visual Neuroscience Group, School of Psychology, University of Nottingham, UK

Corresponding author: A/Prof Allison M. McKendrick
Department of Optometry & Vision Sciences
Level 4 Alice Hoy Building
The University of Melbourne
Parkville
VIC 3010
Australia
allisonm@unimelb.edu.au

Figures: 4

Tables: 0

Word count: 4000 approx

Funding: Australian Research Council DP140100157

Commercial Relationships: Heidelberg Engineering (F), both authors

Keywords: Flicker-defined form, centre-surround, lateral interactions, perimetry, flicker, phantom contour.

Running head: Lateral Interactions in Flicker-Defined Form

Abstract

Purpose: Flicker-defined form (FDF) stimuli have recently been adopted for visual field testing. A key difference between FDF and traditional perimetric stimuli is that the entire display background contains flickering dots. The purpose of this study was to determine whether the perception of FDF stimuli is influenced by lateral interactions involving regions beyond the stimulus border in young healthy observers.

Methods: Experiment 1 measured the effect of surround size and retinal eccentricity on the detection of the FDF contour. Psychometric functions were collected for surround diameters of 20, 30 and 40°, and with stimuli centered at eccentricities of 0, 10 and 20°. Experiment 2 measured the effect of target-surround temporal phase difference on apparent temporal contrast (flicker strength) of the target for both the FDF stimulus and a solid-field stimulus. Psychometric functions were collected for target-surround phase differences of 0, 45, 90, 135 and 180°.

Results: Our results show a mild surround-suppression effect for FDF stimuli that is independent of surround size. Magnitudes of FDF surround suppression were consistent with the reduced temporal contrast energy of the stimulus compared to solid-field stimuli.

Conclusion: FDF stimuli necessarily have both flickering target and background. Our results suggest that visual field defects outside the target are unlikely to markedly influence the detection and perception of the FDF stimulus. Nevertheless, mild surround suppression of contrast arises for FDF stimuli, hence interactions between the background and the target area may influence FDF results in conditions that alter centre-surround perceptual effects.

Introduction

Several recent studies have investigated the clinical utility of the Heidelberg Edge Perimeter (HEP, Heidelberg Engineering GmbH, Heidelberg Germany, http://www.heidelbergengineering.co.uk/products/hep/) for detecting glaucomatous visual field loss [1 2], and have reported on the relationship between HEP thresholds and structural ocular parameters such as retinal nerve fiber layer thickness as measured by optical coherence tomography [1 3 2]. These studies report reasonable performance of the HEP when compared to other clinical perimeters.

A key feature of the HEP is the use of a "flicker-defined form" (FDF) stimulus to measure detection thresholds. The FDF stimulus is a clinical adaptation of a perceptual phenomenon initially described by Livingstone and Hubel [4] and further explored by Ramachandran and Rogers-Ramachandran [5], who referred to the stimulus as a "phantom contour". FDF stimuli are comprised of rapidly counterphasing small dots, where the temporal flicker rate is too high to enable perceptual distinction of the lighter and darker phases of the stimulus. If part of the field of dots, for example within a circular region, is flickered with a different temporal phase to the remainder of the field, that region will perceptually segment from the background despite the relative temporal phase of each individual dot being indistinguishable. This is the basis of the perimetric FDF stimulus used in the HEP. Hence a key difference between FDF and traditional perimetric stimuli is that the entire background of the visual display also contains flickering dot stimuli whose temporal contrast varies with that of the target region. Consequently, it is possible that the clinically measured thresholds may reflect not only the patency of the retinal and visual cortical areas that are spatially concordant with the test-stimulus, but may additionally be influenced by lateral interactions involving the surround beyond the border of the stimulus. Exploring the strength of such effects is the purpose of this study.

Previous studies reveal several features of FDF stimuli that impact upon the measured thresholds. Properties of the target region that are important to FDF detection thresholds include the stimulus area [6], and the dot density [7]. Quaid and Flanagan [7] demonstrated that the number of dots per degree of visual space influences the stimulus detection, specifically, the cumulative area of the dots relative to the total area of the target region is important. The contour boundary is also important to the strength of the percept; phantom contours with longer boundaries are more perceptible [8], and they disappear if the gap between the two discordant temporal phase areas becomes too wide [8, 9].

Here we are not interested in the properties of the target area, but instead are focused on the features of the background upon which it is presented. Spatial interactions between central stimuli and their backgrounds are numerous, and can markedly alter the perceived properties of stimuli including the contrast. An example is the well-studied Chubb contrast illusion whereby an object's apparent contrast varies with the contrast of its background [10]. Centre-surround effects arise at multiple stages of visual processing from the retina through to extrastriate cortex and arise from lateral inhibitory processes at each hierarchical processing stage in addition to feedforward and feedback inhibitory connections (for review see: [11]). Such centre-surround suppression also results for stimuli defined by temporal phase offset [12, 13]. Both the strength and likely neural origin of such effects have been studied. Kremers et al [12] measured the apparent temporal contrast (perceived difference between maximum and minimum luminance across time) of a flickering circle target surrounded by a flickering annulus for a range of different temporal phase offsets between the central target and the surround. The stimulus was similar to FDF with the exception that solid area stimuli were used rather than targets comprised of random dots. That study compared human behavioural data to primate neural responses and showed that the effect of temporal phase offset on apparent temporal contrast was similar in primate lateral geniculate nucleus neurons to the human performance data. Naturally, cortical responses are also critical to human perception, however, several follow-up works from the same group also demonstrate that the spatial scaling of the lateral interactions [13] and monocular contribution [14] is consistent with substantial precortical involvement.

The purpose of this study was to explore the extent to which properties of the surround influence the detectability and the perceived depth of flicker (apparent temporal contrast) of FDF targets. Our rationale for these experiments is twofold: understanding the influence of the FDF background may assist in interpreting key underlying mechanisms, and may also assist in applied interpretation of the FDF task in clinical populations. We explore the effect of altering the background of FDF stimuli (while leaving target area, dot density, and contour length constant) because clinically measured visual field damage can be spatially extensive. If long-range interactions are important to FDF detection thresholds, then the spatial localization of a visual field defect using FDF perimetry may not be as straight-forward to interpret as it seems. For example, if surround properties influence detection thresholds, it is possible that large areas of visual field loss (that reduce the effective size and strength of the surround) may result in alterations to thresholds in other spatial areas that do not overlap directly with the area of conventionally defined visual field loss. Such alterations may have the effect of improving sensitivity in areas near to defects (due to reduced surround suppression), which could then mask subtle defects from detection. Additionally, monitoring of disease progression could be complicated by changes at one location affecting thresholds at another. A potential further complicating factor is that centre-surround contextual effects of contrast and motion processing are significantly affected by normal aging [15-17]. If FDF thresholds are influenced by the surround properties, the interpretation of visual field measurements across age becomes further complicated due to age-related changes to surround inhibition.

In our first experiment we measure FDF detection thresholds for various surround sizes, and for 3 different viewing eccentricities (foveally, 10 degrees and 20 degrees). In our second experiment we measure the apparent temporal contrast of the FDF target for a range of different target-surround phase offsets. We also measure the effect of temporal phase offset on perceived contrast for solid-field stimuli, similar to those used by Kremers et al [12], in order to determine the likelihood of similar mechanisms governing performance in these tasks.

Methods

This study was approved by the Human Research Ethics Committee of The University of Melbourne and adhered to the tenets of the Declaration of Helsinki. All participants gave written consent to take part after explanation of the nature and possible consequences of the study.

Apparatus

Stimuli were generated by custom software written in MATLAB (version 7.0.4, The Mathworks, Natick, MA, USA, http://mathworks.com) and displayed on a 21-inch monitor (19.8-inch viewable, mean luminance 50 cd/m^2, frame rate 120Hz, resolution 800 horizontal x 600 vertical, Trinitron G520, Sony, Tokyo, Japan) via a visual stimulus generator (ViSaGe, Cambridge Research Systems, Kent, UK, http://www.crsltd.com). The monitor was gamma corrected weekly (OptiCal, Cambridge Research Systems, Kent, UK). Participants wore appropriate refractive correction for the 40cm viewing distance that was maintained by a chin rest. Stimuli were viewed monocularly whilst the fellow eye was occluded with an eye patch.

Flicker-Defined Form Stimulus

The general form of the FDF stimulus used in both experiments was a circular target of 5° diameter with a surrounding annulus whose diameter varied in the experiments (Figure 1). Both target and surround consisted of 0.38° diameter non-overlapping square dots randomly positioned to achieve a density of 3.5 dots per square degree. Dots in the centre and surround regions had equal luminance amplitude. Luminance of the dots was sinusoidally modulated at 15Hz temporal frequency. To achieve the FDF effect, the temporal phase of target and surround luminance modulation differed by an amount set in each experiment. Temporal contrast of the FDF stimulus was calculated by the formula

$$C = \frac{L_{\max} - L_{\min}}{L_{\max} + L_{\min}} \qquad (1)$$

where C =temporal contrast and L=luminance of constituent dots (max and min being the values at the peaks and troughs of the sinusoidal temporal modulation). These stimulus parameters were chosen to mimic those of the FDF stimulus used in the commercially available HEP as closely as possible.

Participants

Participants in both experiments were healthy students participating for course credit. Author JD also participated in Experiment 2. All participants had corrected Snellen visual acuity of 6/6 (logMAR 0.0) or better in each eye, spherical equivalent refractive error between -6.00D and +6.00D, normal visual fields and no known ocular disease or amblyopia. All participants performed multiple practice runs of the experiment before data collection commenced to ensure full comprehension of the task. Different individuals participated in Experiment 1 and 2 (see later). Each experiment took approximately six hours per participant to complete, including breaks. This was completed over several sessions.

Experiment 1

In experiment 1 we measured the effect of surround size and retinal eccentricity on detection of the FDF contour. Participants (n=5) were aged 21-23 years. Left eyes were tested.

A two interval forced choice design was employed (Figure 1). In one randomly chosen interval the FDF stimulus was presented with target and surround regions having 180° phase difference to produce the phantom contour effect. The other interval contained the same stimulus but with target and surround regions flickering exactly in phase such that there was no difference between target and surround. Temporal contrast was equal in the two intervals and varied on each trial according to a method of constant stimuli with levels tailored to individual participants. Stimuli were presented for 500ms with a 500ms inter-stimulus interval (Figure 1). Participants used a button press (CB6 response box, Cambridge Research Systems, Kent, UK) to indicate in which interval they saw the contour. Experiment runs consisted of 10 presentations at each of 7 temporal contrasts (total 70 presentations per run). Psychometric functions were built up over multiple runs such that each temporal contrast (minimum of 7) was presented at least 50 times (minimum 350 presentations per psychometric function).

Psychometric functions were collected for three different surround diameters (20, 30 and 40°) and with stimuli centred at three different eccentricities (0, 10 and 20°). Stimuli at 10 and 20° eccentricities were presented on the 45° meridian in the inferior-nasal (lower-right) visual field whilst participants fixated a marker in the top-left of the monitor. Steady fixation was monitored by the experimenter via a mirror. Participants took breaks between experiment runs, and data were collected over multiple sessions across several days.

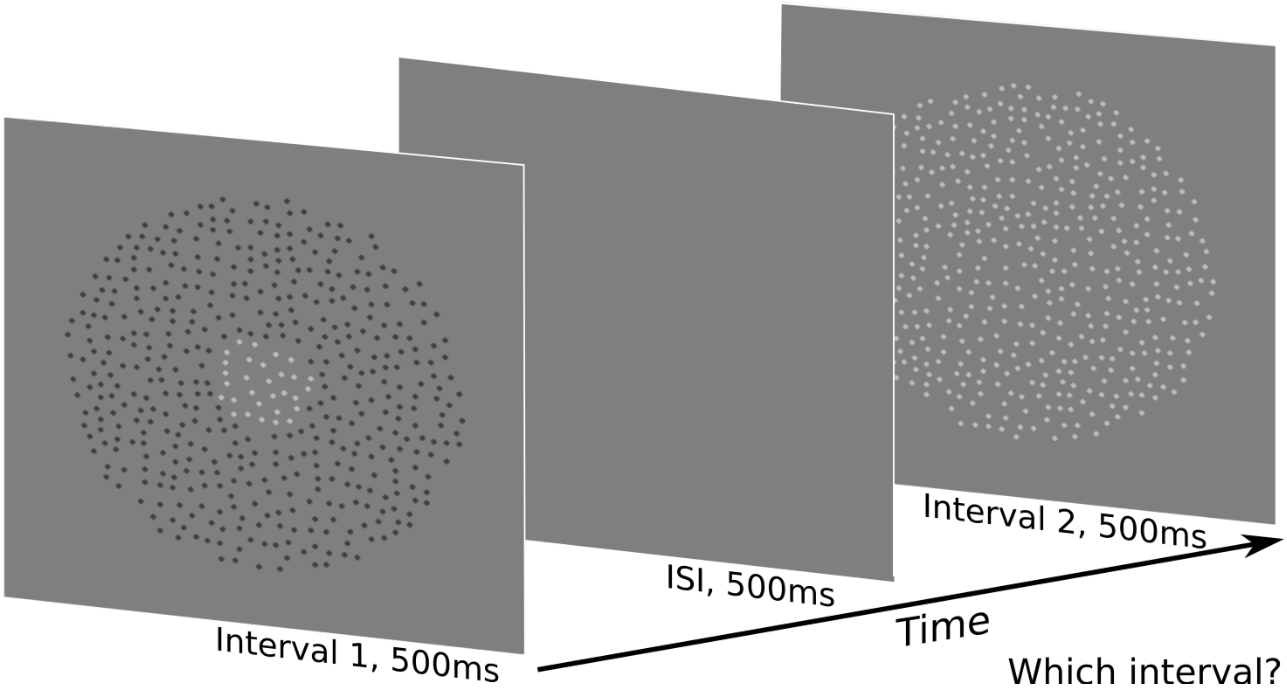

Figure 1: Task and stimuli for Experiment 1. Central targets had diameter 5°, whilst surround diameters varied across conditions (20° in this example). Stimuli with target-surround phase differences of 0° and 180° were randomly presented in one of two intervals. Subjects indicated in which interval they saw the FDF contour. Temporal contrast of both stimuli was equal and varied according to a method of constant stimuli. ISI=inter-stimulus interval.

Experiment 2

Experiment 2 measured the effect of target-surround temporal phase difference on apparent temporal contrast (flicker strength) of the target for both the FDF stimulus and a solid-field stimulus of equal dimensions, similar to that used in a previous study of flicker perception[12] (Figure 2). Participants (n=5) were aged 23 to 28 years. One eye was selected randomly for testing.

In Experiment 2, a two interval forced choice task was used in which the first interval contained a reference pattern and the second interval contained a variable pattern. For both stimuli the reference had 50% temporal contrast, target diameter 5° and surround diameter 20°. The solid field stimulus had a small gap between the central target and surround diameter of 3 min arc. The variable pattern consisted of the central target portions only (i.e. without the surround), and their temporal contrast was varied on each trial according to a method of constant stimuli with levels tailored to individual participants. Stimuli were presented centrally for 500ms with a 50ms inter-stimulus interval. Participants used a button press to indicate whether the variable pattern appeared to have higher or lower temporal contrast than the central target of the reference pattern. Experiment runs consisted of 10 presentations at each of 7 temporal contrasts (total 70 presentations per run). Psychometric functions were built up over multiple runs such that each temporal contrast (minimum 7) was presented at least 50 times (minimum 350 presentations per psychometric function).

For both stimuli, psychometric functions were collected for reference pattern target-surround phase differences of 0, 45, 90, 135 and 180°. Participants took breaks between experiment runs, and data were collected over multiple sessions across several days.

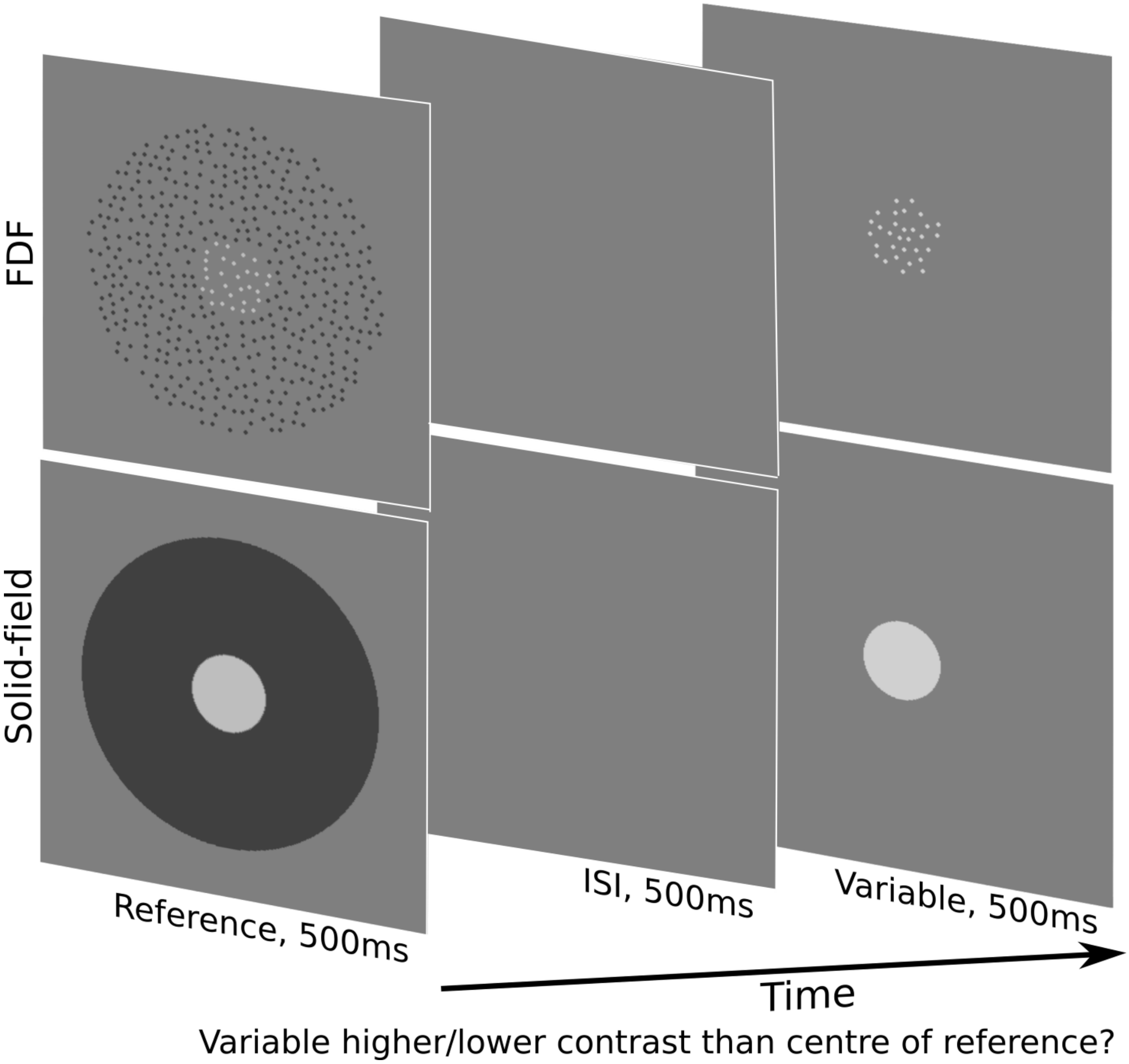

Figure 2: Task and stimuli for Experiment 2. Top row FDF stimuli, bottom row solid-field stimuli. Targets/variables had diameter 5°, reference patterns' surround diameter was 20°. Reference patterns were presented at 50% temporal contrast. Temporal contrast of the variable was varied according to a method of constant stimuli. In this example reference patterns are shown with 180° target-surround phase difference. ISI=inter-stimulus interval.

Data Analysis

Data were analysed in the open-source statistical environment, *R*, version 2.15.0[18]. Psychometric functions were fit with the function

$$\psi(x, \mu) = 0.5 + (0.5 - fn) \times [1 - G(x, \mu, s)] \quad (2)$$

in Experiment 1, or

$$\psi(x, \mu) = (1 - fn) \times [1 - G(x, \mu, s)] \quad (3)$$

in Experiment 2, where x represents temporal contrast in % (see equation 1), μ represents the mean of the fitted cumulative Gaussian, fn represents the lapse rate defining the upper asymptote, G represents the cumulative Gaussian function and s represents the spread (standard deviation) of the fitted cumulative Gaussian. Detection threshold in Experiment 1 was taken as the 75% correct point of the fitted function. The 50% 'higher' point of the fitted function was taken as the apparent temporal contrast (perceptual match) in Experiment 2. Fitting was carried out using the `glm.WH()` (equation 2) or `psyfun.2asym()` (equation 3) functions in the *R* package `psyphy`[19] that follow the procedures recommended by Wichmann and Hill[20]. Fitted psychometric functions' goodness-of-fit was assessed by comparison of model deviance to the deviance distribution of 10000 Monte Carlo data sets simulated from the fitted function[20]. This method derives empirical probabilities that a dataset of this size generated by the fitted function would have deviance as large or larger than that observed. Higher probabilities therefore indicate better fit and psychometric functions with goodness-of-fit $p<0.05$ were tested further until the fit improved.

Comparisons across experimental conditions were made by repeated measures analysis of variance (RM-ANOVA). Paired t-tests were used for comparisons between stimuli.

Modelling

Kremers et al [12] developed a vector summation model based on non-human primate LGN neural responses to a stimulus similar to our solid-field stimulus. They then used the model to fit human psychophysical estimates of apparent temporal contrast of the same stimulus, assuming that the perception of target temporal contrast is determined by a linear combination of the visual system's responses to the target and its surround:

$$R = \sqrt{R_c^{\,2} + R_s^{\,2} - 2 \cdot R_c \cdot R_s \cdot \cos(S - P)}\,. \quad (4)$$

In the model as applied herein, R represents apparent temporal contrast of the target, R_c and R_s represent neural ensemble responses* to the target and surround respectively, S represents target-surround phase offset, and P represents the target-surround phase offset at which R is minimal (equivalent to the temporal lag between target and surround responses). R, R_c and R_s are in units equivalent to temporal contrast (equation 1), whilst S and P are in degrees. We applied this model to the data from Experiment 2 to investigate whether differences in the apparent temporal contrast of the two stimuli could be accounted for by differences in the physical properties of the stimuli. Model parameters were determined by an iterative optimisation procedure that minimised the sum of squared differences between the fitted model and the group-average data.

---

* Similar to the modeling of human psychophysical data by Kremers et al (12), these parameters represent the overall response of the visual system, including a cortical decision mechanism.

Results

Experiment 1

Experiment 1 measured two interval forced choice psychometric functions for detection of the FDF contour at a variety of retinal eccentricities and stimulus surround sizes. Acceptable psychometric function fits (equation 2, all deviance $p>0.09$) were obtained for detection of the FDF contour for all participants and conditions.

Figure 3 shows the effect of retinal eccentricity and stimulus surround diameter on thresholds (75% correct point) and spreads for detection of the FDF contour. As is apparent in Figure 3a, contour detection thresholds were minimally affected by eccentricity (two-way RM-ANOVA, $F(2,31)=2.92$, $p=0.07$) and unaffected by stimulus surround diameter (two-way RM-ANOVA, $F(2,31)=1.50$, $p=0.24$). Figure 3b shows that psychometric function spread was also unaffected by surround diameter (two-way RM-ANOVA, $F(2,31)=1.23$, $p=0.31$), whilst there was a small effect of eccentricity (two-way RM-ANOVA, $F(2,31)=4.84$, $p=0.01$). Post-hoc one-way RM-ANOVAs showed that this effect was primarily for the 15° surround ($F(2,8)=11.35$, $p=0.005$), whist the 10° surround ($F(2,8)=3.52$, $p=0.08$) and 20° surround ($F(2,8)=0.01$, $p=0.94$) were affected less.

There was no interaction between eccentricity and surround diameter for contour detection thresholds or psychometric function spread (two-way RM-ANOVA, $F(4,31)=0.22$, $p=0.93$ for threshold, $F(4,31)=0.75$, $p=0.56$ for spread), indicating that any small effects of eccentricity are independent of surround diameter.

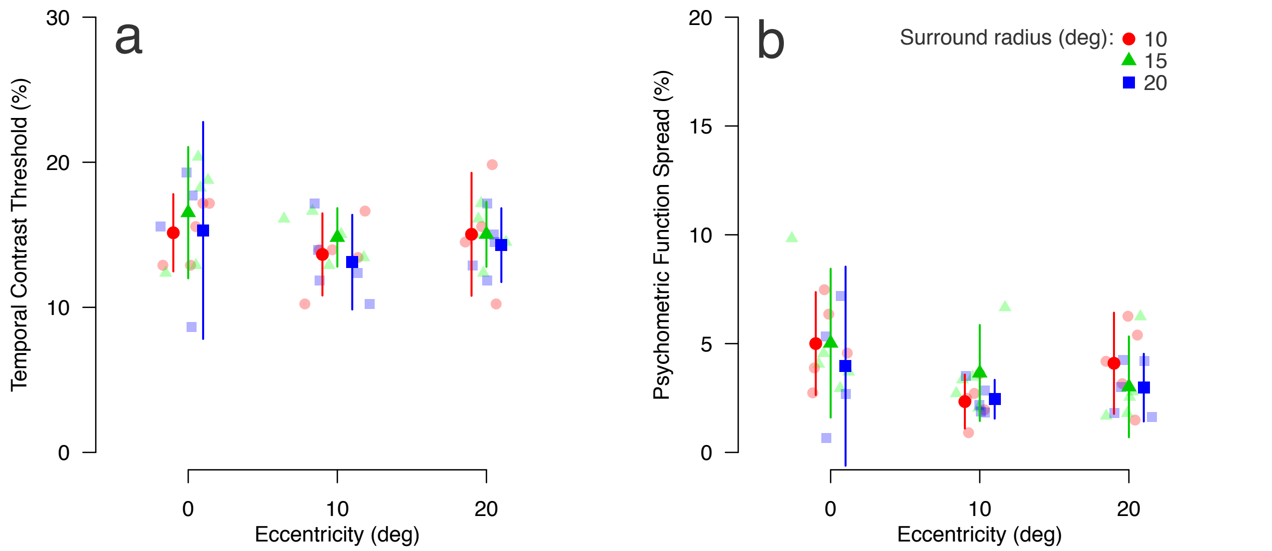

Figure 3: (a) Thresholds and (b) psychometric function spreads for detection of the FDF contour at different eccentricities and surround radii. Bold shaded symbols are group mean data with 95% confidence intervals, lighter shaded symbols represent individual subject data.

Experiment 2

In Experiment 2, participants were asked to indicate whether the variable (target without surround) appeared to have higher or lower temporal contrast than the reference target (with surround), presented with a variety of target-surround phase differences. The 50% 'higher' point on the psychometric function was taken as the perceptual match threshold (apparent temporal contrast of the reference target). Psychometric functions for apparent temporal contrast of both the FDF and solid-field targets were well fitted by equation 3 for all participants and conditions (all deviance p>0.09).

The effects of reference pattern target-surround phase difference on apparent temporal contrast and psychometric function spreads for both stimuli are shown in Figure 4. Two-way RM-ANOVAs indicated interactions between stimulus and phase difference for both threshold (F(4,36)=24.45, p<0.001) and spread (F(4,36)=7.90, p<0.001). Post-hoc one-way RM-ANOVAs showed that apparent temporal contrast was demonstrably affected by target-surround phase difference for the solid-field stimulus (F(4,16)=43.90, p<0.001) but not for the FDF stimulus (F(4,16)=0.75, p=0.57). Psychometric function spread was similarly affected by centre-surround phase difference of the full-field stimulus (post-hoc one-way RM-ANOVA, F(4,16)=26.50, p<0.001), but not of the FDF stimulus (post-hoc one-way RM-ANOVA, F(4,16)=1.24, p=0.33). The different effects of centre-surround phase difference on the perception of the two stimuli are also clearly apparent in Figure 4.

Also shown in Figure 4a is the considerable difference in effects of surround-suppression on the perception of the two stimuli. Across all phase differences, the solid-field stimulus exhibited suppression ratios (apparent contrast/physical contrast, smaller ratio=more surround suppression) of between 0.25 and 0.50, whilst perception of the FDF stimulus was less affected (suppression ratios 0.87 to 0.89, mean paired difference in ratios 0.54, 95% CI 0.41-0.66, paired t-test, p<0.001). Similarly, Figure 4b shows that across target-surround phase differences, mean psychometric function spreads were typically slightly smaller for the solid-field stimulus (range 2.1 to 5.5%) than for the FDF stimulus (range 3.7 to 4.4%, mean paired difference 0.8%, paired t-test, p=0.18). Notably though, when the phase difference was 180°, as in the clinical FDF implementation, there was no meaningful difference between the stimuli in this respect (Figure 4b).

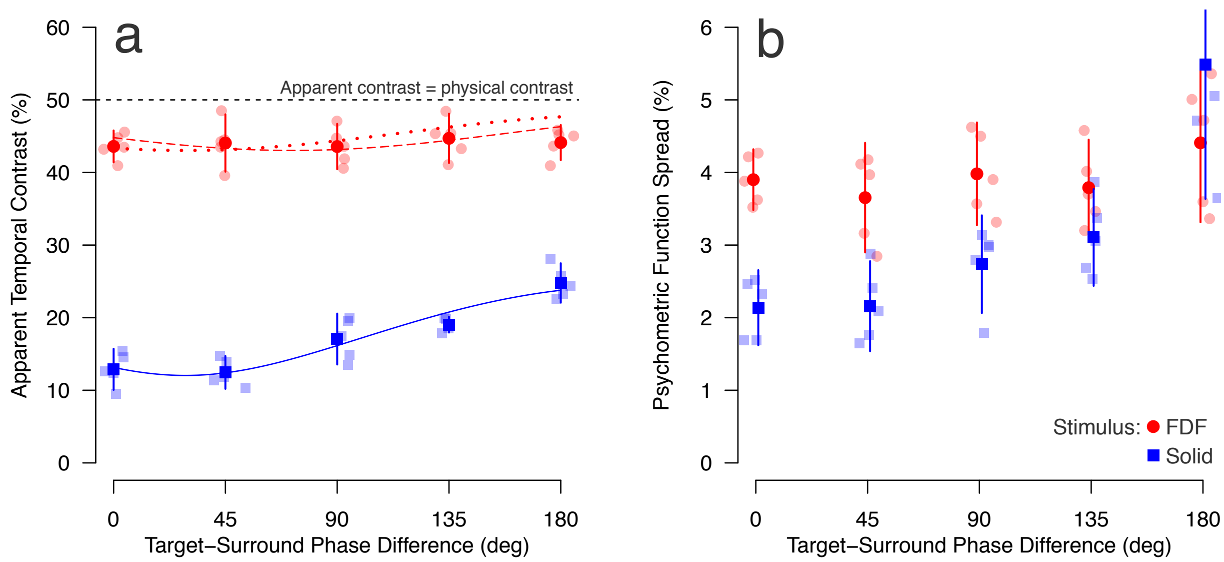

Figure 4: (a) Apparent temporal contrast of FDF and solid-field targets with surrounds of varying temporal phase offset. The solid blue curve represents the optimum fit of the Kremers et al [12] vector summation model to the solid-field data (parameters: R_c =18.2, R_s =6.2, P =28.9). The

red dashed and dotted curves shows the same model where parameters have been adjusted to account for the reduced temporal contrast energy of the FDF stimulus (dashed parameters: R_c =45.5, R_s =2.5, P =72.1, dotted parameters: R_c =45.5, R_s =2.5, P =28.9 [P unadjusted]). (b) Psychometric function spreads for apparent temporal contrast matching data for both stimuli. Bold shaded points represent group means with 95% confidence intervals, lighter shaded points represent individuals' data. Red circles show data for the FDF stimulus, blue squares show data for the solid-field stimulus.

The solid blue curve in Figure 4a represents the best fit of the vector summation model [12] (equation 4) to the solid-field stimulus data. Fitted parameters were R_c =18.2, R_s =6.2, P =28.9. We considered the possibility that the different responses to the FDF stimulus were simply a result of the reduced temporal contrast energy of the stimulus. The dots of the FDF stimulus occupied 40% of the total stimulus area, the remainder of which had zero temporal contrast energy; this reduction in temporal contrast energy may explain the perceptual differences shown in Figure 4a. To explore this we modified the model parameters given above as follows: (1) R_c was increased by dividing by 0.4 to account for the reduced temporal contrast energy of the variable stimulus, equivalent to matching the two conditions for variable stimulus contrast, (2) R_s was reduced by multiplying by 0.4 to account for the reduced surround suppression due to reduced temporal contrast energy of the surround, (3) in two separate predictions P was either not adjusted (red dotted curve in Figure 4a), or was increased by dividing by 0.4 to proportionately increase the target-surround response lag (red dashed curve in Figure 4a). Predicted model parameters for the FDF stimulus were therefore R_c =45.5, R_s =2.5, and P =28.9 (red dotted curve) or P=72.1 (red dashed curve). Both predictions approximately fit the FDF apparent temporal contrast data, as shown in Figure 4a, with the red dashed curve where P was adjusted providing a better fit. For comparison, sums of squared differences between the model and the data were 4.91 for the optimised fit to the solid-field data, 7.07 for the prediction of the FDF data with adjusted P and 16.50 for the prediction of the FDF data with unadjusted P.

Discussion

Our results suggest that the FDF stimulus parameters incorporated in the current commercial perimeter (HEP) are relatively robust to the surround area. Our first experiment shows that the size of the stimulus background (if at least 10 degrees in radius for a 5 degree stimulus), does not influence contrast thresholds in a systematic manner. Our second experiment shows that the apparent temporal contrast of the target region is influenced by the background flicker, however, the effects are relatively mild and independent of the temporal phase offset between the target and the background. Hence, lateral interactions of temporal processing can be demonstrated for FDF stimuli with these parameters, but the magnitude of such effects is relatively small in those with normal vision.

The results shown in Figure 3 imply that the presence or absence of background at a distance of 5 deg or more from the contour boundary does not influence thresholds. Hence, it may be reasonable to assume that in a clinical situation of moderate visual field loss, where there is a significant reduction in effective background area, that thresholds for the target would similarly be unaffected by field loss more than 5 degrees from the target. This assumption may not strictly hold in older adults who show an increased strength of some lateral interactions of contrast processing [16, 21]. Nevertheless, the fact that the FDF stimulus does not result in pronounced surround effects suggests that any clinical differences are likely to be marginal if present.

An additional aim of our study was to explore whether the relationship between target-surround temporal phase offset and surround suppression of apparent temporal contrast (perceived flicker strength) was similar for the FDF stimulus to that measured with solid-field luminance stimuli. Similar to previous work [12], the perceived flicker contrast for the solid-field stimuli varied with temporal phase offset, with the strongest surround suppression when the target and surround flickered in similar phase. While our results were qualititatively comparable to those reported previously [12], there were some quantitative differences that may have arisen due to differences in the size of the target stimuli used in the experiments. Kremers et al [12] used a target of 1 degree surrounded by an annulus with an outer diameter of 10.2 degrees. Our target region of 5 degrees was chosen to match the commercial FDF perimeter (HEP). In comparison to the solid luminance stimulus, the FDF stimulus showed mild suppression of apparent temporal contrast (a physical contrast of 50% was matched to about 40% contrast in the absence of the surround) but this effect was relatively independent of temporal phase offset.

Previous studies implicate pre-cortical areas as important neural processing sites underpinning temporal lateral interactions for solid-field stimuli [12-14]. A key candidate area suggested by these studies is the lateral geniculate nucleus. We are unaware of any neurophysiological reports of neural activity for FDF stimuli specifically. Goodbourn and Forte [8] demonstrate that the phantom contour effect disappears if the gap between the out of phase regions is too wide, and propose that the spatial dependencies are consistent with spatial scaling in V1. It is worth noting that both the solid luminance stimulus and FDF configuration did not have a direct border between the target and surround as there was always a small gap imposed. A key difference between the stimuli was the proportion of stimulus area that contained temporal signal, 40% for FDF vs 100% for solid-field. Application of the vector summation model proposed for solid-field stimuli by Kremers et al [12] showed that the differences in apparent temporal contrast between the two stimuli could be reasonably predicted by accounting for the 60% reduction in temporal contrast energy in the FDF stimulus (Figure 4a). Hence, the form of our observed data does not rule out a common mechanism underpinning perception of the two stimulus types.

Participants informally commented that they found the judgments more difficult in the fovea. Consistent with these reports, psychometric functions were flatter in the fovea, and relatively constant outside this area. Previous studies report elevated detection thresholds in the fovea for FDF stimuli [6, 7]. In this study foveal detection thresholds were minimally, if at all, elevated (Figure 3). However, our observed flatter psychometric functions imply that clinical measurements will show increased test-retest variability for central targets.

The present study included only young, healthy observers. In this population, surround suppression of contrast in FDF stimuli was sufficiently mild to be negligible for clinical purposes. Clinical FDF perimetry is more likely to be used on an older age group, however. Our study does not rule out subtle interactions between the background and the target area influencing FDF results in conditions known to alter the strength of such perceptual effects such as migraine, schizophrenia, older age and some incidences of bipolar disorder [16, 22, 23 24].

In conclusion, FDF stimuli assess the patency of temporal processing of contrast but the fact that the stimuli necessarily have both flickering target and background means that direct spatial comparison of the results to other forms of perimetry using temporally modulated stimuli should be made with care. Our results suggest that visual field defects away from the target area are unlikely to markedly influence the detection and perception of the FDF stimulus in other parts of the visual field as long as dot density is kept low, as in the current commercial implementation.

Acknowledgements

Preliminary analysis of parts of the data was performed by students on the Bachelor of Optometry and Doctor of Optometry degree programs at the University of Melbourne as part of a student group research project.

References

1. Horn FK, Tornow RP, Junemann AG, Laemmer R, Kremers J. Perimetric measurements with flicker-defined form stimulation in comparison with conventional perimetry and retinal nerve fiber measurements. *Invest Ophthalmol Vis Sci* 2014;55:2317-2323.
2. Lamperter J, Russell RA, Schulze A, Schuff AC, Pfeiffer N, Hoffman EM. Structure-function relationship between FDF, FDT, SAP, and scanning laser ophthalmoscopy in glaucoma patients. . *Invest Ophthalmol Vis Sci* 2012;53:7553-7559.
3. Prokosch V, Eter N. Correlation between early retinal nerve fiber layer loss and visual field loss determined by three different perimetric strategies: white-on-white, frequency-doubling, or flicker-defined-form perimetry. *Graefes Arch Clin Exp Ophthalmol* 2014;252:1599-1606.
4. Livingstone MS, Hubel DH. Psychophysical evidence for separate channels for the perception of form, colour, movement and depth. *Journal of Neuroscience* 1987;7:3416-3468.
5. Ramachandran VS, Rogers-Ramachandran DC. Phantom contours: A new class of visual patterns that selectively activates the magnocellular pathway in man. *Bulletin of the Psychonomic Society* 1991;29:391-394.
6. Goren D, Flanagan JG. Is flicker-defined form (FDF) dependent on the contour? *Journal of Vision* 2008;8:15, 11-11.
7. Quaid PT, Flanagan JG. Defining the limits of flicker defined form: effect of stimulus size, eccentricity and number of random dots. . *Vision Res* 2005;45.
8. Goodbourn PT, Forte JD. Spatial limitations of fast temporal segmentation are best modeled by V1 receptive fields. . *Journal of Vision* 2013;13:23.21-18.
9. Victor JD, Conte MM. Temporal phase discrimination depends critically on separation. *Vision Res* 2002;42:2063-2071.
10. Chubb C, Sperling G, Solomon JA. Texture interactions determine perceived contrast. *Proceedings of the National Academy of Sciences* 1989;86:9631-9635.
11. Angelucci A, Bressloff PC. Contribution of feedforward, lateral and feedback connections to the classical receptive field center and extra-classical receptive field surround of primate V1 neurons. *Prog Brain Res* 2006;154:93-120.
12. Kremers J, Kozyrev V, Silveira LCL, Kilavik BE. Lateral interactions in the perception of flicker and in the physiology of the lateral geniculate nucleus. . *Journal of Vision* 2004;4:643-663.
13. Kremers J, Rimmele U. The spatial extent of lateral interactions in flicker perception. *Vision Res* 2007;47:16-21.
14. Teixeira CE, Salomao RC, Rodrigues AR, Horn FK, Silveira LC, Kremers J. Evidence for two types of lateral interactions in visual perception of temporal signals. *Journal of Vision* 2014;14:1-10.

15. Karas R, McKendrick AM. Age related changes to perceptual surround suppression of moving stimuli. *Seeing and Perceiving* 2012;25:409-424.
16. Karas R, McKendrick AM. Aging alters surround modulation of perceived contrast. *J Vis* 2009;9:11.11-19.
17. Betts LR, Taylor CP, Sekuler AB, Bennett PJ. Aging reduces center-surround antagonism in visual motion processing. . *Neuron* 2005;45:361-366.
18. R Development Core Team. *R: A language and environment for statistical computing.* Vienna, Austria: R Foundation for Statistical Computing http://www.R-project.org/; 2012 (accessed 10th July 2013).
19. Knoblauch K, Maloney LT. *Modeling psychophysical data in R*. New York, USA: Springer; 2012.
20. Wichmann FA, Hill NJ. The psychometric function: I. Fitting, sampling, and goodness of fit. *Perception & Psychophysics* 2001;63:1293-1313.
21. Karas R, McKendrick AM. Increased surround modulation of perceived contrast in the elderly. *Optom Vis Sci* 2011;88:1298-1308.
22. Dakin S, Carlin P, Hemslsy D. Weak suppression of visual context in chronic schizophrenia. *Curr Biol* 2005;15:R822-824.
23. Battista J, Badcock DR, McKendrick AM. Migraine increases centre-surround suppression for drifting visual stimuli. *PLoS One* 2011;11.
24. Yang E, Tadin D, Glasser DM, Wook Hong S, Blake R, Park S. Visual context processing in bipolar disorder: A comparison with schizophrenia. *Front Psychology* 2013;4:569.