



Detection and resolution of vanishing optotype letters in central and peripheral vision

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ABSTRACT

Previous studies of peripheral vision have shown that detection acuity is superior to resolution acuity for gratings over a range of contrasts, which is attributed to different limiting mechanisms (contrast insufficiency and neural undersampling) for the two tasks. To extend the analysis to letters in a way that avoided luminance cues, we used “vanishing optotype” characters, conveying second-order information, and constructed from tripole strokes having the same mean luminance as the surround. We measured the minimum letter size for detection and identification tasks for two different pairs of vanishing optotype characters (O vs. + and orthogonally oriented Landolt-C’s) as a function of contrast in central and peripheral vision. Foveally there was no significant difference between detection acuity and resolution acuity for either pair of letters over a range of stimulus contrasts from 20% to 100%, indicating performance is contrast-limited for both tasks. The same result was obtained at 30° eccentricity in the peripheral field for the O vs. + letters, again indicating performance is contrast-limited for both tasks. However, resolution acuity for the Landolt-C letters was significantly worse than detection acuity in the periphery over the same range of contrasts, which suggests performance is limited by neural undersampling for these letters. All of our experimental results are explained by a model of neural sampling in which detection acuity is determined by the size of neural receptive fields relative to the dimensions of the tripole responsible for spatial contrast, whereas resolution acuity is determined by the spacing of receptive fields relative to the spacing between strokes responsible for letter form.

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1. Introduction

The relative importance of optical and neural factors in limiting spatial vision is an issue of long-standing interest and fundamental importance. Stimulus configuration, location in the visual field, and the nature of the task are major factors that affect the balance between these mechanisms. For example, foveal resolution of sinusoidal gratings is typically limited by the optical quality of the eye’s imaging system (Campbell & Green, 1965; Green & Campbell, 1965) yet limitations imposed by underlying neural sampling can be revealed by stimulation of the retina with interferometric fringes that have sufficient contrast to be visible even when their spatial frequency is greater than the Nyquist resolution limit of the foveal cone mosaic (Williams, 1985a, 1985b). In this case, visual resolution, defined operationally as the highest spatial frequency yielding veridical spatial vision, is

limited by neural sampling as demonstrated by the onset of perceptual aliasing when patterns exceed the neural Nyquist frequency. Thus a hallmark of sampling-limited spatial acuity is the failure to resolve salient features of patterns necessary for performing tasks such as identifying letters or the orientation of gratings, even though the pattern’s contrast may be clearly visible and reliably detected (Anderson & Thibos, 1999a, 1999b).

For any given stimulus location in the visual field, resolution acuity may be limited either by optical quality or by neural sampling, whichever mechanism sets the lower limit to visual bandwidth. For example, although grating resolution for foveal stimuli is typically limited by optical factors, highly myopic individuals with eyes (and correcting lenses) of high optical quality may experience foveal aliasing even for conventional viewing of grating targets because of abnormally low neural sampling density owing to retinal stretching (Chui et al., 2005; Wolsley et al., 2008). Similarly, strabismic amblyopes can display near normal grating detection acuity, but greatly reduced optotype recognition acuity (McKee, Levi, & Movshon, 2003). Relatively low sampling density compared to optical bandwidth is also a characteristic of the peripheral

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retina, causing perceptual aliasing for ordinary gratings, either printed or computer generated (Smith & Cass, 1987; Thibos, Still, & Bradley, 1996). Although the optical quality of the eye deteriorates with eccentricity (Charman & Atchison, 2009; Mathur, Atchison, & Charman, 2009a, 2009b; Williams et al., 1996) the sampling density of the retina declines at a greater rate, resulting in undersampling and perceptual aliasing of grating stimuli even in the presence of uncorrected refractive errors and off-axis aberrations (Wang, Thibos, & Bradley, 1997). Retinal sampling limits in this case are set by the relatively coarse array of retinal ganglion cells (Anderson, Detkova & O'Brien, 1995; Anderson, Evans, & Thibos, 1996; Anderson & Hess, 1990; Anderson, Mullen, & Hess, 1991; Artal, Derrington, & Colombo, 1995; Coletta, Segu, & Tiana, 1993; Coletta & Williams, 1987; Coletta, Williams, & Tiana, 1990; Galvin & Williams, 1992; Smith & Cass, 1987; Thibos, 1998; Thibos & Bradley, 1993; Thibos, Cheney, & Walsh, 1987; Thibos, Still, & Bradley, 1996; Wang, Bradley, & Thibos, 1997a, 1997b; Wang, Thibos, & Bradley, 1996; Wilkinson, 1994; Williams, 1985b; Williams & Coletta, 1987) (for a review of this literature, see Anderson, 2006).

In summary, the main evidence that neural sampling is the primary limiting factor for visual resolution of gratings include: (a) the objective demonstration that detection acuity is superior to resolution acuity; (b) the finding that resolution acuity remains robust to significant reduction in retinal image contrast; (c) the subjective perception of spatial or motion aliasing for stimulus frequencies beyond the resolution limit and (d) the agreement between behavioral resolution acuities and predicted Nyquist limits based on anatomically determined density of retinal neurons.

An important clinical application of sampling-limited spatial vision is the non-invasive measurement of localized retinal ganglion cell density in normal subjects of different ages (Anderson & McDowell, 1997; Beirne et al., 2008; Zlatkova, Coulter, & Anderson, 2003) and in patients with diseases that affect ganglion cell density such as glaucoma (Beirne et al., 2003) or retinal ischemia (Chui et al., 2009). Although grating stimuli are commonly used in laboratory experiments, letters remain the preferred target for measuring acuity in clinical and behavioral research. Thus there is a need to extend the sampling theory of visual resolution to include letter stimuli. One approach revealed several possible ways in which neural undersampling could affect letter resolution, with experimental evidence implicating insufficient contrast remaining in the veridical band of spatial frequencies below the Nyquist frequency of the peripheral retina (Anderson & Thibos, 1999b). That work provided evidence of sampling-limited acuity for identifying the orientation of tumbling-E letters having strokes of equal length but rejected the sampling hypothesis for other letters having more complex frequency spectra. Using large, sampled letters viewed foveally, Carkeet et al. (2008) have shown that the Nyquist sampling theorem for gratings does not transfer easily to a simple rule predicting letter acuity from sample spacing. That finding further complicates the use of letter acuity to draw inferences about neural sampling in foveal vision when using adaptive optics technology to overcome optical limitations of the aberrated eye (Rossi & Roorda, 2010).

Despite the lack of an established sampling theory for letter stimuli, it may still be useful to determine empirically if there is a significant difference between detection acuity and resolution acuity for letters. The main barrier to answering this experimental question is that conventional letters are not isoluminant with the background and therefore detection acuity collapses to an increment (or decrement) contrast threshold task rather than a test of spatial vision. However, this lack of isoluminance can be remedied by using letters that are high-pass filtered such that their mean luminance is matched to the background (Howland, Ginsburg, & Campbell, 1978). Such letters are defined by their distribution of

local contrast that exists on a spatial scale that is relatively fine compared to the coarse features that uniquely identify the letter. Targets of this type have been termed 'vanishing optotypes' because of the observation that (at least in foveal vision) when their size is reduced to the point where resolution fails, the targets also become undetectable (Frisén, 1986). This suggests that detection and resolution of such stimuli are both limited by the same underlying mechanism foveally: insufficient retinal contrast. Other visual stimuli employing pseudo-high-pass targets include a version of the Muller-Lyer illusion (Carlson, Moeller, & Anderson, 1984), the Cardiff Acuity Test (Adoh & Woodhouse, 1994) and High-Pass Resolution Perimetry (HRP) (Frisén, 1987). The latter test utilizes the vanishing letter "O" to improve patient acceptance of visual field testing while also producing a test result that is reportedly linked to the density of retinal ganglion cells (Frisén, 1987, 1988). However, we note that, in the present context, the word 'resolution' in that earlier work may be inappropriate since the subject's task is merely one of contrast detection. Nevertheless, as demonstrated in our study, the detection task can be converted to a resolution task simply by requiring the observer to discriminate and identify letters in the vanishing optotype set.

2. Experimental rationale

A conceptual framework for using vanishing optotypes to separately measure detection and resolution acuities is illustrated in Fig. 1, which shows a striped letter defined by local contrast that is isoluminant with the uniform background. Such a stimulus may be created by viewing a grating through the transparent part of a letter-shaped aperture while ensuring the opaque part of the aperture has the same luminance as the space-averaged grating (Thibos & Bradley, 1993). Because masking of a grating by an aperture is a multiplicative process, the spatial frequency spectrum of the product is found by convolution of the grating and aperture spectra. Visually the grating is isoluminant with the surround, which implies the letter is detectable only if the grating is detectable. But for the letter to be resolved (i.e. distinguished from other striped letters and correctly identified) requires that the shape of the aperture be sufficiently well sampled by the array of retinal neurons. Thus a neural model of retinal image processing of such stimuli would posit that detection acuity is determined by the spatial period of the grating relative to the size of neural receptive fields, whereas resolution acuity depends on the size of the aper-

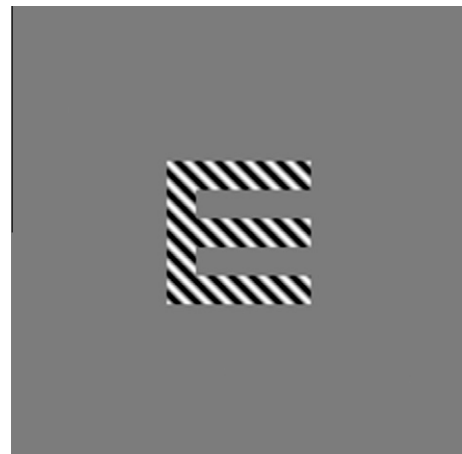


Fig. 1. Spatial construction of an E-shape windowed sinusoidal grating. The space-averaged luminance within the window is the same as the surround and thus the grating contrast must be detectable, but not necessarily veridical, in order for the letter to be identifiable.

ture's features relative to the spacing between receptive fields (Thibos & Bradley, 1993). According to this model, the outline of the aperture creates a spatial envelope of activated neurons responsible for perceived contrast, provided the grating frequency is low enough to be detected by individual neurons in the sampling array. It is immaterial whether the stripes inside the mask are perceived veridically or as spatial aliases caused by neural undersampling. The only requirement for stimulus detection is that the contrast of the gratings be visible. To the contrary, discriminating letter-shaped apertures of different orientations or shapes requires that the retinal mosaic of receptive fields adequately samples the spatial form of the aperture.

The distinction drawn here between the form of the aperture and the scale of the stripes that fill the aperture is analogous to radio communication via amplitude modulation. An audio message to be transmitted (i.e. the shape of the letter) is multiplied by a higher-frequency carrier sinusoid (i.e. the stripes inside the aperture) for transmission. The high-frequency radio signal carries the message in the form of amplitude modulation that can be recovered by rectification followed by low-pass filtering of the "carrier frequency". The main difference between this analogy and our visual counterpart is that the audio message is a graded analog signal, whereas our letter aperture provides binary modulation (transparent or opaque). Nevertheless, the process for recovering the message is the same: rectification (the detection of contrast without regard to sign) and low-pass filtering (recovering the spatial envelope of the contrast signal). In visual terms this would be described by some authors as the recovery of second-order information (Johnson & Baker, 2004) by physiological rectifying filters (Baker, 1999).

The reader may gain some insight into our experimental rationale by viewing Fig. 1 peripherally. Adjust the viewing distance so that the letter subtends approximately 3° (e.g. 3 cm at a viewing distance of 57 cm) and slowly move the target into the peripheral field. At about 10° eccentricity from the fixation point, perception of the stripes will appear non-veridical as they become aliased due to neural under-sampling. However, the form of the letter E will still be recognized as an envelope of visual excitation and thus resolved according to our definition of the term. Further increases in stimulus eccentricity will lead eventually to an inability to correctly perceive the E-shape of the envelope, even though the stimulus contrast remains visible, which marks the acuity limit for resolving the letter. Depending on the peripheral optical quality of the viewer's eye, the target may remain visible (but unresolvable) far beyond 30° of eccentricity (the retinal locus for our experiments). Thus to measure detection acuity in the mid-periphery requires that the letter size be reduced (by moving the object further away in this demonstration) until the spatial contrast that defines the letter is no longer visible.

The stimulus for our experiments, while based conceptually on the prototypically striped letter of Fig. 1, was adapted to the vanishing optotype stimuli used clinically. Using a vanishing Landolt-C, we measured the smallest detectable letter and the smallest resolvable letter (i.e. minimum size for which letter orientation could be identified correctly) as a function of contrast. We refer to these endpoints as detection acuity and resolution acuity, respectively. A second experiment determined detection acuity and resolution acuity for vanishing O and + characters, again as a function of contrast of the stripes that define these vanishing optotype characters.

These two experiments provide several experimental tests of the neural sampling model described above by asking the following questions. First, does detection acuity exceed resolution acuity for vanishing optotypes (indicator 1 above) and, if so, does it matter which letter is used? Second, is resolution acuity robust to contrast reduction (indicator 2 above), as expected if discrimination is

sampling limited? If not, then we infer that resolution acuity is contrast-limited rather than sampling limited. Thirdly, do subjects report the perception of aliasing at any point during the test (indicator 3 above)? Fourthly, does resolution acuity correspond to anatomical measurements of ganglion cell density? To answer this last question, the experimental results were interpreted quantitatively by a neural sampling model based on anatomically realistic dimensions for receptive field size and spacing in human peripheral retina as measured previously in one of our subjects.

3. Materials and methods

All experiments were undertaken with the understanding and consent of the subjects in conformity with the Declaration of Helsinki. Five different tasks were performed using stimuli at four different contrast levels by three observers (authors RSA, SD, and LNT). All observers were experienced in psychophysical testing of the peripheral visual field and had prior experience, but to differing degrees, of the aliasing phenomenon. Although the observers were not naïve to the purposes of the experiment, they had no prior expectations of the results because the psychophysical task was to identify the shape or orientation of the letter-shaped aperture, not the carrier pattern within the aperture. Thus, anticipation that the carrier's stripes are likely to be under-sampled by retinal ganglion cells when letter size is near the acuity limit makes no predictions about whether the aperture *per se* is well-sampled. All testing was performed centrally and then again at 30° horizontally in the temporal field (nasal retina). Stimulus duration was always one second unless truncated by the subject's response, which was registered by a button press. All stimuli were presented on a 12-in. Apple monochrome monitor driven by a Macintosh computer (Apple Computer Inc., Cupertino, CA.) that was running custom stimulus generation/psychophysical software.

Three different characters in the vanishing-optotype set were used: a vanishing O, a vanishing C, and a vanishing + character. All three stimuli were of the same basic construction as indicated diagrammatically in Fig. 2. The stroke consisted of two darker borders either side of a lighter core, in a square-wave tripole-like configuration for which the widths of the components (border:core:border) were in the constant ratio 1:2:1. The mean luminance of the tripole stroke matched the luminance of the gray background. The outer diameter of the character was six times the stroke width. For the letter C, the gap width was equal to the stroke width. The + character consisted of a vertical and horizontal segment drawn with the same square tripole-like stroke. To ensure that the space-

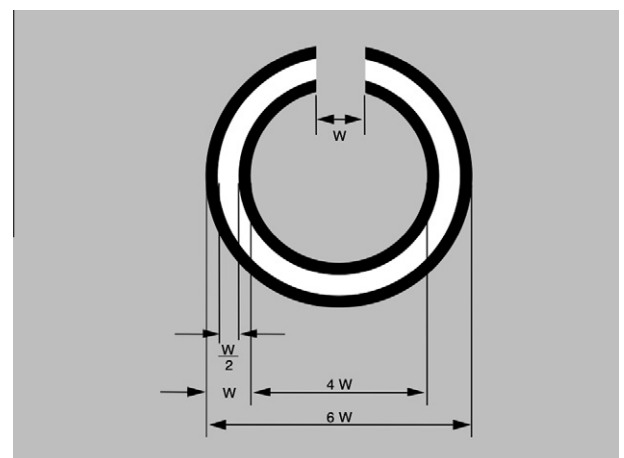


Fig. 2. A schematic of the C stimulus used in this study and the scale relationships between various components.

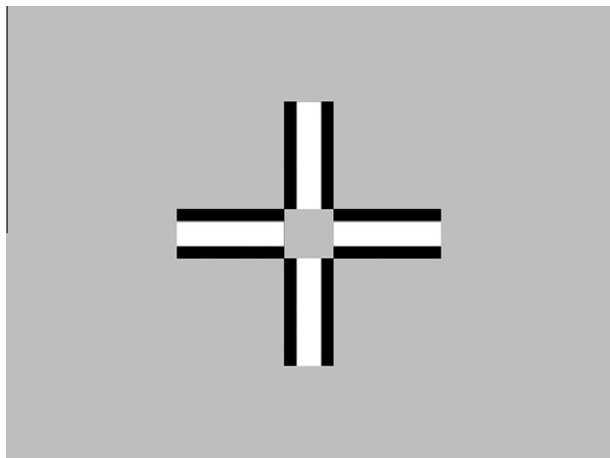


Fig. 3. A schematic of the plus (+) stimulus used in this study.

average luminance of the + character was the same as the background, the intersection of the horizontal and vertical components was removed and constrained to be the same luminance as the background as shown in Fig. 3.

Stimulus contrast was varied by manipulating the luminances of the border and core portions of the stroke in a balanced manner so that the space-averaged luminance of the stimulus was always equal to the background. Four calibrated levels of contrast were 0.93, 0.48, 0.21 and 0.09, where contrast is defined as $(\text{core luminance} - \text{border luminance}) / (\text{core luminance} + \text{border luminance})$. Keeping the space-averaged luminance of the stimulus the same as the background prevented detection of the letter by a luminance cue, i.e. the subject needed to detect the spatial contrast inherent in the tripole to detect the stimulus.

The five tasks performed by the observers were:

- (1) Detection of the O stimulus; no discrimination or resolution of any spatial detail was required.
- (2) Detection of the C stimulus; no discrimination or resolution of any spatial detail was required.
- (3) Detection of the + stimulus; no discrimination or resolution of any spatial detail was required.
- (4) Identification of the direction of the gap in the C stimulus, confined to two possible orientations: gap 'right' or gap 'up'.
- (5) Identification for a 2-'letter' set: the letter O and the + character.

Tasks 1–3 (detection tasks) were run as two-interval forced-choice paradigms with stimulus size as the variable. On any given trial, the subject indicated whether the stimulus appeared in the first temporal interval or the second. Tasks 4 and 5 (letter discrimination) were run as two-alternative forced-choice paradigms, again with stimulus size as the variable. On any given trial, the subject indicated which of two characters was presented. To change character size the entire stimulus, tripole and window, were scaled proportionally to maintain constancy of their relative sizes. Wetherill and Levitt staircases were used (Wetherill & Levitt, 1965) and terminated after ten reversals. For detection tasks, the average stroke width W for the last eight reversals was taken as the minimum angle of detection (MAD). For identification tasks, the average stroke width W for the last eight reversals was taken as the minimum angle of resolution (MAR). Both angles represent the minimum stroke width for which the task could be performed correctly 93.8% of the time (i.e. convergence of a two alternative forced choice, three down – one up staircase).

Since optical blur preferentially reduces contrast and may produce phase reversals that could confound our experiments,

appropriate optical correction of the eye for the test eccentricity was used during all experimental runs. The appropriate optical correction was determined firstly using retinoscopy either on-axis for foveal correction or off-axis for peripheral trials, with subsequent subjective refinement using a maximum perceived contrast criterion while viewing a high spatial frequency grating. Correction was provided via the subject's own glasses or using trial lenses during foveal testing, or appropriately positioned trial lenses during peripheral testing.

4. Results

The effects of contrast on minimum angle of detection (MAD) and minimum angle of resolution (MAR) for vanishing optotypes are shown in Fig. 4 for foveal vision and in Fig. 5 for peripheral vision 30° in the temporal field. Symbols show average performance for the three observers with error bars representing one standard error of the mean (SEM) across subjects.

Two important features are evident in the foveal data shown in Fig. 4. First, detection acuity and resolution acuity both improve (minimum angles get smaller) monotonically with contrast for all letters, which indicates that foveal performance on these tasks is contrast-limited. Second, comparing Fig. 4a and b reveals that MAD and MAR are approximately equal for characters O vs. + in foveal vision. Although MAR was slightly greater than MAD for the tumbling C character, the magnitude of this difference was small compared to the inter-subject variation and thus ruled insignificant. These foveal results confirm the design concept of vanishing optotypes as characters that can be correctly identified provided they have sufficient contrast to be detected. From these findings we conclude that resolution of high-pass letters by foveal vision is limited by contrast, not neural sampling, a conclusion consistent with the grating literature (Anderson, 2006; Anderson, Evans, & Thibos, 1996; Campbell & Green, 1965; Williams, 1985a).

There are some similarities between peripheral and foveal results, as well as some very important differences. As expected, performance is substantially poorer overall in peripheral vision compared to the fovea, as can be seen by comparing ordinate scaling in Figs. 4 and 5. As was the case at the fovea, MAD for the C, O and + characters (Fig. 5a) are practically identical. Detection acuity again declines monotonically with contrast, implying that the task of detecting a high-pass filtered optotype is limited by contrast in peripheral vision, just as it is foveally. In particular, the task of detecting the letter O is clearly limited by contrast in both foveal and peripheral vision.

Resolution acuity for O vs. + is similar to detection acuity at 30° eccentricity, implying that O and + can both be identified correctly in peripheral vision provided there is sufficient contrast for the characters to be detected. Resolution acuity improves (MAR declines) as contrast increases, implying that discriminating O from + is also contrast-limited in peripheral vision. The one exception to these general trends is MAR for the Landolt-C identification task, which, although somewhat more variable than the O vs. + comparison, is largely independent of contrast over the range tested. These latter data indicate that identifying Landolt-C orientation is the only task in our study that is not contrast limited, and thus is potentially sampling-limited, but only in peripheral vision.

To test the hypothesis that resolution acuity in peripheral vision is sampling limited for Landolt-C letters but not for O vs. +, detection acuity is compared with resolution acuity in Fig. 6. The ratio of MAR to MAD is shown for foveal vision (filled symbols) and peripheral vision (open symbols) for each subject separately using a staggered ordinate axis. For each subject, three out of four ratios are close to unity over the full range of stimulus contrasts tested, which is inconsistent with sampling-limited behavior. Only for

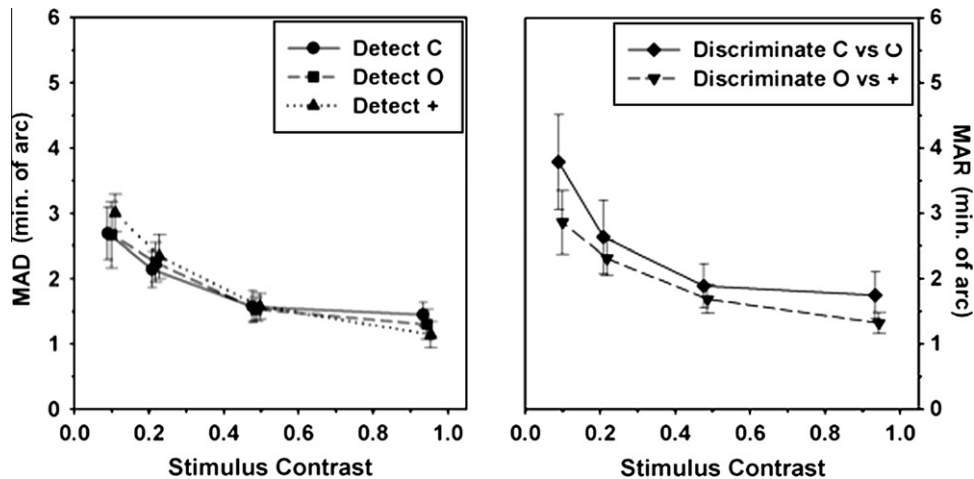


Fig. 4. Foveal data. The left panel shows performance for detection tasks (circles, squares and triangles show data for detection of C, O and + stimuli respectively). The right hand panel shows performance for discrimination tasks (diamonds for discriminate gap in C, and inverted triangles for discriminate O from +). The symbols for different tasks have been slightly offset along the contrast axis (by 0.01) to prevent symbols from overlying one another. Error bars represent SEM for the three observers.

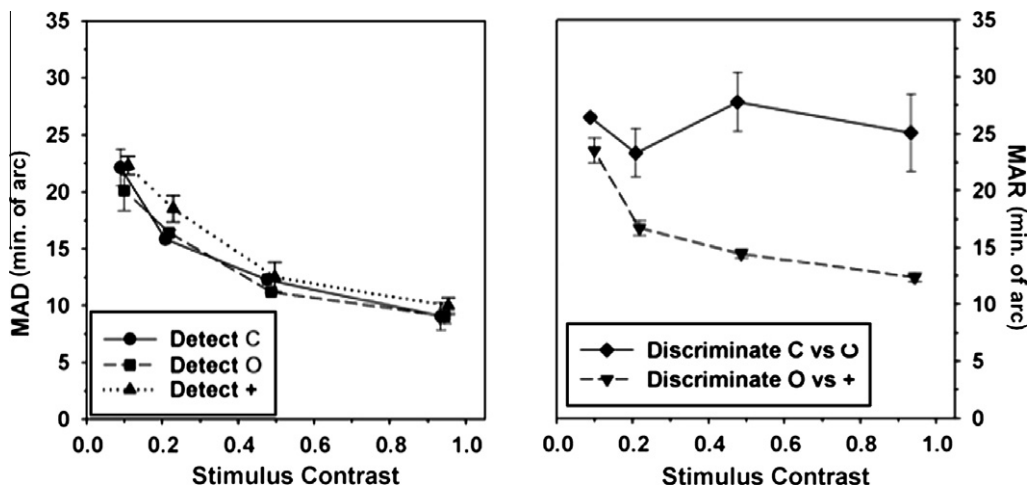


Fig. 5. Same as Fig. 4, except showing data gathered from 30° in the temporal field.

the Landolt-C task in peripheral vision is the ratio MAR/MAD significantly greater than unity (in the range 2.5–3 for our subjects). For this task and retinal location, there is a two to threefold range of letter sizes for which the letter target is clearly detectable, yet unresolvable, which is consistent with sampling-limited behavior.

5. Discussion

The notion of sampling-limited resolution of gratings is a relatively simple concept because extended gratings have highly localized spatial frequency spectra that approach a delta function. Thus a grating's spectrum is clearly either below or above the Nyquist frequency set by a regular sampling mosaic. But when a grating is truncated down to a small patch containing just a few periods, the frequency spectrum expands to occupy a broad range of spatial frequencies, some of which may be above and some below the Nyquist frequency. Thus even the Tumbling-E, which is the most grating-like of all letters in the Roman alphabet, has a broad, complex spectrum that is affected in several different ways when undersampled (Anderson & Thibos, 1999a, 1999b). To this complexity we now add the tripole structure of strokes used to construct vanishing optotypes, which further complicates the quantitative modeling of sampling-limited behavior. To avoid this

complexity of stimuli characterized in the spatial frequency domain, we offer instead a simpler explanation in the spatial domain for why neural under-sampling of vanishing optotype letters can cause resolution acuity to be significantly worse than detection acuity for some tripole letters, but not for others.

The upper panels (a and b) of Fig. 7 display the + and C characters at the minimum size required for detection by subject RSA in the periphery. A previous experiment using extended gratings provided an estimate of neural receptive field size and spacing for this same subject (Anderson, Evans, & Thibos, 1996). Those values are used to illustrate a schematic array of neural receptive fields on the same absolute scale as the letters. Inspection of this figure reveals that the receptive field diameter is approximately $W/2$ (half the width of the tripole) which means the integrated intensity detected by each receptive field is approximately equal to the background intensity, regardless of the letter's location relative to the array. Thus the contrast in the neural image carried by this sampling array is near zero, which explains why this is the minimum stroke width for detection. At this minimum size, some 20 or more neurons are poised to begin detecting spatial contrast when letter size increases, which we take as an estimate of the minimum number of samples needed for perceptual visibility. Notice, however, that the spacing between receptive fields is too large to veridically

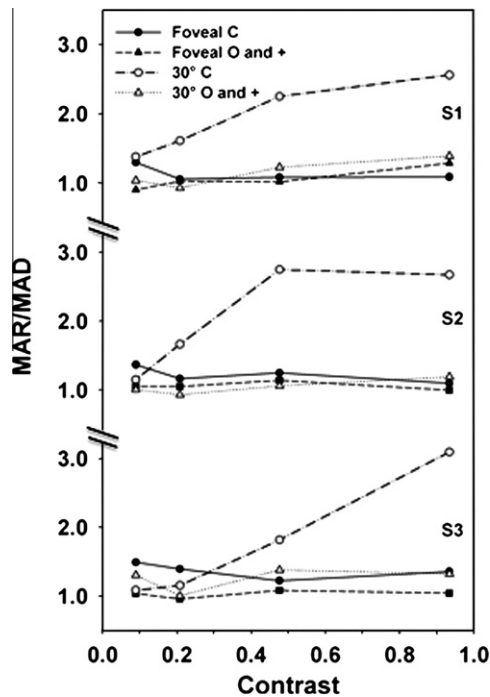


Fig. 6. Discrimination/detection performance ratios for Landolt-C targets (circles) and O and + targets (triangles) for foveal testing (filled symbols) and peripheral testing (unfilled symbols). Data for the three subjects is shown separately on a staggered ordinate axis. See text for additional detail.

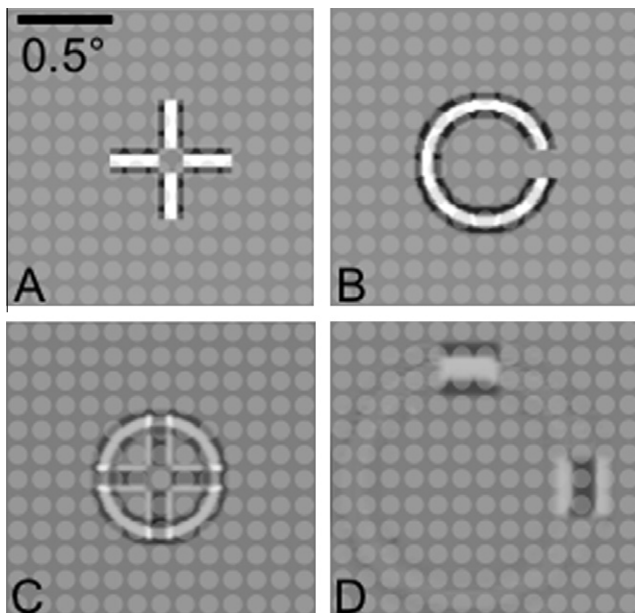


Fig. 7. Panels A, B show the + character and letter C scaled spatially to be at the threshold size for detection. Panel C shows the difference image for the O and + characters scaled spatially to be at the threshold size for resolution. Panel D shows the difference image for the 'right' C and the 'up' C, scaled spatially to be at the threshold size for resolution. Overlaid on each stimulus is an array of receptive fields with diameter (0.1°) and spacing (0.12°) estimated for the same subject in a previous study that used extended grating stimuli (Anderson et al., 1996). Calibration bar in panel A applies to all panels. In each case, the stimulus to detection or discrimination excites approximately 20–30 receptive fields at threshold. Count of the receptive fields that overlap the stimulus; A: 20, B: 20, C: 32, D: 18.

represent the individual border and core components within the tripole. Thus the tripole pattern will be undersampled when letter size is near the detection limit, which causes perceptual aliasing of

the tripole, in the same way that undersampling leads to aliasing of the striped pattern inside the E-shaped aperture in Fig. 1.

The lower part of Fig. 7 illustrates the task faced by the visual system when attempting to discriminate a pair of letters, which is a necessary precursor of letter identification. As has been done previously for gratings (Anderson & Thibos, 1999a; Campbell & Robson, 1968) and for letters (Anderson & Thibos, 2004), we argue here that the stimulus information available for target discrimination is contained in the 'difference image'. Thus the available signal for discriminating O from + is shown in Fig. 7c as the algebraic subtraction of the + image from the O image. In a similar fashion, the available signal for discriminating two orientations of the Landolt-C is shown in Fig. 7d as the algebraic difference between the two letter images. The difference image in panel c is depicted at the minimum size for discrimination by subject RSA and is overlaid onto the same neural array as in panels a–b. Inspection of Fig. 7c reveals that the letter is just detectable at this size because the period of the tripole closely matches the size of the receptive field. This close agreement is evidence that optical blur due to residual refractive errors and aberrations in peripheral vision was not a major limiting factor in our experiments. More importantly, the spacing between receptive fields is small compared to the separation of major features in the difference image. In short, the critical features in the difference image in panel 7c are well-sampled even though the tripole stroke may be undersampled.

A very different situation for the just-resolvable Landolt-C is depicted at the same scale in panel 7d. Here the period of the tripole is significantly larger than receptive field size and thus the just-resolvable target will be well above threshold for detection. However, the difference image is so sparse that for the gap's location to be well-sampled and reliably-signaled, the letter must grow two to threefold in size so that the major features in the difference image (the two gaps) cover several stimulated neurons and are separated by several un-stimulated neurons, as shown in panel d. In short, the letter features of the difference image in panel d are well sampled at the minimum size for resolution, but would be undersampled if the letter was reduced to its minimum size for detection.

To summarize these observations, it appears from our experimental results that threshold discrimination of O and + characters in peripheral vision is supported by approximately the same number of activated neurons (about 20–30) as supports threshold discrimination of two orientations of the Landolt-C, despite the fact that the Landolt-C is significantly larger. Presumably this minimum number of neurons is set by the summation properties of the visual system to compensate for internal noise and spatial irregularity in the sampling array. To achieve the requisite number of activated neurons, the Landolt-C must be 2–3 times larger because most of the neurons sampling the letter provide no useful information for performing the discrimination task since they respond equally to both stimulus orientations. Since the number of neurons sampling the stimulus is the essential feature of our argument, we conclude that resolution of Landolt-C vanishing letters is limited by neural sampling density. A similar argument cannot be made for the O vs. + discrimination because $MAD = MAR$ for these letters. Instead, a simpler explanation for MAR is that making the letter even smaller would make it invisible. Thus resolution of O vs. + fails for letters slightly smaller than MAR because of a failure to detect the stimulus contrast rather than because of insufficient sampling density.

To graphically demonstrate our explanation for the limits to recognition of vanishing optotypes, Fig. 8 shows the appearance of high contrast target pairs at different sizes when sampled by a fixed, slightly irregular sampling array mimicking the array of ganglion cells of the peripheral retina. In sampling the image, each neuron in this array linearly sums (averages) the energy within its receptive field center. Such a sampling demonstration was

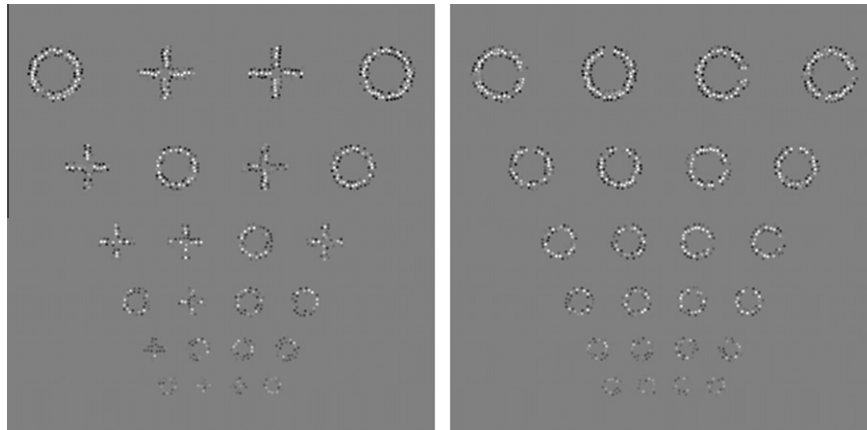


Fig. 8. Appearance of high-contrast O and + targets (left) and Landolt C targets (right) when sampled by noisy array at different sizes. O can be discriminated from + all the way to the bottom indicating similar limits to detection and discrimination, after which contrast limits performance. Although the C can be detected all the way to the bottom, discrimination fails after about the third row owing to insufficient samples to reliably indicate gap orientation.

employed by Carkeet et al. (2008) to simulate foveal cone sampling of conventional letter targets. By observing these sampled images, it is immediately apparent that sampled characters can be identified much further down the chart for the O vs. + pairing (left chart, almost to the bottom row) than for the Landolt-C pairing (right chart, only to perhaps the third row). While the Landolt-C looks fairly circular all the way down the chart, the gap direction is not discernable below the top few rows because there are insufficient cells available to register the location of the gap. The letter is thus very detectable all the way down the figure, but resolution fails about halfway down. For the O vs. + however, the characters can be both detected and discriminated even at the bottom of the figure. Any loss of discrimination at the bottom appears to be because summation within the receptive fields causes demodulation of contrast within the tripole strokes. This further supports the notion that discrimination of the O and + is a contrast-limited task even in peripheral vision where optical degradation of contrast is less important. Thus, stimulus size contributes in two ways: it makes the area larger, thereby facilitating detection, and it controls the number of receptive fields detecting the gap, thus aiding resolution. Which limit applies is dependent on the task and the letters under consideration.

However, it should be noted that this task involves only two alternatives that are very dissimilar. If the number of alternatives were to increase, the dissimilarities between individual characters would decrease and the task may switch to become sampling-limited.

A recent study by Evans et al. (2010) using gratings has indicated that the level of supra-Nyquist discrimination performance is dependent on the degree of spatial jitter in the sampling array. We would expect this to apply most strongly when the number of letter alternatives is small (2AFC used by Evans et al. and in the present study) and the degree of uncertainty is thus low. Under such conditions the target does not have to clearly appear as e.g. an 'O', but merely be identified as 'not the other one'. Looking at the sampled charts it is clear that the O and + targets can be discriminated without actually looking much like an O or a +. If the number of alternatives was greater, the degree of uncertainty would increase and the subject would require a much larger, better sampled letter to confidently identify it from a long list of alternatives. In this simulation we have employed a fairly irregular array, as would be expected to exist at 30° in the periphery. More sophisticated simulations employing different amounts of array irregularity and different numbers of letter alternatives may provide better insight into the limits to letter resolution at different eccentricities, but are beyond the scope of this paper.

We conclude that detection acuity is limited by contrast for vanishing optotypes in peripheral vision whereas resolution acuity may be sampling-limited or contrast-limited, depending on the letters to be discriminated. Since detection acuity for vanishing optotypes in foveal and peripheral vision is limited by stimulus contrast (rather than by sampling), we would expect MAD to be closely related to receptive field size rather than retinal cell density. When compared to the High-Pass Resolution Perimetry literature, our data for detection of a high-pass O are similar to those of Frisén (Frisén, 1987, 1988). Specifically, our results confirm that performance on the conventional HRP task is hindered appreciably by contrast reduction, a finding that argues against it being limited by a sampling process at the level of the retinal ganglion cells or at any other stage in the visual pathway. On the other hand, resolution acuity for high-contrast, high-pass letters may be either contrast or sampling limited, depending on the specific letters being discriminated. This was a novel and unexpected finding that was not anticipated by knowledge that grating resolution is sampling-limited (Thibos, Walsh, & Cheney, 1987), nor by the literature on the detection of static (Hess, Baker, May, & Wang, 2008) or moving (Smith et al., 1994) second-order stimuli, in peripheral vision. In designing a clinical resolution perimetry test to measure retinal ganglion cell loss in diseases such as glaucoma, it is essential to carefully consider the target set to be employed, bearing in mind that the mechanism that limits performance may vary depending on the letters chosen.

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