

Cone spacing and the visual resolution limit

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It is commonly assumed that the visual resolution limit must be equal to or less than the Nyquist frequency of the cone mosaic. However, under some conditions, observers can see fine patterns at the correct orientation when viewing interference fringes with spatial frequencies that are as much as about 1.5 times higher than the nominal Nyquist frequency of the underlying cone mosaic. The existence of this visual ability demands a closer scrutiny of the sampling effects of the cone mosaic and the information that is sufficient for an observer to resolve a sinusoidal grating. The Nyquist frequency specifies which images can be reconstructed without aliasing by an imaging system that samples discretely. However, it is not a theoretical upper bound for psychophysical measures of visual resolution because the observer's criteria for resolving sinusoidal gratings are less stringent than the criteria specified by the sampling theorem for perfect, alias-free image reconstruction.

There are at least two reasons to measure the visual resolution limit. First, the visual resolution limit is one of many benchmarks that specify the limits of human visual performance. A more interesting reason is that such measurements might allow us to draw inferences about the underlying architecture of the visual system. In this paper we address difficulties that arise in comparing visual resolution with the theoretical resolution limit of the cone mosaic. The theoretical tool often invoked for this purpose is the sampling theorem.^{1,2} It states that a band-limited signal that is sampled at regular intervals can be completely recovered from the sample values without aliasing if the highest frequency in the signal does not exceed $1/2s$, where s is the spacing between samples. This critical frequency is commonly called the Nyquist limit of the sampling array. Attempts to relate visual acuity to the anatomical spacing of photoreceptors have treated the Nyquist frequency of the cone mosaic as a theoretical upper bound on the visual resolution of the entire visual system.³⁻⁵

Coletta and Williams⁶ introduced a psychophysical technique for estimating cone spacing outside the fovea, complementing another technique for measuring cone spacing in the living fovea.^{7,8} These techniques make possible a comparison of cone spacing with measurements of visual resolution in the same retinal locations of the same observers. Such a comparison could disentangle the limitations imposed by the cone mosaic and postreceptoral mechanisms across the retina.

In order to determine whether the cone mosaic can determine the resolution limit of the visual system as a whole, one must employ a psychophysical technique that pushes the cone mosaic to its own theoretical limits. Under many conditions of ordinary viewing, the spacing of cones does not limit resolution. Vision at low light levels or with improper refraction are familiar examples. The use of interference fringe stimuli minimizes optical blurring, and the use of high intensities reduces quantum and neural limitations, increasing the likelihood that visual resolution is set by cone sampling. The sinusoidal nature of interference fringes is also convenient because it is compatible with the sampling theorem, which is expressed in frequency terms. It would be

desirable if the resolution measure were implemented with a forced-choice psychophysical procedure so that it would be immune to shifts in the observer's criterion.

At the same time, the measure should not stray from the intuitive sense of what it means to resolve a pattern, to separate a pattern into its separate components. For example, the highest spatial frequency at which interference fringes can be detected is not a measure of resolution because of the existence of aliasing.^{3,6-14} Observers can detect moiré patterns formed between gratings and the cone mosaic, even though they cannot distinguish the stripes of the original grating.

The first experiment demonstrates the effect of cone aliasing in the parafoveal retina and describes an attempt to establish an objective measure that captures visual resolution while ignoring the effects of aliasing. The second experiment refines this measure but nonetheless shows that the visual system can correctly extract information about the orientation of fine gratings even when the spatial frequency of the gratings exceeds the Nyquist frequency of the cone mosaic.

EXPERIMENT 1: CONTRAST SENSITIVITY FOR DETECTION AND ORIENTATION DISCRIMINATION

Most of the experiments described here were performed in the parafoveal retina, where aliasing by the cone mosaic has the appearance of two-dimensional spatial noise that is due to disorder in the mosaic. We attempted to establish a resolution measure that could be reasonably compared with the cone Nyquist frequency by asking observers to indicate the orientation of an interference fringe in addition to detecting simply its presence. The assumption that is implicit in this technique, which we evaluate below, is that observers can resolve a grating if they can identify its orientation.

Method

The apparatus is described in detail in Ref. 7. A brief description of this apparatus and the modifications required for these experiments can be found in Ref. 6. The test field

consisted of a 2-deg disk of 632.8-nm coherent light at 500 trolands (Td). An interference fringe of any desired spatial frequency, orientation, and contrast could be introduced into the test field without changing the space-averaged luminance of the field. An 8-deg annulus of incoherent light surrounded the test field. The luminance and wavelength (630 nm) of the annular surround closely matched the test field. A fixation cross hair was embedded in the surround. When the observer fixated the cross hair, the test field was positioned at 3.8 deg of eccentricity in the nasal retina.

Contrast thresholds were determined simultaneously for both fringe detection and orientation discrimination. On each trial, an interference fringe was presented in one of two 500-msec intervals chosen at random. The intervals were marked by tones and were separated by 500 msec. The fringe presented on each trial was either horizontal or vertical (also chosen at random). On each trial, the observer made two responses. The observer indicated the interval in which the stimulus appeared and then indicated the grating orientation. No feedback about performance was provided. One spatial frequency was tested per run; different spatial frequencies were tested in random order.

In each run, contrast thresholds were determined with four randomly interleaved staircases, corresponding to detection and discrimination thresholds for both horizontal and vertical fringes. The initial contrasts for each staircase were determined by a method of descending limits. A maximum-likelihood procedure, QUEST,¹⁵ determined the fringe contrast presented on each trial. A single run ended when 25 trials had been presented for each condition. The QUEST procedure fits the data with a Weibull function whose slope (β parameter) was fixed at 3.5, and 75% correct performance was chosen as the criterion for threshold.

Results and Discussion

Contrast-sensitivity functions (CSF's) for fringe detection and orientation discrimination are shown in Fig. 1 for two observers. Each data point is the mean of two runs. Contrast sensitivity for both tasks is low at low spatial frequencies as a result of masking by laser speckle, as has been previously described for the fovea.¹⁶ For both observers, the orientation-discrimination CSF and the detection CSF agree at low spatial frequencies. However, there is a range of higher spatial frequencies from 32–35 cycles/deg to 50–55 cycles/deg for which observers cannot correctly discriminate fringe orientation, although they can still detect the interference fringe. The detection of these high-frequency fringes is mediated at least partly by aliasing noise produced by the cone mosaic.⁶

The orientation-discrimination task meets all the criteria established so far for an objective measure of visual resolution that could be compared with the Nyquist frequency of the cone mosaic. The limit established with this technique was compared with acuity measurements made by the method of adjustment, in which observers determined the highest spatial frequency at which they could see a fine, oriented pattern amid aliasing noise. Acuity determined by the method of adjustment was 33 cycles/deg for observer DRW and 34 cycles/deg for observer NJC, which agrees well with the forced-choice measure of about 35 and 32 cycles/deg, respectively. This result suggests that forced-choice orientation discrimination is a measure that is consistent with the

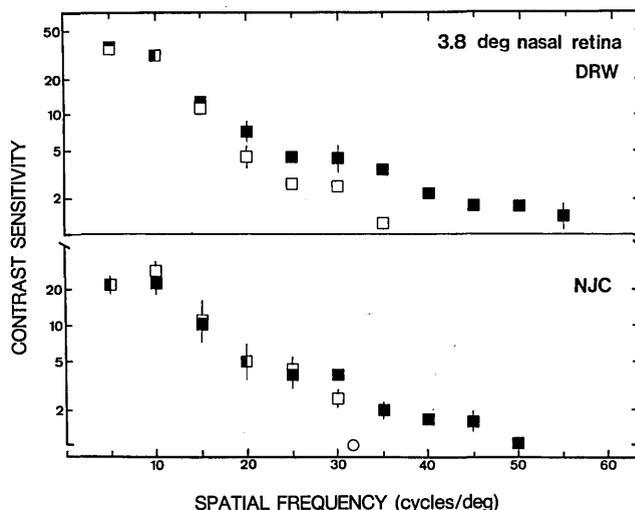


Fig. 1. Contrast sensitivity for interference fringes as a function of spatial frequency at 3.8 deg in the nasal retina for observers DRW and NJC. Contrast sensitivity is shown for detection of gratings (■) and for orientation discrimination (□). Data are the average for vertical and horizontal gratings. Also shown is the 75% correct level (○) for orientation discrimination (observer NJC) for 100% contrast gratings. If the contrast threshold for either the horizontal or the vertical fringe could not be measured at maximum contrast, no point was plotted.

subjective criteria that each observer establishes for resolving a grating.

EXPERIMENT 2: THE ORIENTATION-IDENTIFICATION LIMIT AND CONE SPACING

The following experiment demonstrates that a resolution criterion based on orientation fails to produce estimates that agree with the Nyquist frequency of the cone mosaic. The experimental procedure was modified to estimate efficiently the orientation-identification limit for comparison with estimates of cone spacing in the same retinal locations of the same observers. Psychometric functions were obtained for the identification of unity contrast horizontal and vertical fringes as a function of spatial frequency. These functions show that, in the parafovea, observers can correctly identify grating orientation at spatial frequencies exceeding the cone Nyquist frequency.

Method

The stimulus display and retinal location were identical to those used in the first experiment. During each 500-msec trial, a horizontal or a vertical interference fringe, randomly chosen, was introduced into a uniform field. The grating contrast was always 100%. The observer's task was to choose which orientation was presented. Observers were instructed to fixate carefully throughout the experiment. They monitored the accuracy of their own fixation by comparing the position of the field's afterimage with the center of fixation, thereby providing some subjective evidence that fixational errors were small.

Each run consisted of 150 stimulus presentations. There were 15 trials at each of the two orientations at each of five randomly interleaved spatial frequencies. On alternate runs another set of five spatial frequencies was tested, the

values of which were interdigitated with those of the first set. No feedback was provided after each trial. The use of five spatial frequencies in each run and the lack of feedback were intended to discourage observers from developing ulterior strategies for discriminating between horizontal and vertical fringes if they could not perceive their orientation. We describe the task as orientation identification, rather than simply orientation discrimination, on the basis of these features of the experimental design.¹⁷

Results and Discussion

The mean percent correct, representing the average for horizontal and vertical fringes, is plotted as a function of spatial frequency for three observers in Fig. 2. For observers DRW and RMK there were 4 runs per spatial frequency; for observer NJC there were 10 runs. Error bars represent ± 1 standard error of the mean based on the variability between runs. These average data were fitted with a Weibull-like function constrained to drop from 100 to 50% correct with increasing spatial frequency. The expression for this function is

$$f(x) = (0.5)\exp -(x/\alpha)^\beta + 0.5,$$

where x is spatial frequency (in cycles/deg), α determines the horizontal position of the psychometric function, and β determines its slope. Parameters α and β were objectively estimated with a least-squares curve-fitting algorithm. There is no theoretical motivation for the use of this particular function, nor is it a particularly good description of performance at higher frequencies, for reasons discussed below. Nonetheless it describes the data reasonably well out to spatial frequencies for which performance first reaches the chance level (50%), thereby providing an objective estimate of the orientation-identification limit. This limit was estimated, somewhat arbitrarily, by the spatial frequency producing 75% correct performance on the smooth-curve fit to the data.

Fringe orientation depends on the orientation of the two interferometric point sources imaged in the pupil. To guard against any artifact that might have resulted from changing the pupillary entry point, 30 additional trials per run were blank trials in which no fringe was presented and in which the positions of the point sources in the pupil were set just as they were when a fringe was presented. Chance-level performance was observed on these blank trials, suggesting that observers were not choosing the correct orientation on the basis of some cue other than orientation that might have covaried with the pupillary entry point.

When a sinusoidal grating is abruptly truncated, an artifact is produced at the edges of the field^{18,19} that can produce spuriously high estimates of resolution. An additional control experiment was performed to exclude the possibility that observers were using this potential cue. The contrast of the interference fringe was smoothly reduced from the center of the test field, and the space-averaged luminance was kept constant. The interference fringe was windowed by a photographic transparency that was conjugate with the retina. The transmission function of the transparency was a two-dimensional Gaussian with a full width at $1/e$ of 36 arcmin. This stimulus was embedded in a field of incoherent light whose luminance profile was the complement of the Gaussian envelope of the interference fringe, so that the

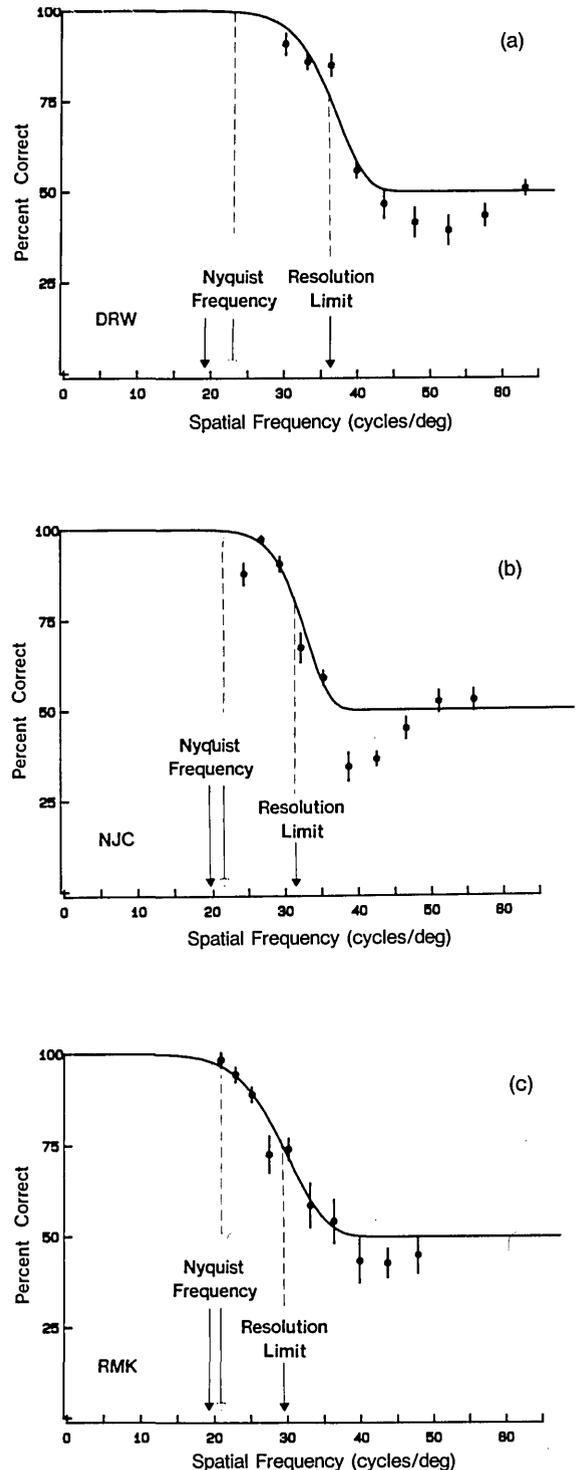


Fig. 2. Psychometric functions for orientation identification at 3.8 deg of eccentricity for three observers. Gratings were vertical or horizontal interference fringes of unity contrast. Error bars represent ± 1 standard error of the mean based on the variability between runs. Means are based on 4 runs (120 trials per frequency) for observers DRW and RMK and 10 runs (300 trials per frequency) for observer NJC. The orientation-identification limit was chosen to be the spatial frequency required for 75% correct responses, calculated from the smooth-curve fit to the mean data for both horizontal and vertical gratings. The nominal Nyquist frequency is calculated from Østerberg's cone spacing data²¹ (filled arrows) and from psychophysical measurements of cone spacing (open arrows) obtained on the same individuals by the technique described by Coletta and Williams.⁶

space-averaged luminance across the field was constant. The spatial-frequency spectrum of the stimulus was Gaussian, centered at the fringe frequency with a half-bandwidth at $1/e$ of only 1.06 cycles/deg. This condition constrained the stimulus to a narrow range of frequencies near the nominal frequency of the fringe, thereby eliminating potential edge artifacts. The orientation-identification limit measured under these conditions was similar to that measured with a sharp-edged test field of about the same size, suggesting that observers were not using this potential artifact. This result is consistent with the subjective reports of all the observers, who insisted that they could see an oriented pattern across the entire test field at spatial frequencies near the orientation-identification limit.

These estimates of visual resolution can now be compared with estimates of cone spacing in the same retinal locations in the same observers. The open arrows in Fig. 2 are the estimates of the cone Nyquist frequency obtained psychophysically for each observer by the orientation-reversal technique described by Coletta and Williams.⁶ The orientation-reversal effect can be seen in Fig. 2, where the data tend to drop below 50% correct performance at higher spatial frequencies, although the apparent magnitude of the effect is reduced here by averaging the results for horizontal and vertical fringes. There is a range of spatial frequencies for which striations appear in the spatial noise produced by cone aliasing. These striations are perpendicular to the true fringe orientation and appear when the fringe spatial frequency equals the "modal frequency" of the cone mosaic. The reciprocal of this frequency is a measure of cone spacing, and half the frequency corresponds to the Nyquist frequency of the cone mosaic. For example, the modal frequency of the cone mosaic (average of forced-choice estimates for horizontal and vertical gratings) is 44 cycles/deg for observer NJC, which yields a cone Nyquist frequency of 22 cycles/deg.

The cone Nyquist frequencies at the same retinal location where the orientation-identification measurements were made are 23, 22, and 21 cycles/deg for observers DRW, NJC, and RMK, respectively. The orientation-identification limits were 37, 31, and 29 cycles/deg for observers DRW, NJC, and RMK, respectively, substantially higher than the nominal Nyquist frequencies.²⁰ The ratio of the orientation-identification limit to the nominal Nyquist frequency depends on the probability criterion chosen for the orientation-identification limit. Defined at 75% correct performance, this limit averages 1.5 times higher than the nominal Nyquist frequency for these same observers. We will refer to this phenomenon as supra-Nyquist orientation identification.

It is unlikely that this effect can be explained by an error in the estimate of cone spacing. The available anatomical estimates at this eccentricity in the human eye agree closely with the psychophysical estimates of Coletta and Williams.⁶ Österberg's measurements of cone spacing at this retinal eccentricity²¹ predict a nominal Nyquist frequency of about 19 cycles/deg (shown as filled arrows in Fig. 2). The anatomical estimates of Curcio *et al.*²² (not shown in Fig. 2), based on data from four human eyes, predict a nominal Nyquist frequency of about 22 cycles/deg.²³ The cone counts of Österberg and Curcio *et al.*, expressed in areal instead of linear terms, would have to be too low by factors of 2.6 and 2.2, respectively, to account for the effect.

The psychophysical measurements are bolstered by the fact that all three observers, including one who was naive, insisted that they could see a fine pattern of the correct orientation extending across the test field at high spatial frequencies that were above their own nominal Nyquist frequency. Acuity measurements made by the method of adjustment, as well as the orientation-discrimination limits inferred from the contrast sensitivity measurements of Fig. 1, were similar to those obtained by the forced-choice orientation-identification technique.

Observers may have relied more heavily on information from the portion of the target that fell on the highest cone density, i.e., that portion nearest the fovea. However, this hypothesis does not account for much of the discrepancy between the orientation-identification limit and the cone Nyquist frequency. The nominal Nyquist frequency, calculated from the results of the orientation-reversal technique, even at the very inner edge of the 2-deg target would be only about 24 cycles/deg averaged across the three observers, although resolution averages 32 cycles/deg.

In principle, the orientation of the interference fringe could be computed from the response of a single photoreceptor that scanned the retinal image. If the temporal modulation introduced in the receptor(s) was greater for horizontal than for vertical eye movements, the observer could deduce that the grating was vertical, and vice versa. An experimental test of this hypothesis is to determine whether supra-Nyquist orientation identification is observed for flashes that are too short to permit scanning. In practice, this experiment is complicated by the fact that the use of short-duration grating pulses reduces contrast sensitivity to begin with, and the gratings in question are less than five times the contrast threshold even at maximum contrast. However, tests with one observer (NJC) showed that orientation identification exceeded the nominal Nyquist frequency with flashes as short as 75 msec, which is probably too short a time for a scanning strategy to be employed successfully.

Supra-Nyquist Orientation Identification and Retinal Eccentricity

The filled symbols in Fig. 3 show the orientation-identification limit at various retinal eccentricities for three observers. The mean of at least three runs is plotted at each eccentricity. The test-field diameter was scaled to be 80 times Österberg's cone spacing value²¹ at each retinal location tested. For example, a 40-arcmin field was used at the foveal center, and a 2-deg field was used at 3.8 deg, where cone spacing is about three times larger. The psychophysical estimates of the cone Nyquist frequency from the same observers⁶ are shown with open symbols. The data are also compared with anatomical measures of the Nyquist frequency for human cones. The data of Österberg²¹ are represented by the solid line; those of Curcio *et al.*²² are represented by the dashed line. The \times indicates the mean Nyquist frequency at the foveal center calculated from the anatomical data of Österberg,²¹ Curcio *et al.*,²² and Miller.²⁴ Supra-Nyquist orientation identification persists out to eccentricities of at least 10 deg, with performance dropping below the nominal Nyquist frequency of the cone mosaic between 10 and 20 deg of eccentricity.

There is equivocal evidence for supra-Nyquist orientation identification in the fovea. Observer NJC could identify

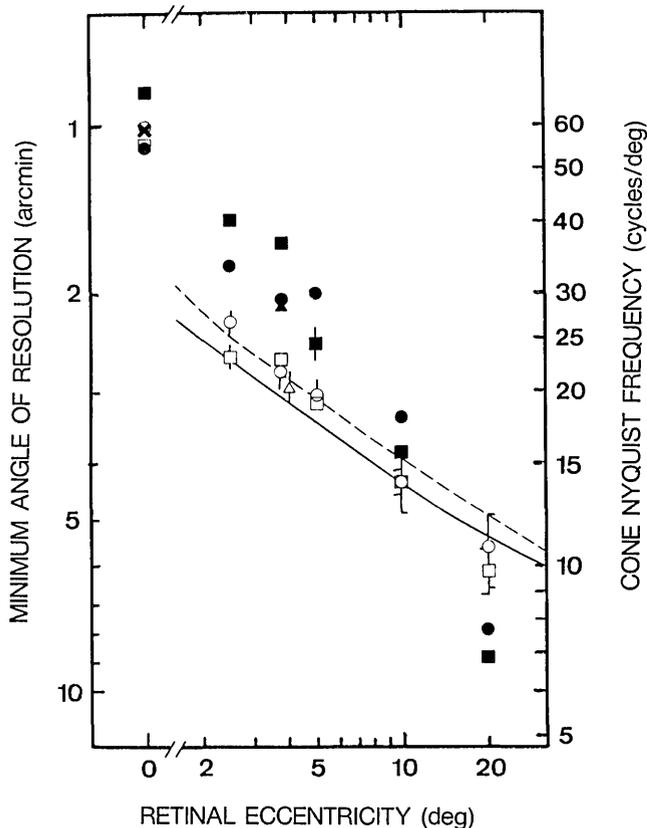


Fig. 3. Orientation-identification limit and cone Nyquist frequency as a function of retinal eccentricity. Filled symbols depict forced-choice orientation-identification limits for interference fringes for observers DRW (squares), NJC (circles), and RMK (triangles). All data are for temporal retina, except points at 3.8 deg, which are for nasal retina. Data are the mean ± 1 standard error of the mean for vertical and horizontal fringes. Open symbols depict the cone Nyquist frequency obtained by the psychophysical technique described by Coletta and Williams⁶ for the same subjects. Solid and dashed lines are nominal Nyquist frequencies calculated from the anatomical cone spacing data of Østerberg²¹ and Curcio *et al.*,²² respectively. The X indicates the nominal Nyquist frequency calculated from the anatomical cone spacing data at the fovea from Østerberg,²¹ Curcio *et al.*,²² and Miller.²⁴

orientation correctly up to 55 cycles/deg, whereas her Nyquist limit as predicted from the moiré zero psychophysical technique⁸ was 59 cycles/deg. However, observer DRW could correctly identify orientation at 68 cycles/deg, which was above his Nyquist limit of 57 cycles/deg.

DISCUSSION

Comparison with Previous Studies

The evidence presented here for supra-Nyquist orientation identification differs from previous estimates of grating acuity in the near extrafovea, for reasons that are not entirely clear. Earlier estimates lie equal to or below the Nyquist frequency instead of above it.^{4,5,25,26} However, these previous studies also differed in experimental method. We maximized retinal contrast by using interference fringes, used fields containing a large number of fringe cycles, and used forced-choice methodology. Since the aliasing noise that characterizes the appearance of high-frequency extrafoveal gratings was not identified in other studies, it seems likely

that the psychophysical techniques employed in those studies were not so sensitive as the technique used in the present study.

The difference cannot be attributed entirely to the use of interference fringe stimuli in the present study. Two earlier studies^{4,5} in which interference fringes were used to examine visual acuity within 10 deg of the fovea did not describe the spatial noise produced by cone aliasing. However, continuously presented fringes were used in the earlier studies, whereas pulsed fringes were used in the present study. Pulsing the fringe in an otherwise unchanging field helps the observer to distinguish aliasing noise from the laser speckle that is continuously present in coherent fields.

These earlier studies also used the method of adjustment, rather than orientation identification, to estimate resolution. The resolution limits of Enoch and Hope⁶ correspond roughly to the nominal Nyquist frequency out to 7 deg, the largest eccentricity that they studied. Our subjective observations suggested that the crisp appearance of interference fringes begins to be disrupted by aliasing noise for spatial frequencies near the nominal Nyquist frequency of the cone mosaic. It is possible that the resolution criterion adopted by the observers in the study of Enoch and Hope was influenced by the appearance of the aliasing noise, which they evidently did not distinguish from laser speckle.

It is more difficult to account for the difference between the present data and those of Green,⁴ who found that acuity followed the cone Nyquist frequency out to only 2 deg, falling substantially below the Nyquist frequency at greater retinal eccentricities. The contrast-sensitivity data in Fig. 1, which were collected at 3.8 deg, provide no support for the notion that postreceptoral mechanisms restrict visual resolution to values below the cone Nyquist frequency in either observer. The contrast threshold for orientation identification drops smoothly with increasing spatial frequency to about 20% at the Nyquist frequency for both observers. Only between 10- and 20-deg eccentricity does performance fall below the Nyquist frequency (Fig. 3). Postreceptoral factors are clearly limiting visual resolution at these largest eccentricities. Thus the present data support the generally held belief that, beyond 10 deg at least, the limitations on visual resolution in the peripheral retina are mainly postreceptoral.

Sampling Properties of the Cone Mosaic

How can the cone mosaic provide information about fringe orientation at spatial frequencies above its Nyquist frequency? Nagel²⁷ and Yellott^{28,29} have pointed out that cone spacing, considered strictly by itself, does not obliterate all information about sinusoidal gratings even when the gratings exceed the Nyquist frequency of the cone mosaic.³⁰⁻³²

This point is demonstrated in the top half of Fig. 4, which shows a horizontal sinusoidal grating (left) and a vertical grating (right) sampled by the extrafoveal cone mosaic. The mosaic was constructed from a photograph of a whole mounted rhesus retina supplied by Hugh Perry. The visual angle of the mosaic corresponds to about 1 deg, and the retinal eccentricity was 3.8 deg, where most of the psychophysical observations were made. The spatial frequency of the fringe was 1.25 times the nominal Nyquist frequency. Nonetheless, it is possible to discern the original gratings in their proper orientation. These fine gratings are not an

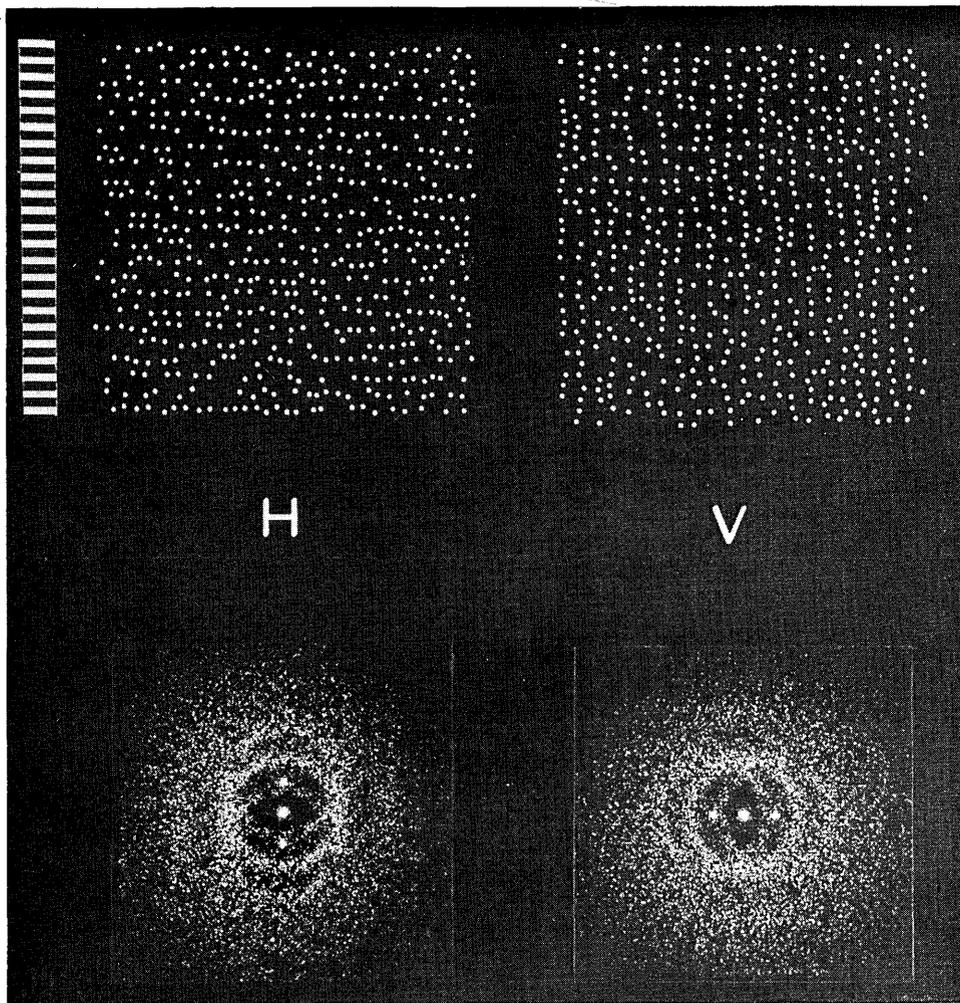


Fig. 4. Sampling properties of the primate extrafoveal cone mosaic. Effects of sampling horizontal (left) and vertical (right) gratings that exceed the nominal Nyquist frequency are shown in the spatial domain in the upper half of the figure. Dots represent locations of individual cones at 3.8 deg in the monkey parafovea. The sample is roughly 1 deg of visual angle across. The grating spatial frequency was 1.25 times the nominal Nyquist frequency. The lower half of the figure shows the effects of sampling in the two-dimensional frequency plane. The optical transform of the sampled horizontal grating is shown at the lower left; that of the vertical grating is shown at the lower right.

illusion or solely the result of aliasing. Some observers find it easier than others do to resolve the gratings in these simulations. However, with modest experience, observers can identify the orientation, spatial frequency, and phase of the original grating. The conspicuousness of the gratings can be accentuated by holding the plane of the page nearly parallel to the line of sight and peering down the rows of bright dots that correspond to the locations of the bright bars of the fringe. Small amounts of defocus also help, which suggests that spatial frequencies associated with the dots themselves tend to mask the grating in this simulation.

The fact that cone spacing does not obliterate supra-Nyquist gratings can also be appreciated in the spatial-frequency domain, as Yellott^{28,29} has pointed out. The lower half of Fig. 4 shows the optical transforms that correspond to the sampled gratings shown at the top. The technique for generating these optical transforms is described by Coletta and Williams⁶ and is similar to that originally used by Yellott²⁸ with cone mosaics. The three dots in the transforms correspond to the delta functions of the original fringe. The annular distribution of power around each of the delta functions corresponds to the spectrum of the mosaic alone: the

so-called desert island spectrum first described by Yellott.²⁸ The effect of cone sampling in the frequency plane is to convolve the spectrum of the mosaic with the spectrum of the grating stimulus (which is equivalent to multiplication of the grating and the mosaic in space). The convolution replicates the power spectrum of the mosaic around each of the delta functions of the fringe. The annular distributions of energy in the two replicas of the mosaic spectrum cast some energy at lower spatial frequencies than that of the original grating, corresponding to the aliasing noise. However, the delta functions that characterize the orientation and the spatial frequency of the grating survive sampling by the mosaic.

The ability of observers to identify the orientation of supra-Nyquist gratings in these simulations has been established by using a forced-choice procedure. Coletta and Williams⁶ employed the same orientation-identification technique used in the psychophysical experiments described above with the simulated mosaic of Fig. 4 instead of the actual extrafoveal retina. Interference fringes were imaged on a photographic transparency of the monkey cone mosaic. These sampled fringes were then imaged on the observer's

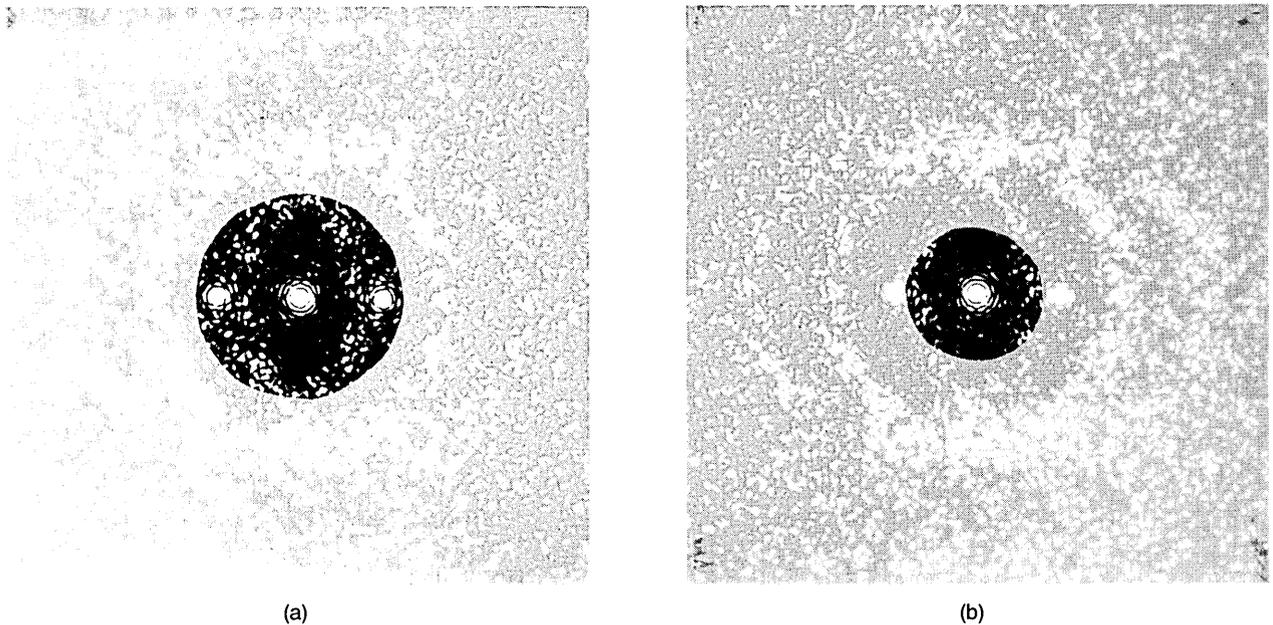


Fig. 5. Description in the frequency plane of two possible explanations for supra-Nyquist orientation identification. Both images show the optical transform of a vertical sinusoidal grating at 1.25 times the nominal Nyquist frequency of the cone mosaic sampled by the extrafoveal primate mosaic. The dark disk at the center of each transform represents the window of visibility, which is a hypothetical spatial filter in the postreceptoral visual system. (a) The supra-Nyquist resolution hypothesis: the spatial bandwidth of the filter is sufficient to pass the delta functions corresponding to the original grating. (b) The aliasing hypothesis: the spatial bandwidth of the filter is no greater than the Nyquist frequency, and supra-Nyquist orientation identification is mediated by the aliasing noise passing predominantly through the left- and right-hand edges of the window.

fovea. This procedure endowed the fovea with a sampling rate about 2.5 times lower than it normally enjoys, rendering its sampling properties roughly comparable with those of the extrafovea. The observer's performance exceeded 75% correct out to spatial frequencies that were more than 1.5 times the nominal Nyquist frequency of the artificial mosaic, just as when the actual extrafoveal cone mosaic was used (see Fig. 6 of Ref. 6). Indeed, the psychometric functions obtained with the simulation agree quantitatively with the actual psychometric functions in two ways. They not only capture the phenomenon of supra-Nyquist orientation identification; they also show the orientation-reversal effect at still higher spatial frequencies.

Two Hypotheses for Supra-Nyquist Orientation Identification

The first explanation for the supra-Nyquist orientation-identification effect is that it reflects the capacity of the postreceptoral visual system to use information at the spatial frequency of the original fringe even when the spatial frequency exceeds the cone Nyquist frequency. We will refer to this possibility as supra-Nyquist resolution. One way of characterizing this explanation is shown in Fig. 5(a). The spatial bandwidth of postreceptoral mechanisms is represented by a window of visibility³³ in the frequency plane. All spatial frequencies that fall within the window are faithfully extracted by the postreceptoral visual system; those that fall outside the window are lost. In Fig. 5(a) the window is larger than the Nyquist frequency of the cone mosaic. The delta functions corresponding to the original fringe are passed by the window, so that the visual system can extract the original signal (plus some aliasing noise). The exact properties of this window need not concern us; we have chosen a circular window with a sharp edge for simplicity.

Characterizing the information accessible to the brain with a single spatial filter is an oversimplification, but it captures the essential hypothesis that the brain can extract frequencies above the Nyquist frequency of the cone mosaic.

The role played by the packing arrangement of cones in the extrafoveal mosaic is unclear. The extrafoveal mosaic is less regular than the fovea,³⁴⁻³⁷ and the costs and/or benefits of this disorder have been the subject of much debate.^{12,37-40} Yen⁴¹ has shown that, in the absence of noise, it is possible to reconstruct frequencies perfectly up to the average Nyquist frequency even when the spacing of the sample points is nonuniform. French *et al.*⁴² proposed a model of the effects of irregularity in which disorder demodulated the contrast of high spatial frequencies in addition to introducing aliasing noise. However, their predictions were based on the assumption that the visual system was misinformed about the locations of its cones. A model that does not make this assumption⁴³ suggests that the effect of disorder is less severe than that predicted by French *et al.*, even when the effects of photon noise are considered.

In the specific case of grating resolution, disorder in the cone mosaic may provide some benefit.^{28,29} Disordered mosaics produce spatial noise that bears little resemblance to the highly regular grating stimulus. A visual system organized to extract regular features from the retinal image may benefit from the differences between supra-Nyquist gratings and aliasing noise. In the fovea, where the mosaic is much more regular, there is little evidence for supra-Nyquist orientation identification. If it exists, it is not nearly so pronounced as it is just outside the fovea. This is not necessarily a reflection of the difference in packing order between fovea and extrafovea, however, and may reflect postreceptoral factors. When viewing foveal fringes that are 1-1.5 times the foveal Nyquist frequency, observers report a rap-

idly flickering percept at the very center of the fovea that lacks a distinct pattern and is surrounded by a higher-contrast annulus of zebra stripes. The reason why it is difficult to see a distinct pattern in this frequency range is not clear. The fine alias predicted at the foveal center is not clearly seen until higher fringe frequencies (about 90 cycles/deg), for which the zebra stripe pattern is lower in its average frequency.

It is possible that *a priori* information plays an important role in accounting for supra-Nyquist orientation identification in the parafovea. The set of possible stimuli presented to the observer during the psychophysical experiment is limited, which could constrain the observer's perceptual solution to each stimulus from the set. For example, in the orientation-identification experiment, the visual system has only to find the one-dimensional pattern of fine stripes at two orientations that best matches the observed distribution of quantum catches. Other kinds of pattern need not be considered.

An alternative hypothesis to account for supra-Nyquist orientation identification is that it is mediated solely by an anisotropy in aliasing noise. It may be that the postreceptoral visual system is incapable of extracting the supra-Nyquist signals that are passed by the cone mosaic. This possibility is described by Fig. 5(b): the window of visibility has a cutoff frequency at the Nyquist frequency. The delta functions corresponding to fringes higher than the nominal Nyquist frequency are not passed by the window. However, energy is passed in the form of roughly crescent-shaped regions in the frequency plane at the left and right edges of the window. These correspond to aliasing noise in the spatial domain that would be weakly anisotropic. The broadband noise would be stretched on the average in the same general direction as the stripes of the original fringe and could possibly provide crude but correct information about the fringe orientation. We will refer to this explanation as the aliasing hypothesis. (At still higher frequencies approaching twice the Nyquist frequency, the aliasing noise becomes anisotropic in the perpendicular direction, accounting for the orientation-reversal effect.⁶)

There is some subjective evidence against this hypothesis. Our observers reported that the apparent spatial frequency of interference fringes increased monotonically with increasing spatial frequency out to the orientation-identification limit (1.5 times the cone Nyquist frequency). The aliasing hypothesis predicts that the apparent spatial frequency should begin to decline for spatial frequencies higher than the nominal Nyquist frequency. However, these subjective reports have not been confirmed with an objective psychophysical procedure, so that the aliasing hypothesis cannot be firmly rejected. The supra-Nyquist resolution and aliasing hypotheses that have been proposed here to explain supra-Nyquist orientation identification are not mutually exclusive. It is possible that any information about grating orientation directly extracted from the original signal could be reinforced by the anisotropic aliasing noise.

Implications for Efforts to Relate Visual Acuity and Anatomical Spacing

The above considerations show that there is no reason in principle why observers could not make use of information from spatial frequencies above the Nyquist frequency. The

balance of the psychophysical evidence available so far suggests that observers may actually be capable of doing so. Under the conditions that we have employed, resolution defined by this measure can be 1.5 times that anticipated from sampling theory. Use of the sampling theorem to draw inferences about anatomy from these psychophysical data would overestimate the density of neural elements by a factor of 2.25. This is likely to be an unacceptable margin of error.

Psychophysical tasks that provide estimates of the Nyquist frequency of the cone mosaic have already been found: the orientation reversal provides one estimate,⁶ and Coletta and Williams⁴⁴ have recently described a motion illusion that may estimate this value even more directly. However, a psychophysical task has not been found that estimates the Nyquist frequency and also captures our intuitive sense of the term resolution. The orientation-identification measure implies that orientation information alone is sufficient for visual resolution. One might argue that true resolution would require the observer to obtain more information about the stimulus. But how much more information would be sufficient? One could devise a criterion that required observers to extract information about spatial frequency as well as orientation. However, the disordered mosaic need not prevent an observer from extracting this information as well, at least in principle.

The conditions specified by the sampling theorem to permit alias-free reconstruction of a sampled image are more stringent than those demanded either by observers or by the operational definitions of resolution prescribed by psychophysical experiments. The sampling theorem specifies the requirements that an imaging system must meet to produce a flawless reconstruction of the entire two-dimensional luminance profile of the grating. Visual resolution does not require perfect reconstruction in this sense. The visual system has the less demanding task of computing from the quantum catches in the receptors a small number of attributes of the grating, such as spatial frequency and orientation, with some tolerable amount of error. The accuracy with which these attributes can be computed depends on a host of factors, including the effects of noise, the locations of receptors, the efficiency of postreceptoral mechanisms, and their capacity to use *a priori* information. The manner in which performance depends on these factors is not specified by the sampling theorem. Ideal performance for the particular acuity task employed would provide a useful benchmark for comparison with psychophysical performance,⁴⁵ but an appropriate ideal observer has yet to be constructed for grating acuity tasks.

The concept of an optical-resolution limit has proven difficult to formulate; it is not clear that the resolving power of an optical instrument is a particularly meaningful figure of merit.⁴⁶ Even the cutoff frequency of a diffraction-limited system can be surpassed under some circumstances.⁴⁷ The concept of visual resolution suffers from a similar lack of generality, and the theoretical limits of performance are set by the task as much as by the underlying visual architecture. The sampling theorem correctly specifies the highest frequency possible for image reconstruction without aliasing. However, it does not necessarily prevent an observer from extracting enough critical features of a supra-Nyquist grating to be confident that he sees it.

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$$f_N = (1/2)(0.291)(2D/\sqrt{3})^{1/2},$$
 where D is the cone density in cones per square millimeter and 0.291 converts millimeters on the retina to degrees of angular subtense. This estimate is negligibly different from one based on direct measurements of the modal frequency of the disordered extrafoveal mosaic,⁶ with the Nyquist frequency defined as half of the modal frequency.
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