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The relationship between visual resolution and cone spacing in the human fovea

Ethan A. Rossi¹ and Austin Roorda^{1,2}

¹Vision Science Graduate Group, University of California, Berkeley, Berkeley, California 94720, USA

²School of Optometry, University of California, Berkeley, Berkeley, California, 94720, USA

Abstract

Visual resolution decreases rapidly outside the foveal center. The anatomical and physiological basis for this reduction is unclear. We used simultaneous adaptive optics imaging and psychophysical testing to measure cone spacing and resolution across the fovea, and show resolution is limited by cone spacing only at the foveal center. Immediately outside the center, resolution is worse than cone spacing predicts and better matches the sampling limit of midrange retinal ganglion cells.

Neural sampling of the retinal image plays an important role in limiting human visual resolution at all locations in the visual field except the fovea, where optical aberrations usually impose a fundamental limit¹⁻⁵. When aberrations are minimized, the instantaneous postreceptoral information is believed to be limited by the spatial sampling of the cone photoreceptor mosaic in the fovea and possibly beyond¹⁻⁵. To the first order, this limit can be considered to be the Nyquist sampling limit of the cone mosaic (N_c). Foveal cones each connect via a cone bipolar cell to at least two retinal ganglion cells (RGCs) and since the majority of the RGCs in the central retina are of the midrange class, it is presumed that each cone in the central fovea connects to both an ON- and OFF-center midrange retinal ganglion cell (mRGC)⁶⁻⁷. This is the so-called “private line” hypothesis⁸ which forms the basis of the argument that cone spacing should limit resolution wherever this retinal circuitry is in place. At some point outside the fovea, signals from multiple cones converge onto single mRGCs, compromising resolution, and thus at some point visual resolution no longer matches N_c but instead matches the Nyquist limit of mRGCs⁶⁻⁷.

The eccentricity where convergence in the mRGC network begins is not clear, with anatomical evidence suggesting between 3.5 degrees⁶ to 6 degrees⁷ from the foveal center. Psychophysical studies which sought to compare N_c to visual resolution vary considerably, with estimates of the match between N_c and resolution persisting to anywhere from 2

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Competing Financial Interest: Roorda: patent: Method and Apparatus for Using Adaptive Optics in a Scanning Laser Ophthalmoscope. The patent covers both the imaging and stimulus delivery applications of the technology described in this paper.

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degrees to 10 degrees from the foveal center¹⁻⁵. Consequently, the relationship between visual resolution and N_c remains unknown (see Supplementary Information). The large variability in psychophysical investigations stems in part from the difficulty in directly measuring both N_c and optically optimal visual resolution in the same individuals^{3,5}, forcing comparisons of their resolution measurements with sampling limits derived from different eyes, primarily from histological reports^{1-2,4}. It is now well established that cone spacing, especially in the central fovea, is highly variable between individuals⁹, making these comparisons susceptible to error. The adaptive optics scanning laser ophthalmoscope¹⁰ (AOSLO) overcomes these limitations, allowing simultaneous measurement of the minimum angle of resolution (MAR), the cone spacing, and the precise location and motion of the stimulus across the retina.

An AOSLO was used to project an adaptive optics corrected tumbling E stimulus onto the retina at several locations within the central fovea (0–2.5° from the foveal center⁸) of five observers. Adaptive optics minimizes blur by measuring ocular aberrations and compensating for them with an adaptive element, improving optical quality for imaging and high resolution stimulus delivery¹⁰⁻¹². Adaptive optics significantly improves vision¹¹ and has been shown to reduce the MAR at the preferred retinal locus of fixation (PRLF) by ~33% in normal observers¹². In a four alternative forced choice task, observers reported the orientation while fixating the stimulus or a peripheral target. Each observer was tested at retinal locations temporal to the PRLF; one (S4) was also tested at superior, inferior and nasal locations. A video of the retina was acquired on each trial, encoding the exact location of retinal stimulation (see Supplementary Videos 1 & 2).

Retinal imagery is overlaid with a topographic map of stimulated cones in Fig. 1 for observer S3. A map was generated for each observer by precisely determining each cone that interacted with the stimulus over the course of each trial (see Supplementary Methods and Supplementary Video 3). The expected falloff in MAR with increased distance from the PRLF was observed (Fig. 2a). Fixational variability caused some test locations to deviate slightly from the horizontal meridian (Fig. 1), so actual distances from the PRLF are shown in Fig. 2. The magnitude and rate of reduction in MAR matched the performance reported in the literature from studies that measured resolution across the fovea using high contrast laser interference fringes¹⁻² (see Supplementary Information). An important value to note is the E_2 value (the eccentricity in degrees at which the threshold doubles); the mean E_2 of the MAR (E_{2m}) for all observers was ~1.275° (n = 5).

N_c along the horizontal temporal retina is plotted in Fig. 2b. Where cones were well resolved, center-to-center inter-cone distance (ICD) was measured directly from identified

cone centers and used to calculate N_c , where: $N_c = \frac{\sqrt{3}}{2} \times ICD$. This conversion is required because the Nyquist limit for a triangularly packed cone photoreceptor mosaic is based upon the spacing between rows of cones³. An assessment of mosaic regularity confirmed that this was an appropriate method for calculating N_c (see Supplementary Information). Cones were resolved at the PRLF for one observer (S3); cones became resolved for other observers between 0.14°–0.5° from the PRLF. N_c at the PRLF for these observers (and S2 at 0.4°) was therefore estimated from retinal imagery (see Supplementary Information). Similar to E_{2m} ,

we can compute E_{2c} , the value at which N_c doubles; mean E_{2c} was $\sim 2.224^\circ$ ($n = 5$), nearly double E_{2m} .

MAR is plotted against N_c at test locations in Fig. 2c. MAR agreed well with estimates of N_c at the PRLF, in agreement with previous researchers¹⁻⁵. However, MAR decreased at a greater rate with increasing eccentricity than was predicted by N_c . If MAR exactly matched N_c , data points would be expected to fall on the dashed 1:1 line shown in Fig. 2c. The slope is the important factor in this comparison, as a slope of 1 demonstrates that MAR is governed by N_c . A linear regression line was fit to the data of each observer independently. The mean slope was 0.6355 (SD = 0.1058; $n = 5$). This value was significantly different from 1 (t-test; one sample; $p = 0.00153$), indicating that MAR was worse than predicted by N_c at locations eccentric to the PRLF. Choosing a different threshold for acuity (i.e. 75% vs. 82.5%) would only have resulted in horizontal translations of the regression line fits. Choosing a different metric to represent N_c would have changed the slope; for the most extreme case, of a square mosaic, the slope would still only have been ~ 0.73 . Bland-Altman analysis¹³ confirmed poor agreement between MAR and N_c across test locations (see Supplementary Information). This discrepancy does not seem to be explainable by the nature of the stimulus (see Supplementary Information) or task, as the tumbling E task has been shown to be a sampling limited task¹⁴.

The area where visual resolution most closely matched N_c ($0-0.5^\circ$) corresponded well with the anatomically distinct foveola, the nearly flat floor of the foveal pit⁸. This retinal area has several features that are seemingly optimal for high spatial resolution, including: maximum cone density, elongated waveguides, the absence of rods and S-cones, and the lack of overlying vasculature and nerves⁸⁻⁹. However, we believe the discord between resolution and N_c seen outside the foveola was primarily due to differences in retinal circuitry across the fovea. Since the fibers of Henle displace RGCs from the photoreceptors of the central retina to which they form connections, foveal circuitry has historically been difficult to characterize^{6-8,15}. Careful study of these fibers leads to new predictions of mRGC receptive field density across the visual field¹⁵. Using a theoretical model of mRGC receptive field density¹⁵, we estimated the Nyquist limit of the mRGC mosaic (the spacing between neighboring ON- or OFF-center mRGC receptive fields) at the resolution test locations along the horizontal meridian (see Supplementary Information) and compare it to MAR in Fig. 2d. An individual regression line was fit for each observer; the mean slope was 1.0111 (SD = 0.1105; $n = 5$), this value does not differ significantly from 1 (t-test; one sample; $p = 0.8333$), indicating that MAR for this task is governed by the Nyquist limit of the mRGC mosaic across the fovea. Cortical mechanisms ultimately utilize the information provided by the earliest stages of visual processing in the retina to make a decision in a visual resolution task; that those decisions so closely match the theoretical sampling limits imposed by the first stages of retinal processing is remarkable.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgments

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Figure 1. Cone stimulation map for subject S3

Cones appear as bright circles arranged in a triangular lattice pattern. Stimulated cones are shown as topographic maps overlaid in color. Color bar shows normalized level of cone stimulation.

Figure 2. Visual resolution matches the Nyquist limit of the mRGC mosaic, not the cone Nyquist limit

a, Visual acuity as a function of eccentricity. Symbol legend is inset in (d). For observer S4, t, n, s, and i denote temporal, nasal, superior and inferior locations. Error bars are $\pm$ s.e.m. and omitted when smaller than symbol. **b**, Cone Nyquist limit across the horizontal temporal retina. Lines colored by subject in the same way as symbols (see legend inset). Solid lines are measurements; dashed lines are predictions. **c**, Cone Nyquist limit and MAR for temporal test locations. Cone Nyquist limit is mean of cones within an elliptical area subtending ± 2 SD of mean stimulated location. Error bars are $\pm$ s.e.m. and omitted when smaller than symbol. Dashed black line is the 1:1 line. **d**, Nyquist limit of mRGC and MAR. Only results along horizontal meridian are shown for S4. Dashed black line is the 1:1 line.