Peripheral photoreceptor activity during accommodation and emmetropization

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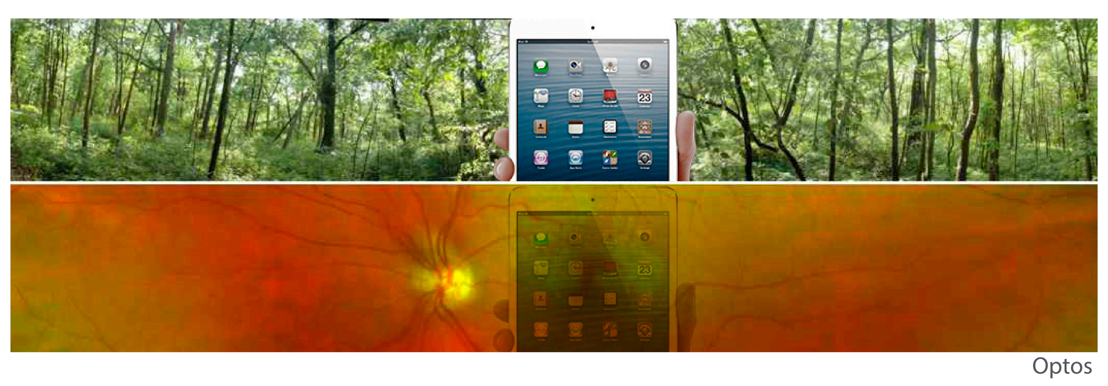
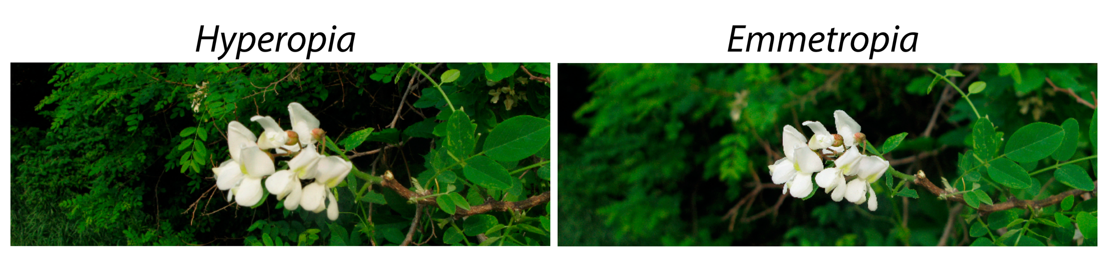
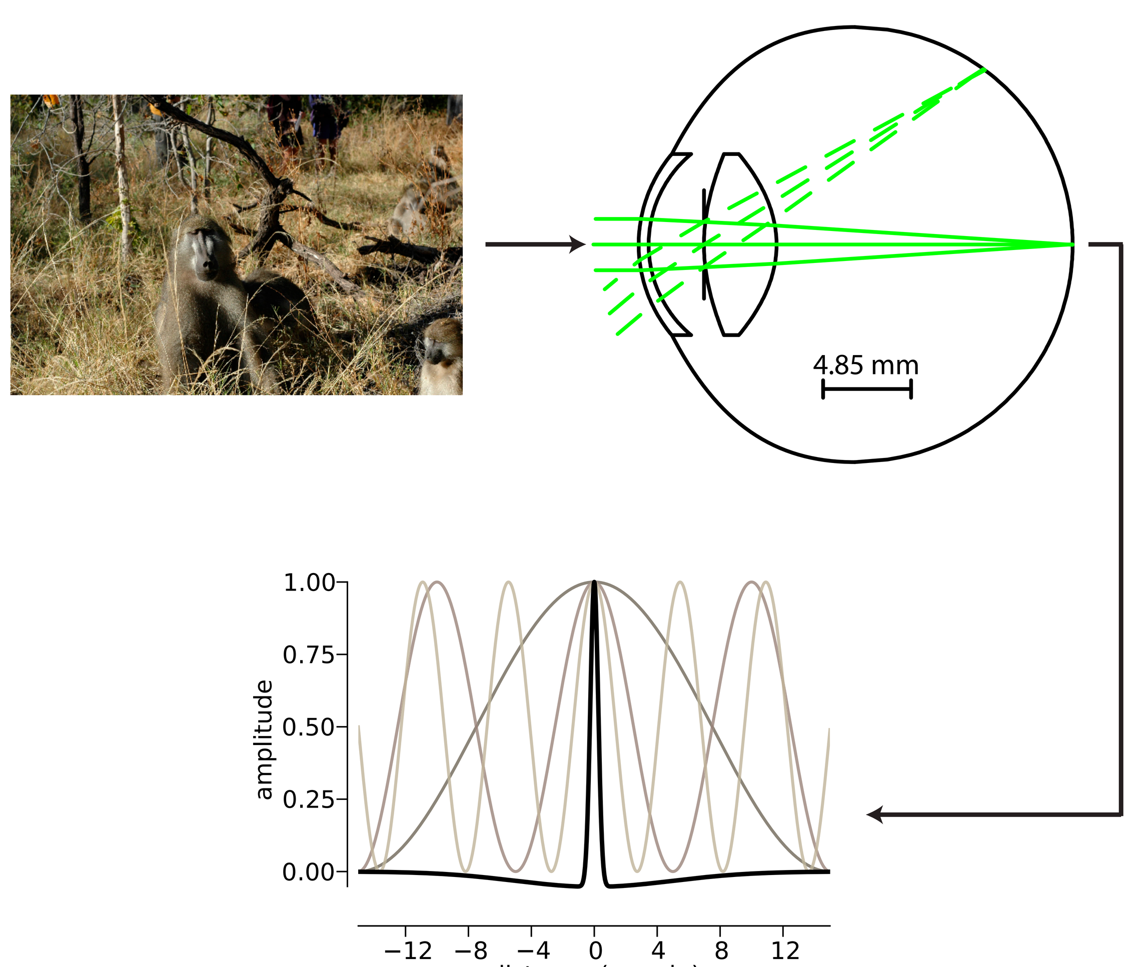
Introduction - Myopia results when the eye grows too long for its optics. The importance of the peripheral retina in emmetropization has recently been appreciated and our group has argued that activity differences (contrast) between neighboring cone photoreceptors is associated with signaling eye growth. However, there has not been a systematic analysis of how peripheral photoreceptor activity might be stimulated by natural images during near accommodation over the period of life which emmetropization occurs. The present work uses mathematical modeling to develop a theoretical framework of emmetropization based on the observation that the peripheral retina is often exposed to distant scenes when the fovea is accommodated to near objects.

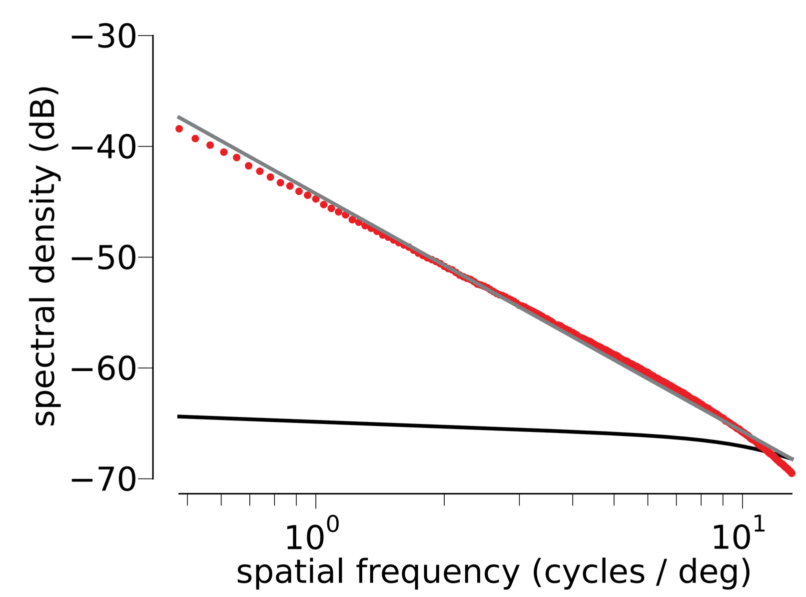






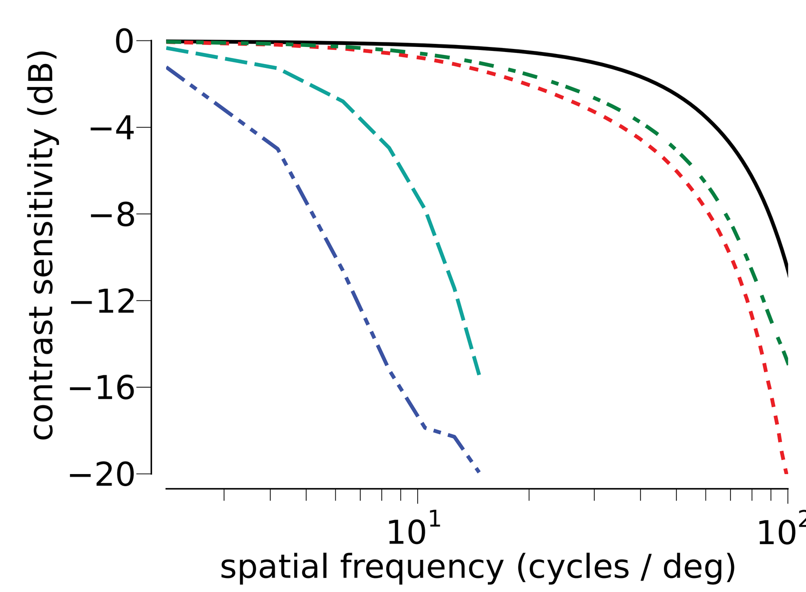
Methods - The OSLO ray tracing software (Lambda Research) was used to derive modulation transfer functions of a schematic eye [1] for several eccentricities and accommodation states. The amplitude spectrum of calibrated natural images [2] were computed with a fast Fourier transform and fit with a $1/f$ power law. The activity of photoreceptors was modeled as a difference of Gaussians. Finally, the transfer functions, power spectrum and photoreceptor model were combined to obtain the response from the peripheral cone photoreceptor mosaic to the average natural scene.

1.



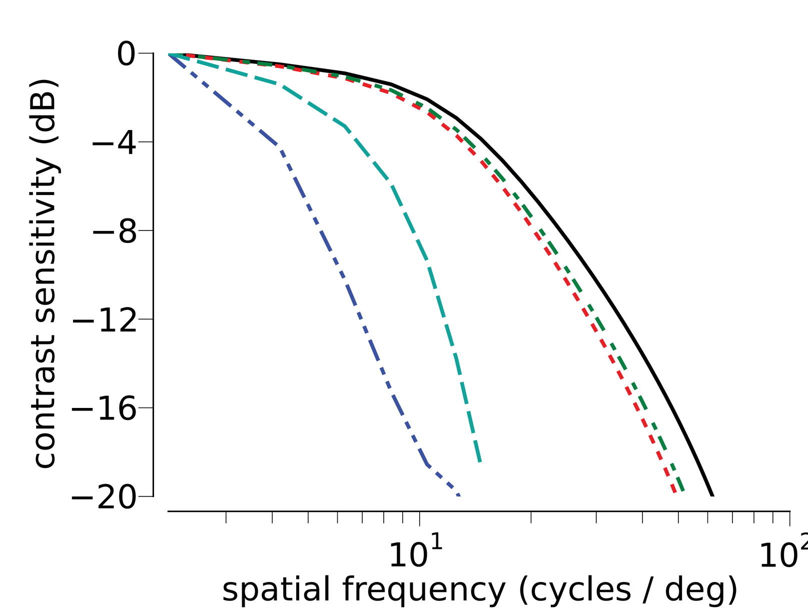
The spatial frequency content of a typical scene was estimated for a database of natural images [2]. The mean power spectrum (red) was fit with a power law (gray) according to (Eq1). The spatial frequency spectrum, $s(f)$, reaching the eye (black) was corrected for eye movement with (Eq2), which assumes a Brownian motion model (Eq3) [3].

2.



The off-axis (10 degrees) optical contrast sensitivity functions (CSF) for numerous accommodation states were modeled using the Navarro schematic eye [1].

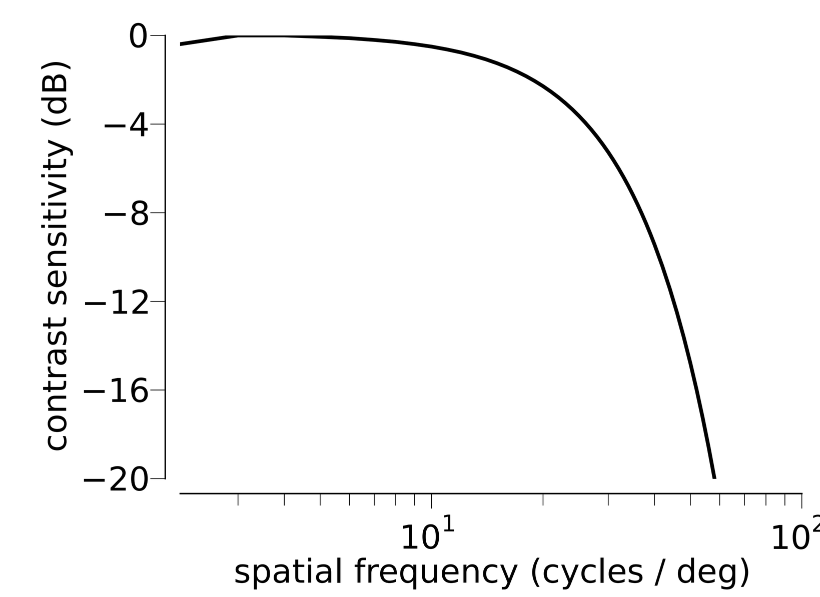
3.



The spatial frequencies transferred to the retina, $r(f)$, after accounting for the optics was estimated through convolution of the power spectrum, $S(f)$, with the optical CSFs, $g(f)$ (Eq 4).

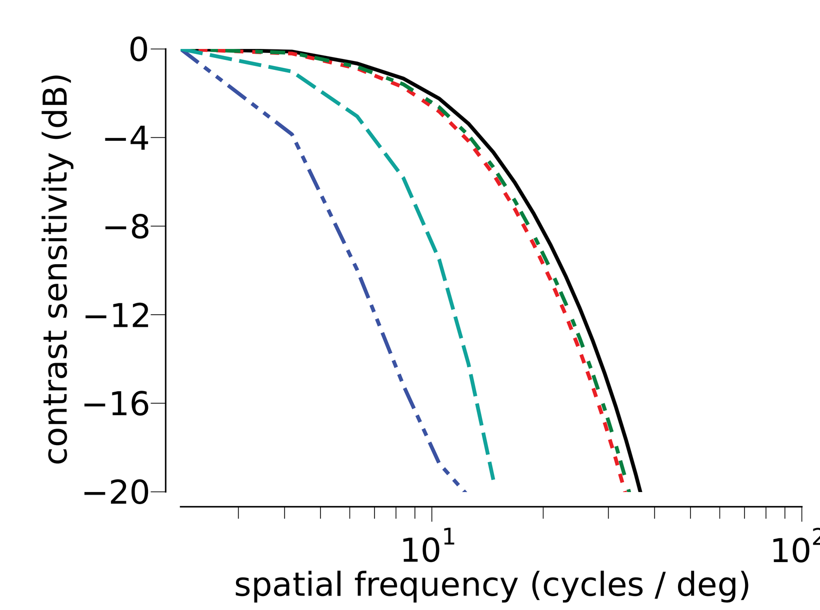
- diffraction limited case
- infinity, distant object
- reading, near object (book)
- reading, distant object
- reading under accommoded, distant object

4.

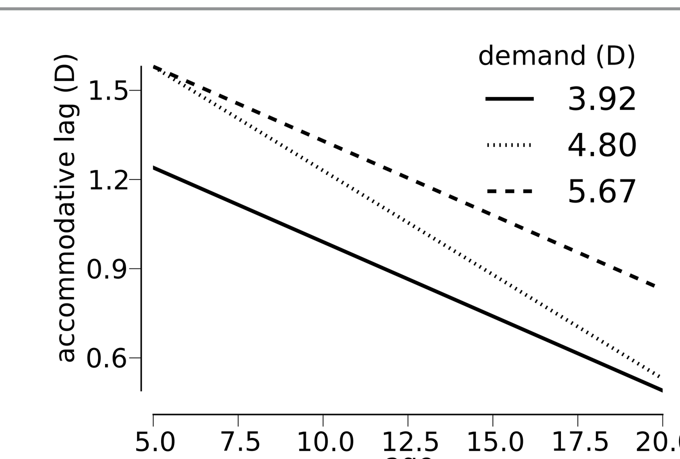


A cone receptive field at 10 deg eccentricity with lateral inhibition from neighboring cones was modeled as a difference of Gaussian (DoG). We then decomposed the DoG into spatial frequency components to determine transfer properties, $c(f)$.

5.



The expected activity, $a(f)$, of a peripheral cone photoreceptor was computed through convolution of the frequency spectrum reaching the retina, $r(f)$, and the contrast sensitivity of a cone in the periphery, $c(f)$, which can be integrated with (Eq 5) to find the relative activity, A, of a single cone.



Accommodative lag as a function of age, from [4].

$$s(f) = \frac{1}{f^{\alpha}} \quad \text{(Eq1)}$$

$$S(f) = \sum_{\omega=1}^{80} s(f)Q(f,\omega) \quad \text{(Eq2)}$$

$$Q(f,\omega) = \frac{fD}{f^2\frac{D^2}{4}+\omega^2} \quad \text{(Eq3)}$$

$$r(f) = S(f)g(f) \quad \text{(Eq4)}$$

$$A = \int_0^F r(f)c(f)\,df \quad \text{(Eq5)}$$

Results - Accommodation to near objects results in a significant loss of medium and high spatial frequencies for images of distant objects in the peripheral retina relative to the fovea reducing the relative activity of photoreceptors there. This loss of frequency content is partially ameliorated by accommodative lag that has been observed in young children but decreases during emmetropization. The outcome of this analysis (Table 1) indicates that the accommodation state of the eye substantially modulates the mean activity of a cone photoreceptor.

Table 1. Normalized cone activity as a function of optical state and object distance.

object	accommodation	cone response
0D	0D	0.92
2.46D	2.46D	0.89
0.16D	2.46D	0.20
0.16D	0.67D	0.43

Table 2. Hypothesis comparison.

observation	eye grows to clarity	eye grows to blurriness
reading causes myopia	?	high contrast text produces large differences in activity between adjacent cones: ↑ eye growth
opsin mutations cause myopia	?	the mutation increases contrast in cone mosaic ↑ eye growth
emmetropia proceeds normally after fovea ablation	this is contrary to our analysis which shows that the periphery "sees more blur" as the eye grows	the periphery "sees more blur" as the eye grows ↓ eye growth as emmetropia approaches
form deprivation causes myopia	the eye elongates because images are blurred	absence of contrast increases gain so that photoreceptor noise results in large signal differences: ↑ eye growth

Conclusion - Contrary to the common intuition that during emmetropization the eye grows until images are clear, we compute that considering the statistical environment and the optical transfer functions characteristic of common accommodation states the peripheral retina systematically "sees more blur" and photoreceptor activity in the peripheral retina decreases as the eye goes through emmetropization. Thus, it is fined grained, sharply focused images which produce high amounts of photoreceptor activity in the periphery that signal the eye to grow during development and the reduction in that activity that occurs as the eye approaches emmetropia that is responsible for the secession of eye elongation.

References

1. Escudero-Sanz & Navarro 1999 J. Opt. Soc. Am. A. 16:1881-91.
2. Tkačik et al. 2011 PLoS One 6:e20409.
3. Kuang et al. 2012 Current Biology 22: 510-514.
4. Anderson et al. 2009. Optometry and vision science. 86(6): 685–94.

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