Title	Understanding the role of retinal cone photoreceptors in color perception, blur, and emmetropization
Authors(s)	Vohnsen, Brian
Publication date	2020-09-04
Publication information	Vohnsen, Brian. “Understanding the Role of Retinal Cone Photoreceptors in Color Perception, Blur, and Emmetropization.” SPIE, September 4, 2020. https://doi.org/10.1117/12.2567037.
Conference details	Light in Nature VIII, Online Event, 24 August - 4 September 2020
Series	Proceedings of SPIE, 11481
Publisher	SPIE
Item record/more information	http://hdl.handle.net/10197/13054
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Publisher's version (DOI)	10.1117/12.2567037

Brian Vohnsen, “Understanding the role of retinal cone photoreceptors in color perception, blur, and emmetropization,” Proc. SPIE 11481, Light in Nature VIII, 1148107 (August 21, 2020).
DOI: https://doi.org/10.1117/12.2567037

Understanding the role of retinal cone photoreceptors in color perception, blur, and emmetropization

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ABSTRACT

The photoreceptors are responsible for the conversion of optical images into neural signals that are conveyed to the visual cortex where vision is triggered. Rod photoreceptors provide night vision whereas cone photoreceptors provide daylight vision and color perception. The photoreceptors have commonly been represented as discrete but dense array of pixels despite of their elongated cellular structure. Earlier studies have suggested that they act as biological waveguides transmitting images from the inner to the outer segments. However, this understanding may not fully encompass their role in vision which is more related to that of optical antennas organized in such a way that optical image contrast and resolution is optimized. Here, we discuss the role of the photoreceptors analyzed as three-dimensional adaptable detectors of light (voxels) using electromagnetic principles. We show that this understanding is compatible with how light is perceived when being incident onto the retina at different angles in the effect commonly known as the Stiles-Crawford effect. We discuss how this can explain the reduced sensitivity to aberrations and chromatic blur of the three-dimensional retina when compared to the common two-dimensional understanding of image formation in the eye. We show how the same principles may impact on emmetropization and ultimately how it may play a key role to prevent the onset or progression of myopia.

Keywords: Photoreceptors, visual pigments, absorption, directionality, leakage, cross coupling, emmetropization, myopia.

1. INTRODUCTION

The last optical step in vision is the absorption of light in the retinal cone and rod photoreceptors onto which images of the outside world is continuously projected by the anterior optics of the eye. The photoreceptors are elongated cells with a large length-to-diameter aspect ratio (up to 50:1 at the fovea) that has led them to be considered as biological waveguides.[1,2] The densely packed foveal cones are similar in shape to the cylindrical rods where the latter are only present away from the central part (foveola) of the foveal pit. At the fovea, cones are cylindrical and similar in shape to the slightly longer parafoveal rods, whereas in the parafovea, perifovea and peripheral retina, cones are shorter and tapered from the inner to the outer segment by the connecting ellipsoid containing high-index mitochondria. The visual pigments are contained in the outer segments in stacked lipid bilayers with rhodopsin in the rods and with short (S), medium (M) and long (L) wavelength sensitivity of opsins in membrane invaginations of the three cone types.[3] This unique structure and arrangement underpins the psychophysical Stiles-Crawford effect of the first kind (SCE-I) which is recognized by the angular sensitivity of the retina to an obliquely incident ray of light.[2,4-10] Thus, the effective visibility of an incident ray of light depends essentially on a Gaussian function in the pupil plane with a characteristic directionality parameter ρ_{SCE}. In the waveguide picture of the photoreceptors this is explained by the angular sensitivity in coupling efficiency[2] but importantly this interpretation has a number of shortcomings: (i) the SCE-I is largely absent in the rods despite of their structural similarity to foveal cones, (ii) no account is taken of cross-coupling between adjacent photoreceptors, and (iii) what happens to the nonguided components of light? The waveguide understanding of photoreceptors is widespread both in visual optics and in retinal imaging.[11-13] Yet, the present author has argued that structural and optical directionality does not dictate waveguiding and indeed the layered structure of the retina and photoreceptor cells may suffice[7] for the mode-like appearance of light in high-resolution cone-mosaic imaging.[1] On account of this, a simpler geometrical absorption model was introduced that allowed for photoreceptor leakage and cross-coupling from outer segments to explain the SCE-I as well as the more important integrated SCE-I, namely the integrated visual sensation of light through the natural pupil in natural viewing conditions.[8] This successfully explained observations with a flickering pupil as well as the traditional SCE-I.[10]

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In this contribution the volumetric absorption model of photoreceptors[8] is examined in more depth in relation to how the eye and retina develops from infant to adulthood in the process of emmetropization. Understanding this process may ultimately explain optical parameters of the eye that can influence myopia onset and development as well as trigger accommodation of the eye.[14] The approach is also used to analyze how the eye and retina may respond to monochromatic aberrations in generating effective retinal images[15,16] as the SCE-I filters obliquely incident light and relatedly dampen the visual impact of ocular chromatic aberrations.

The methodology is summarized in Section 2 which is followed by results and discussion in Section 3 and finally the conclusions in Section 4.

2. METHODOLOGY

Children are typically born hyperopic with an axial eye length that is approximately 2/3 of the adult size. The process of emmetropization ensures that the eye grows rapidly in the first few years of life before slowing down to 0.1 mm/year or less. However, emmetropization is increasingly failing causing a drastic increase in myopia prevalence with increased risk of retinal complications and even vision loss.[17] At the age of 13 years the average rate of axial length growth for emmetropes is about 0.05 mm/year but the equivalent rate for myopes can be even 3 to 4-times higher.[18] In the infant eye the foveal cone photoreceptors are less dense, wider and shorter than in the adult eye and in early childhood cones migrate towards the foveal center as the foveal region and pit continues to develop. Even at the age of 4 years is the foveal cone density and cone outer segment length only half of what it is in adults.[19]

The most apparent difference between indoor and outdoor vision is the size of the natural pupil. Thus, it seems plausible that the difference in optical vergence with a large or small pupil may be a determining factor to avoid myopia. In this study, we suggest that the vergence is intricately linked to the outer segment length and photoreceptor density in such a way that emmetropization works to optimize contrast and limit cone-to-cone crosstalk. The situation is shown schematically in Fig. 1.

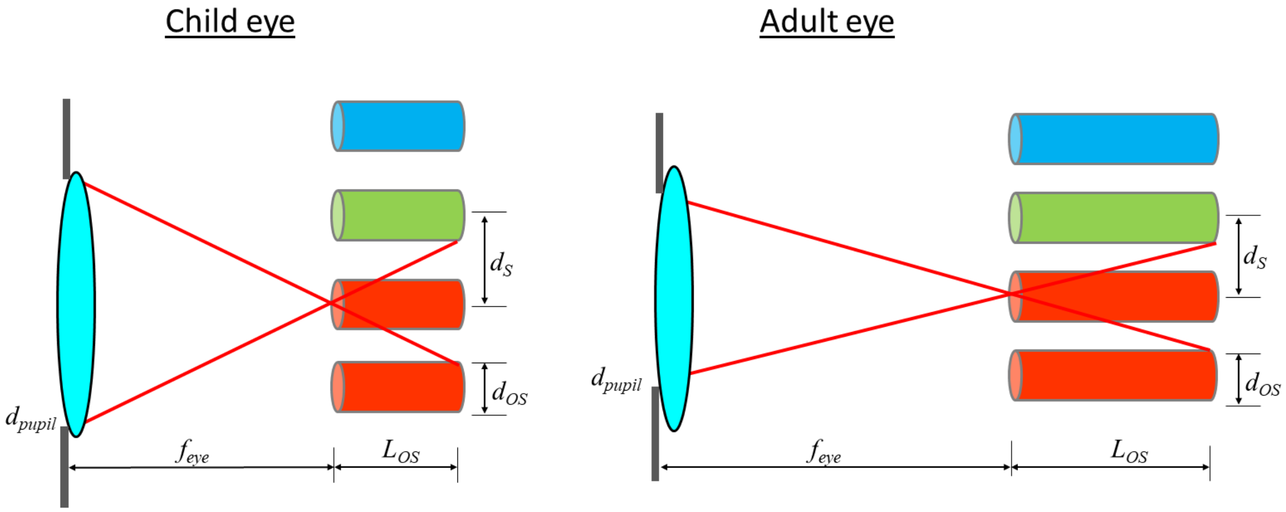

Figure 1. In the infant eye (left) the outer segments are shorter and cones are less dense at the fovea whereas in the adult eye the outer segments are longer (right). To avoid leakage of light from the outer segments to adjacent cones, and thus to ensure high visual contrast, the pupil must be small.

Simple optical principles set an upper limit on the optical vergence of the contributing rays in an eye with axial length, L_{eye}, from a pupil diameter, d_{pupil}, in relation to the outer segment length, L_{OS}, diameter, d_{OS}, and photoreceptor density, σ, that will ensure that cross-coupling between adjacent cones is avoided. For a hexagonal photoreceptor packing the spacing between cones, d_s, can be written as[20]

$$d_s = 1.075 / \sqrt{\sigma} \ . \tag{1}$$

Thus, to avoid cross-coupling of rays between adjacent cones the following relation must be satisfied

$$d_{pupil} < L_{eye} \frac{2d_s - d_{OS}}{L_{OS}} \ . \tag{2}$$

When this is obeyed, the highest possible contrast of the retinal images is obtained while aberrations are small or negligible. However, aberrations may increase the cross-coupling further, and thus lower the visual contrast, in particular for large indoor pupils.

3. RESULTS AND DISCUSSION

The consequences of Eq. (2) are discussed in the following for emmetropization of an (i) infant eye with axial length of 17 mm, (ii) a child with 21 mm and (iii) an adult with 24 mm, and for comparison also a myopic eye with axial length of 28 mm. The results of Eq. (2) are summarized in Table 1. From the results it can be concluded that as the eye grows cross-coupling between adjacent foveal cone photoreceptors becomes increasingly likely unless the pupil is kept small (outdoor pupil).

Table 1. Maximum pupil diameter for foveal vision without cross-coupling between adjacent cone photoreceptors. A cone population of 5%(S), 30%(M) and 65%(L) has been assumed. An outer segment diameter d_{OS} = 2 μm is assumed (although in the newborn infant cones are initially wider). The very large pupil estimates for the infant and child shows that cross coupling is not of concern in the first 3 years of life (i,ii) but then becomes a matter of concern as foveal cone photoreceptors become longer and denser.

Item	**Assumed ocular parameters**	**Max. d_{pupil} S-cones**	**Max. d_{pupil} M-cones**	**Max. d_{pupil} L-cones**	**Max. d_{pupil} all cones**
(i) Infant eye L_{eye} = 17 mm	σ = 30,000 cones/mm^2 L_{OS} = 25 μm	36.4 mm	14.1 mm	9.1 mm	7.1 mm
(ii) Child eye L_{eye} = 21 mm	σ = 80,000 cones/mm^2 L_{OS} = 25 μm	26.9 mm	10.0 mm	6.2 mm	4.7 mm
(iii) Adult eye L_{eye} = 24 mm	σ = 160,000 cones/mm^2 L_{OS} = 50 μm	10.6 mm	3.8 mm	2.2 mm	1.6 mm
(iv) Myopic eye L_{eye} = 28 mm	σ = 160,000 cones/mm^2 L_{OS} = 50 μm	12.3 mm	4.4 mm	2.6 mm	1.9 mm

3.1 Emmetropization

The above results suggest that emmetropization takes place in such a way that cross-talk between adjacent foveal cone photoreceptors is minimized and thereby image contrast is highest. This also provides the highest visual acuity. The foveal cones would dominate this process whereas the parafoveal and perifoveal cones are spaced further apart, shorter, and tapered, and would therefore not be subject to the same strict vergence requirement. If the pupil is larger than specified by Eq. (2) then image contrast and visual contrast degrade. A large pupil would compromise contrast and thus the only feasible response of the eye is to increase axial length and thereby lower vergence across the outer segments. Thus, the onset of juvenile myopia make take place in the transition from case (ii) to (iii) in Table 1. The myopic eye with large axial length tends to have a reduction in foveal cone density.[21] From Eq. (2) a reduction in peak density from 160,000 to 150,000 cones/mm^2 will increase the estimated maximum pupil diameter from 1.9 to 2.0 mm. In turn, a hyperopic eye (not included in Table 1) would give a smaller pupil from Eq. (2) or would possible have slightly shorter outer segments.

The approach taken in this study can be used to estimate a visual contrast as the ratio between light within an outer segment in relation to the light contained within and in the neighboring outer segments and also a visual acuity factor derived from the actual cone density. The values found are in good agreement with known visual optics data.

3.2 Monochromatic and chromatic aberrations

For large pupils, rays would potentially cross the retina at larger angles potentially increasing cross-coupling as well as cause more aberration-related vergence. Yet, this would be secondary to the vergence set by the pupil diameter itself. In turn, chromatic aberrations would cause differences in angles across the retina, but the different density of the individual cone types and their larger spacing, will dampen the blur caused by chromatic errors in agreement with expectations as chromatic aberrations of the eye have normally little impact on vision.

4. CONCLUSIONS

The present study is the first to discuss the relation of emmetropization and myopia in terms of optical vergence across the elongated retinal cells. The results suggest that the commonly-assumed waveguide nature of the photoreceptors is imperfect and is accompanied by significant leakage. This is not entirely surprising given the internal structure of the cells and the irregular packing of the visual pigments. The fact of leakage has been used previously in self-screening models of the hue-shift that accompanies the so-called Stiles-Crawford effect of the 2nd kind.[6,22] Thus, it is fitting that the leakage model can provide a plausible mechanism to understand emmetropization without resorting to waveguiding in complex photoreceptors cells. Finally, the same approach could be taken for the peripheral rod photoreceptors but as visual acuity in scotopic conditions is low this would not take on an essential role for contrast.

ACKNOWLEDGEMENTS

This research has been supported by the European Union’s H2020 ITN network "MyFUN" grant agreement no. 675137.

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