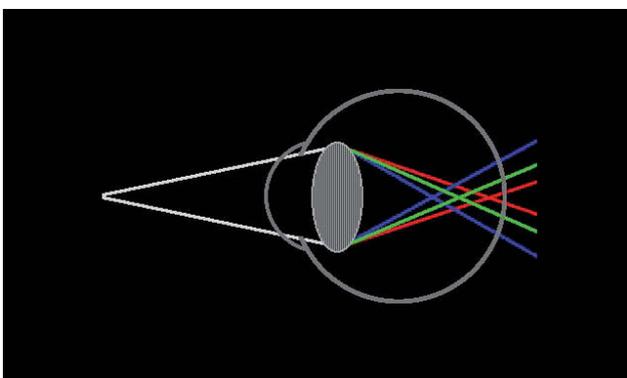


## Aberrations of the Eye - Crude Flaws or Ecological Design?

Dear Editor:

The recent editorial by Professor Rafael Navarro<sup>1</sup> in the Journal of Optometry entitled "Darwin and the Eye" celebrates the bicentennial of Charles Darwin's birth. The editorial invites discussion of the influence of creationism and evolution on our views of the optics of the eye, and provides a thoughtful critique. Professor Navarro is puzzled by the mixture of "smart solutions and crude flaws" that seem to coexist in the eye's design. The words we use routinely to describe aberrations reveal a deep zeitgeist regarding the photographic "camera" model of the "chambered" eye and the role that aberrations play in vision science. Zeitgeist refers to ideas that are prevalent in a period and place and that are expressed in literature, philosophy, and religion. Creationism and Darwinism both nurture the notion that aberrations are defects that distort and impair the retinal image; they are removed in part by accommodation, emmetropization, neural adaptation, spectacles and contact lenses as well as laser surgery. Whether by intelligent design or by evolution, the idea of a perfect aberration-free eye, like a Leica or a Canon camera, forming a perfect image of the world on the retina is appealing. James Gibson<sup>2</sup> contributed to the Zeitgeist by insisting that the optics of the eye and the resulting retinal image are irrelevant for ecological optics. In Gibson's view, information from the environment is structured into the optic array, and the eye simply "picks up" invariant relationships in the array that specify the environment. In this model the "perfect" eye all but disappears!



**FIGURE 1**  
Accommodating eye illustrating vergence, refraction and dispersion across the pupil and effects across the retina. (Link to movie in electronic PDF version, available at: [www.journalofoptometry.org](http://www.journalofoptometry.org))

Ecological optics<sup>2</sup> started a revolution in visual optics and perception sixty years ago. Gibson described an exquisite solid geometry termed "ambient optic array" that represents the environment from an observer's point of view. The geometry is a solid visual "cone" comprised of an array of solid angles, having all a common apex at the point of observation. Surfaces and objects in the environment serve as bases of the solid angles, and the solid angles are separated by "transitions of brightness and color" that represent salient features of the environment, like edges. The geometry of the ambient optic array has its base in the environment and apex at the pupil centre or nodal point. The solid geometry is reversed in geometrical optics, where the area of the pupil is a common base for a large array of solid angles (composed of pencils or bundles of rays), each having a separate apex located in the environment. The two geometries are congruent when the ambient optic array is extended to every point of observation across the area of the extended pupil. Once pupil area, refraction and dispersion are included in the model, diverging rays and wavefronts with optical vergence enhance Gibson's transitions of brightness and color at edges, and the retinal image is overlaid with a polychromatic blur that specifies relative depth<sup>3</sup> and that drives accommodation.<sup>4-6</sup> Vergence, refraction and chromatic dispersion across the pupil for an accommodating eye are illustrated in *figure 1*.

In the prevailing model of the eye, aberrations are imperfections, distortions, crude flaws or noise that blurs the retinal image, especially at high spatial frequencies (30 c/deg or 6/6 Snellen acuity). But defocus and chromatic aberration provide strong signals with ecological validity at intermediate spatial frequencies<sup>7,8</sup> (3 c/deg), where their effects are moderate. The eyes of fishes, chicks, guinea pigs, tree shrews, cats, marmosets and monkeys compensate for positive and negative vergence by changing its axial length.<sup>9-11</sup> Hyperopic defocus accelerates the rate of elongation and thins the choroids of chicks, while myopic defocus slows the rate of elongation and thickens the choroid.<sup>12</sup> Emmetropization and accommodation both operate in monochromatic light, and accommodation responds without feedback from defocus<sup>4</sup> or higher-order aberrations.<sup>13</sup> This suggests a sensitivity to the wavefront vergence across the exit pupil of the eye, rather than to blur of the retinal image alone.

While our idealized model of the eye remains constrained by zeitgeist and dogma, Darwin's eye, less encumbered by word or name or myth, embraces nature's "crude flaws" as distance and relative depth...

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## Reply

*Dear Editor:*

In his interesting letter, Professor Philip B. Kruger suggests that, from an Ecological Approach, optical aberrations should not be viewed as optical design flaws (this would be a sort of zeitgeist); on the contrary, aberrations can be beneficial, providing information such as distance and relative depth to the visual system. This is a complex issue that deserves a detailed analysis of its different aspects. Let us start with the case of the chromatic blur suggested by Prof. Kruger.

### OPTICAL DESIGN

From an optical design perspective, the physiological chromatic aberration (CA) is mostly explained by the chromatic dispersion of salty water,<sup>1</sup> which is the main constitutive material of the eye. To correct CA, optical designers combine high- and low-dispersion glasses (flint and crown types of glass, respectively). However this strategy is hardly applicable to biological tissue with high water content. Refractive indexes show small differences (ranging between 1.336 and 1.41 in the eye, depending on whether there is a lower or a higher concentration of proteins), and the resulting chromatic dispersion show small variations as well. Here nature seems to have limited resources, and hence CA is left uncorrected.

### CHROMATIC BLUR AND RETINAL SAMPLING

CA mainly affects short wavelengths (blue). Interestingly, short wavelengths are also more affected by scattering, both intraocular and that due to the atmosphere. Atmospheric scattering causes the sky to look blue. From an Ecological perspective, in natural environments, blue used to be the color of backgrounds such as the sky or the sea, with only a few exceptions (flowers mainly). Here the human retina seems to be fully adapted to both internal (chromatic blur) and external (blue backgrounds) factors: the density of short-wavelength-sensitive cones is only about 1/10 of the total density of the three types of cones.<sup>2</sup> Thus, the resolution of "blue" cones is less than 1/3 of that of the cone mosaic. This seems to be a smart way of saving resources, since blue light is

more affected by chromatic blur and scattering and is usually associated to backgrounds. In this sense, the retina seems to be adapted to the poorer information carried by the "blue" chromatic channel, investing into that range of the visible spectrum only 10% of its units, instead of the proportion (33%) that would correspond to that portion of the spectrum. This seems to be a good adaptation to the environment and to its physical and physiological limitations.

### ACCOMMODATION AND VERGENCE

Prof. Kruger cites experimental evidence that the visual system shows "a sensitivity to the wavefront vergence across the exit pupil of the eye, rather than to blur of the retinal image alone".<sup>3</sup> To that evidence I can add that each ray of light carries information of the vergence error, and that the average across all rays passing through the pupil is a measure of the refractive error.<sup>4</sup> On the other hand, aberrations induce an asymmetry between the blur (PSF) produced by positive and negative defocus, both with monochromatic (due to spherical aberration) and polychromatic (due to CA, as shown in Prof. Kruger's movie) light. Earlier studies by Prof. Kruger and others suggest that this asymmetry could be used by the visual system to drive the accommodation response in the right direction (see References in Prof. Kruger's letter). Therefore, here we have two types of evidences, suggesting that the visual system may use information from the wavefront or from the type of blur, but the visual system could use other additional sources of information as well. Vergence errors, optical defocus, image blur, contrast, etc. provide different ways or metrics to describe the same physical phenomenon in different domains: beams, (second order) aberrations, image quality, spatial frequencies, etc. For instance, a potentially rich source of information is the rapid change of image contrast associated to microfluctuations of accommodation. The visual system might use all sources of information when available or might prefer a specific type of information to drive accommodation.

### MULTIPLE CUES AND LEARNING

There are many evidences suggesting that the visual system may learn to use all cues and information available, provided that enough resources (neurons) are devoted to that task. In fact, different strategies or metrics can be used in

parallel as a sort of cross-checking to increase robustness. For instance, a triple check could include wavefront vergence, asymmetric blur (PSF) and image contrast (MTF) analyses. When one type of information is missing (for example blur asymmetry, if one corrects aberrations), still two (at least) other sources of information can be available to the visual system to drive accommodation.

#### OPTICAL-TO-NEURAL OR NEURAL-TO-OPTICAL ADAPTATION?

Going back to my former Letter to the Editor:<sup>5</sup> there the main point was that the explanation for the apparent design flaws in the eye requires considering the whole system, which comprises optical as well as neural components.<sup>6</sup> Here the paradox arises when one analyzes the type of optical design of the eye and compares it with the strongly inhomogeneous retinal photoreceptor mosaic and with the even more inhomogeneous cortical projection of the visual field. The optical system of the eye is that of a very wide angle lens. Its design principles (symmetry in the distribution of elements and lack of axis and rotational symmetry) seem aimed at achieving maximum field homogeneity.<sup>7</sup> The idea of design flaws soon disappears if one assumes that the design goal is homogeneity rather than optimal central performance. However, the paradox then arises as this type of optical design seems opposite to foveated vision. The retinal design seems contrary to that of the optics, as the goal for the neural system seems to be maximum central performance at the cost of a strong retinal inhomogeneity. I can only find one plausible explanation for this paradox (or mismatch between optical and neural design): the optics and the fovea could develop at different stages of evolution. The paradox disappears if one assumes that the wide-angle eye developed earlier than foveated vision and its associated visual abilities (vision of details, recognition, etc.).<sup>7</sup> The fovea is characterized by a high cone density, also connected to a high proportion of neurons in the visual cortex. The hypothesis to explain the paradox is that most of the resource investment associated to the development of the fovea (and of its related capabilities) focused on the increase in the number of neurons of the visual cortex. If we consider optics alone, a better (supernormal) visual acuity could be possible, since the adaptation of the optical system of the eye might be relatively simple, changing its design to improve the central performance to nearly double its optical resolution at the cost of a worse peripheral performance. (In fact hawks, owls and other similar species show a higher visual acuity than humans). However, increasing the neural resolution by

a factor of 2, while keeping full functionality, implies increasing the number of neurons by a factor of 4. This seems difficult for our current cranial volume. From a neural perspective, the brain might lack resources to get a true benefit from better optics (on-axis). Then, a plausible explanation is that the fovea developed by progressively increasing the central density of cones until the resolution of the cone mosaic at its very center matched optical resolution. During that process the optics of the eye did not need to change substantially, but probably the visual cortex expanded in the process with a significant increase in the number of neurons.

#### CONCLUSION

As I have tried to explain, I do not believe that the eye has design flaws. Paradoxes and/or design-flaw interpretations may appear when one analyzes optics by itself. However, the brain, and not the eye, is the organ that is responsible for vision. The retina is mainly neural tissue and an extension of the brain, whereas the optics only projects an image onto that sensitive tissue. Consequently, vision cannot be understood in terms of optics alone; on the contrary, optics serves to the neural system. Then, any explanation should necessarily consider the main neural process. Nevertheless I agree with Professor Kruger that there was a widely extended zeitgeist regarding ocular aberrations. Unfortunately, such zeitgeist has influenced both research and clinical practice; for instance, we have lately heard of the promise of "supernormal vision" made by refractive surgery.

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