Pergamon

0042-6989(95)00225-1

Vision Res., Vol. 36, No. 8, pp. 1067–1079, 1996

Printed in Great Britain
0042-6989/96 $15.00 + 0.00

Images of Cone Photoreceptors in the Living Human Eye

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Received 22 March 1995; in revised form 7 August 1995

Though the photoreceptor mosaic has been imaged through the intact optics of the eyes of several species, it has not been clear whether individual photoreceptors can be resolved in the living human eye. We have constructed a high-resolution fundus camera and have resolved cones with a spacing as small as 3.5 μm in single images of the fundus. The high contrast of these images implies that almost all the light returning from the retina at this wavelength (555 nm) has passed through the apertures of foveal cones. The average power spectra of our retinal images show that it is possible to recover spatial frequencies as high as 150 c/deg in eyes with normal optical quality, a conclusion that was confirmed with estimates of the optical quality of these eyes obtained with a Hartmann–Shack wavefront sensor. These results emphasize the superiority of the eye's optics over the spatial sampling limits of the retina when the eye's optical quality is optimized. They also show that it would be possible to routinely resolve retinal structures as small as photoreceptors in the normal living eye if its aberrations could be corrected.

Fovea Cones Fundus imaging Resolution Point-spread function

INTRODUCTION

Blurring by the eye's optics limits both the finest patterns that can be imaged on the retina and the smallest retinal features that can be imaged outside the living eye. Helmholtz (1873) and numerous authors since (Snyder & Miller, 1977; Yellott, 1982, 1983; Williams, 1985, 1992; Land, 1990) have pointed to a rough match between this optical limit and the limit imposed by the grain of the foveal cone mosaic. That is, the highest spatial frequency passed by the eye's optics in bright light is roughly equal to the Nyquist limit of the foveal cone mosaic. The notion underlying this match is that evolution has engineered the eye's optics to give the retina access only to the low spatial frequencies it adequately samples while removing the spatial frequencies above the Nyquist limit that would alias. Despite this apparent match at the foveal center, it is well known that, under laboratory conditions in which the eye is carefully refracted, the optics are superior to the retinal grain everywhere else in the visual field (Jennings & Charman, 1981; Navarro *et al.*, 1993; Williams *et al.*, in press). A match between the optics and sampling seems to be the exception rather than the rule across the animal kingdom in compound eyes (Snyder, 1979; Wehner, 1981) as well as in vertebrate eyes (Snyder *et al.*, 1986, 1990). Snyder *et al.* argued that the optical cutoff almost always exceeds the Nyquist limit because the benefit of superior optics in increased contrast sensitivity at subNyquist spatial frequencies outweighs the increased risk of aliasing.

This relationship between optics and retinal grain has interesting implications for experiments in which the eye's optics are used in reverse to view the living retina. For example, if the optics were good enough to pass spatial frequencies as high as the cone sampling frequency, which is twice the Nyquist frequency, it should be possible to resolve them in the intact eye (Land & Snyder, 1985). In several snake species as well as the cane toad, single photoreceptors were resolved through the intact optics by capitalizing on their large photoreceptors and good optics (Land & Snyder, 1985; Zwick *et al.*, 1995; Jagger, 1985). For four vertebrate species including humans, Snyder *et al.* (1986, 1990) showed that the optical cutoff frequency is roughly twice the Nyquist limit of the photoreceptor mosaic in at least some portion of the retina, leading to the prediction that individual photoreceptors could be potentially resolved through the intact optics of these species. Specifically, Snyder *et al.* (1986, 1990) pointed out that human cones at 10 deg from the foveal center have a sampling frequency of about 26 c/deg which is potentially low enough for the mosaic to be resolved through the intact optics, assuming a diffraction-limited 2 mm pupil.

Despite these theoretical predictions, there has been no compelling evidence that receptors can be resolved in an

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