Imperfect optics may be the eye's defence against chromatic blur

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The optics of the eye cause different wavelengths of light to be differentially focused at the retina. This phenomenon is due to longitudinal chromatic aberration, a wavelength-dependent change in refractive power[1]. Retinal image quality may consequently vary for the different classes of cone photoreceptors, cells tuned to absorb bands of different wavelengths. For instance, it has been assumed that when the eye is focused for mid-spectral wavelengths near the peak sensitivities of long- (L) and middle- (M) wavelength-sensitive cones, short-wavelength (bluish) light is so blurred that it cannot contribute to and may even impair spatial vision[2,3]. These optical effects have been proposed to explain the function of the macular pigment[4], which selectively absorbs short-wavelength light, and the sparsity of short-wavelength-sensitive (S) cones[5]. However, such explanations have ignored the effect of monochromatic wave aberrations present in real eyes. Here we show that, when these effects are taken into account, short wavelengths are not as blurred as previously thought, that the potential image quality for S cones is comparable to that for L and M cones, and that macular pigment has no significant function in improving the retinal image.

In natural, polychromatic light, the retinal image is affected by interactions among longitudinal chromatic aberration (LCA), wave aberrations and transverse chromatic aberration (TCA). Wave aberrations are local deviations in the path of light entering the eye through different points in the pupil. They can be caused by irregularities in the cornea and lens, for example, and they can produce complex distortions in the retinal image even in monochromatic light. TCA is an angular displacement across the retina of the images for different wavelengths. Whereas LCA is dependent solely on the change in refractive index of the eye's optical elements with wavelength, TCA derives both from this index change and from misalignments between the cornea, lens and fovea[6,7]. The range of LCA is very consistent across individuals, but wave aberrations and TCA are subject to individual differences[8,9]. We measured these quantities at a series of wavelengths in three subjects to investigate the image quality of the eye in white light.

Retinal image quality can be characterized by the modulation transfer function (MTF), a spatial-frequency-dependent measure of the relative contrast attenuation from object to image caused by the optics of the eye. The MTF is computed as the modulus of the Fourier transform of the point spread function (PSF), the retinal image produced by an infinitely distant point light source. In Fig. 1 the thin solid curve represents the optimal MTF for a 550-nm monochromatic source, imaged through a 6-mm pupil in a theoretical model eye with LCA but no other aberrations. The thin dotted curve shows the MTF for the same model eye for a 450-nm source that is blurred by 0.7 dioptres. This is the amount of defocus that would result from LCA in the human eye if the eye were optimally focused for 550 nm. At 450 nm, the MTF is degraded, with contrast at some spatial frequencies reduced to zero. The thick curves show the corresponding MTFs for one of the subjects in this study with the empirically determined wave aberrations and the same degree of LCA-induced defocus at 450 nm relative to 550 nm as the model eye. For this subject, the 550-nm (solid) and 450-nm (dotted) curves are very similar. In real eyes, the wave aberrations decrease the variability in MTF across wavelengths that would occur in an eye subject to LCA alone. Figure 2a summarizes this effect for the three subjects, showing the area under the MTF (calculated for 0–100 cycles $\deg^{-1}$) as a function of wavelength. The range of LCA for these subjects was consistent with published values[1]. For each subject, the degree of defocus at 550 nm was offset from 0 dioptres to optimize the area under the MTF at this wavelength. This constant offset was then added to the defocus at each wavelength to preserve the range of LCA across the spectrum. In the theoretical model eye with LCA alone (thick curve), MTF area decreases on either side of a sharp peak, varying by 27-fold from minimum to maximum. However, for the three subjects, MTF area is relatively constant across all wavelengths, with a mean variation of less than twofold. The monochromatic aberrations in the real eyes attenuate the MTF at mid-spectral wavelengths, but they actually improve the MTFs at the spectral extremes. This does not imply that image quality at any given wavelength could not be further improved with the appro-

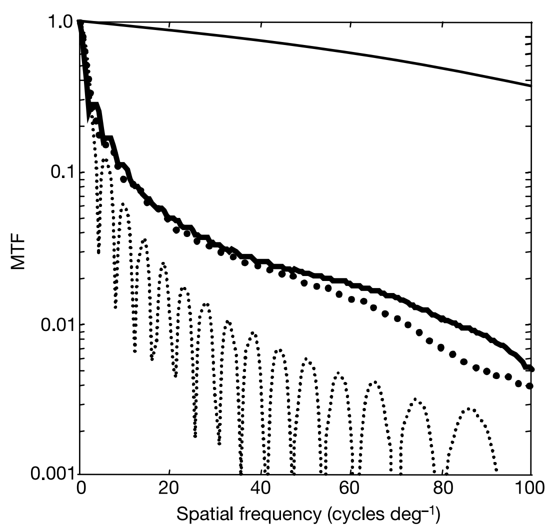

Figure 1 MTFs at 550 nm (solid curves) and 450 nm (dotted curves) for two eyes: (1) a theoretical model eye subject to LCA but with no wave aberrations (thin lines) and (2) a real human subject's eye (thick lines). The other two subjects showed similar results. The MTFs shown here and in subsequent figures are radial averages of two-dimensional MTFs.

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priate defocus correction under monochromatic conditions. Figure 2b compares the three subjects' mean MTF area as computed above (solid curve) with the mean MTF area attained when each wavelength's MTF area is individually optimized (dashed curve). This improves both long-wavelength and short-wavelength MTFs, producing a spectrally flat function for these subjects.

Of course, the visual system generally operates under polychromatic conditions, and the small variability in MTFs across the spectrum afforded by the wave aberrations has several consequences for the retinal image available to the cone photoreceptors in natural light. Because wave aberrations are measured under and defined for monochromatic light, the PSF for polychromatic light has been simulated computationally here by compositing the monochromatic PSFs for individual wavelengths. The MTF from this composite PSF gives a measure of polychromatic retinal image quality. The MTF associated with a specific spectral sensitivity function, for example the S-cone fundamental, is computed from a weighted PSF, in which the weights represent the relative sensitivity at each wavelength. The polychromatic PSF must also take into account each individual's TCA, which shifts the position of each monochromatic PSF on the retina. Figure 3a shows the MTFs for the L-cone, M-cone and S-cone fundamentals[10] in equal-energy white light for the model eye with LCA alone and with optimal resolution at 550 nm. In this case, the S-cone MTF lies well below those of L and M cones, because of the image blur caused by LCA at short wavelengths. The individual peaks in the S-cone function represent spatial frequency ranges of alternating contrast reversal, in which light and dark are exchanged. Figure 3b–d shows MTFs computed for each cone class for the eyes of the three subjects, taking into account each subject's LCA, TCA and monochromatic wave aberrations at a series of wavelengths. Their wave-aberration and TCA magnitudes are given in the legend to Fig. 3. The same defocus adjustment as described above to optimize the MTF volume at 550 nm was used. Even when the MTF is thus optimized for mid-spectral light, and despite individual differences in TCA and wave aberrations, the potential image quality for the S cones approaches, and sometimes exceeds, that of L and M cones for all subjects. Furthermore, regions of contrast reversal are eliminated. These calculations do not take into account the different sampling mosaics for the different cone classes; they simply show the potential image quality for each cone class if the cone classes were to be similarly distributed in the retina. Although the MTF of the S cones is degraded much less by LCA than has been conventionally assumed, the sparsity of S cones still limits their spatial sensitivity. In addition, individuals with exceptionally low wavefront error might have cone MTFs more similar to those shown for the LCA-only theoretical eye. However, the subjects used here have wave aberrations that are representative of the general population[11].

The S-cone fundamental's relatively narrow spectral bandwidth compared with those of L and M cones also contributes to potential S-cone image quality by limiting the influence of TCA displacement in the composite PSF. However, because the L and M cones have relatively wide bandwidths, with sensitivity extending into the short-wavelength range, the polychromatic images available to these cones also benefit from the aberration-induced reduction in variability in monochromatic MTFs. Without wave aberrations, foveal vision might be subject to differential blurring of objects with different spectral reflectances and to contrast reversals caused by changes in an object's spatial frequency content with the subject's movement through the environment. Perceptual artefacts could also occur with large changes in the spectral distribution of the environmental illumination.

The improvement in short-wavelength image quality shown here brings into question one possible role of macular pigment in the eye. Macular pigment selectively absorbs wavelengths below 530 nm, with a peak absorption at 460 nm (ref. 12). Although it has often been proposed that macular pigment attenuates short-wavelength light at the retina to alleviate the deleterious effects of LCA, Fig. 4 shows that macular pigment actually provides little if any improvement in the MTF. The two upper curves represent polychromatic MTFs for the LCA-only theoretical eye for two luminance functions: (1) a combination of L-cone and M-cone fundamentals[10] that does not include macular pigment and (2) the same luminance function including macular pigment[12] with a peak absorption of 90%. The

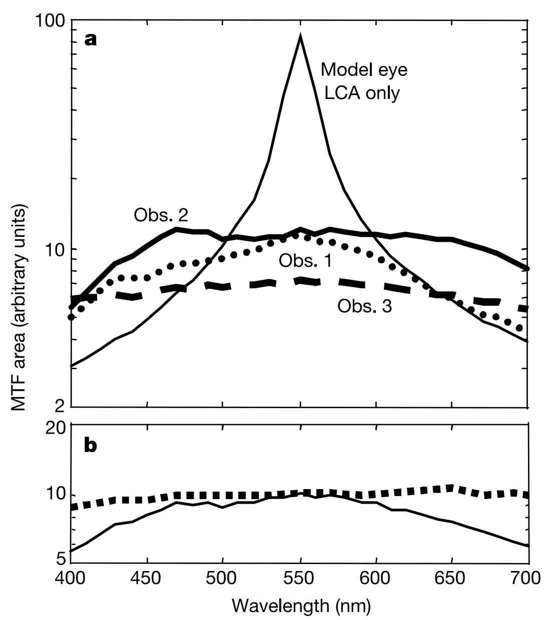

Figure 2 MTF area. **a**, Area under the MTF (arbitrary units) as a function of wavelength for a theoretical model eye with LCA only and for three subjects with measured wave aberrations. **b**, Mean MTF area for all three subjects when defocus is set to optimize area at 550 nm (solid line) and when each wavelength is individually optimized (dashed line). The dashed line shows that MTF area at any single wavelength can be improved further by correcting focus at that wavelength.

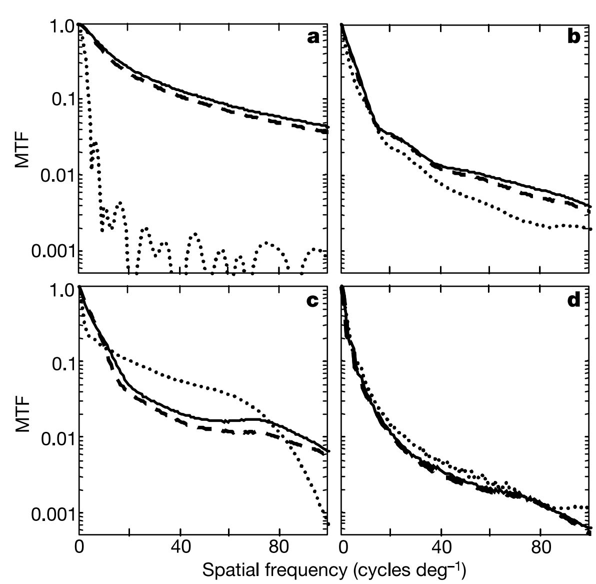

Figure 3 Polychromatic MTFs computed with a 6-mm pupil for L cones (dashed line), M cones (solid line) and S cones (dotted line) for theoretical model eye with LCA only (**a**) and three subjects (**b**, observer 1; **c**, observer 2; **d**, observer 3) with measured LCA, TCA and wave aberrations. RMS wavefront errors (at 530 nm) for the three subjects were 1.83, 0.84 and 2.11 μm. Their TCA magnitudes were: 0.30, 0.13 and 0.18 arcmin nm^{-1}. Similar results were found with a 4-mm pupil (not shown). A comparison of the average results for 6-mm and 4-mm pupils is shown in Supplementary Information.

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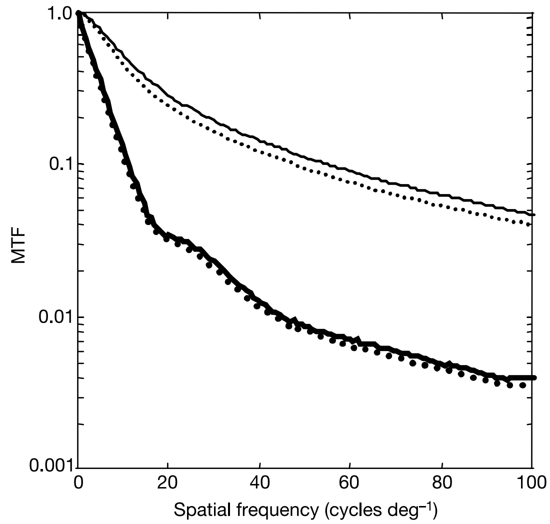

Figure 4 Polychromatic MTFs for the theoretical model eye (thin lines) and for one subject (thick lines) with (solid lines) and without (dotted lines) the effect of macular pigment absorption at short wavelengths. Macular pigment produces only a trivial improvement in the MTF. The other two subjects showed similar results.

two lower curves represent MTFs under the same conditions for one subject in this study. The other subjects showed similar results. For the model eye, macular pigment provides at best a 20% improvement in MTF. For the real eye, the two MTFs are nearly identical. Although macular pigment might serve very important purposes in the eye, such as protecting the retina from oxidative damage from short-wavelength light[13–15], it apparently does not affect image quality.

It has been widely assumed that chromatic defocus from the eye's optics degrades the retinal image of short-wavelength light. But this assumption has not previously been tested in a manner that takes into account all of the eye's optical aberrations, measured at multiple wavelengths. We have shown that there is actually little variability in the eye's image quality, as quantified by MTF, across the visible spectrum. Wave aberrations cause the visual system to sacrifice resolution at a single wavelength but allow it to gain approximate constancy in spatial sensitivity across the spectrum. This constancy might provide an even more effective solution to the problems of chromatic blur than could be attained by attenuation and sparse sampling of short-wavelength light in an eye with perfect optics. □

Methods

Apparatus

Wave-aberration data were collected psychophysically with a spatially resolved refractometer[16]. For an array of pupil entry locations, the subject visually aligns a monochromatic test spot with a stationary reference location on the retina that enters through the pupil centre. Moving the test spot on the retina corresponds to a change in its angle of incidence at the pupil. The angle needed to align the spot with the reference position for each pupil entry location provides an estimate of the wavefront slope at that location. In a separate optical channel, a fixation cross with a high-spatial-frequency background (namely text) is displayed through a small, centred pupil. The cross is used as both the fixation target and the reference point for aligning the test spot; the text acts as an accommodative cue. A Wratten 58 (green) filter is used in this channel to limit the illumination spectrum of a fluorescent source and to maintain accommodation in the mid-spectral range.

Subjects

Three adult subjects, one female and two male (ages 27, 36 and 48 years), participated in this study. Measurements were performed on the right eye only. Each subject's pupil was dilated with 0.5% tropicamide solution to ensure that all test spots would be visible. The effective diameter of the entire pupil-sampling array is 7.32 mm.

Procedure

The subject's head was stabilized with a dental-impression bite bar on a three-dimensional translating stage. The experimenter monitored the subject's pupil position to align the pupil centre to the optical axis of the apparatus to correct the position during experimental runs. In each run, the test spot was stepped through 37 entrance pupil locations in pseudo-random order, and the subject used a joystick to move the spot's image to the centre of the fixation cross for each pupil location. Aberrations were measured at six different wavelengths (450, 490, 530, 570, 620 and 650 nm) by placing interference filters (10 nm half-width) in the test spot channel. Each subject completed three runs at each wavelength. Spherical refractive error was subjectively corrected for each subject by means of a translating focusing block to bring the high-frequency background into focus. The same spherical correction was used for all runs at all wavelengths.

Data analysis and computational methods

The data from the spatially resolved refractometer provide estimates of the local slope of the wave aberration at different pupil locations. Zernike polynomial coefficients up to the seventh order (35 Zernike terms) were determined by least-squares fits of the derivatives of the Zernike polynomials to these data. For each subject, each run was fitted individually, and the mean Zernike coefficients across the three runs for each wavelength were used to reconstruct the wave aberration in the pupil plane for that wavelength. Zernike coefficients for wavelengths from 400 to 700 nm were interpolated and extrapolated at 10-nm steps from a polynomial fit to the coefficients for the six measured wavelengths[16]. The change in second-order Zernike defocus with wavelength was used as an estimate of LCA. Transverse chromatic aberration (TCA) was determined by measuring wave aberrations at two distinct wavelengths (476 and 601 nm) by using a single magenta filter. TCA was estimated as a linear function of the difference in PSF positions for these two wavelengths and extrapolated from 400 to 700 nm.

The reconstructed wavefronts were used to compute the monochromatic PSF and two-dimensional MTF for each wavelength. A pupil diameter of 6 mm was used for all PSF and MTF calculations. This is near the average pupil size for 20–40-year-olds under illumination on the order of 100 cd m^{-2} (ref. 17). One-dimensional MTFs were calculated as the radial average of the two-dimensional MTFs.

Polychromatic PSFs for the cone spectral sensitivity functions[10] and macular pigment[12] were created by summing the PSFs for each wavelength after they had been (1) scaled by the spectral sensitivity for that wavelength and (2) linearly translated to account for TCA at that wavelength. For each subject, second-order defocus was individually adjusted by a constant value to produce optimal MTF volume to 100 cycles deg^{-1} at 550 nm. This constant was added to the defocus term at all wavelengths to maintain the range of LCA across the spectrum.

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