

# Retinal contrast losses and visual resolution with obliquely incident light

Matthew J. McMahon\* and Donald I. A. MacLeod

*Department of Psychology, University of California, San Diego, La Jolla, California 92093-0109*

Received January 2, 2001; accepted May 10, 2001; revised manuscript received May 14, 2001

To determine whether vision with obliquely incident light is degraded by contrast losses originating in the retina, laser interference fringe patterns were produced on the retina for various directions of incidence of the two interfering beams. Contrast-modulation flicker [Vision Res. **38**, 985 (1998)] was used as a psychophysical measure of contrast at the level of the photoreceptors. Fringe contrast was shown to be maximal when the interfering beams were equal in perceived brightness, not in physical intensity. The effective fringe contrast was slightly reduced with oblique incidence for high spatial frequencies, but the reduction was too slight to be an important factor in visual resolution. The loss was similar whether the incident beams were displaced from the pupil center in a direction parallel or perpendicular to the grating bars. © 2001 Optical Society of America

OCIS codes: 330.1070, 330.4060, 330.5310, 330.5370, 330.6110, 330.6130.

## 1. INTRODUCTION

An effective way to determine the neural limitations on spatial visual performance is to design experiments that quantify resolution losses at specific stages in the visual system. Previous researchers have compared visual resolution for CRT grating stimuli with resolution for gratings produced by laser interference. Since the interference fringe is immune to optical blurring and diffraction, the difference between conventional and interferometric measures has been used to quantify the losses in contrast produced by the anterior optics.<sup>1,2</sup> In this paper we attempt to further partition resolution losses in the visual system by quantifying the contrast loss originating in the retina with obliquely incident light. The magnitude and basis of this contribution has been controversial, as a summary of previous work will illustrate.

In 1958, Campbell<sup>3</sup> measured grating acuity through a 1-mm artificial pupil. Acuity was similar when the pupil was centered on the natural pupil and when it was displaced 4 mm in a direction parallel to the grating bars. However, displacing the pupil 4 mm in a direction perpendicular to the grating bars produced an eightfold reduction in visual acuity. Campbell reported that the acuity decrement persisted when spherical aberration was corrected, when it was measured with monochromatic light, and when the grating target luminance was increased to compensate for the decreased brightness of the displaced pupil condition.

To determine whether the effect was due to degradation of contrast by the anterior optics, Campbell and Gregory<sup>4</sup> repeated the experiment with interference fringe stimuli. Their stimuli, monochromatic Fraunhofer single-slit fringes, were immune to degradations by optical aberrations or diffraction by the pupil of the eye. The acuity effect was still present, though much smaller in magnitude (a factor of 2), suggesting that some of the original Campbell effect was retinal in origin. Subsequently, similar experiments by Enoch also suggested a small retinal

component for the directional acuity effect, although it depended only weakly on the orientation of the test grating.<sup>5</sup>

Another consequence of varying the angle of incidence of light falling on the retina was demonstrated by Stiles and Crawford<sup>6</sup> in 1933. They showed that a test light imaged on the retina through the center of the pupil appears much brighter than the same test light when it is imaged through the pupil margin. Wright and Nelson<sup>7</sup> proposed that light entering the eye more obliquely is less likely to be "trapped" within a cone than is axially incident light. This waveguide-type model of the Stiles-Crawford effect has persisted, with slight modifications.<sup>8</sup>

To test the hypothesis that the Campbell effect was also due to the waveguide properties of foveal cones, Green<sup>9</sup> measured laser interference fringe contrast for varying angles of incidence of the interferometric point sources. This technique, like the one of Campbell and Gregory,<sup>4</sup> used interference to effectively bypass blurring by the anterior optics. Green found that when the intensity of the decentered beams was increased to compensate for the Stiles-Crawford brightness difference, there was no loss in resolution. From this, he concluded that the only contribution of the retina to the Campbell effect was through the decreased brightness of obliquely incident light. In similar interferometry experiments, Thibos<sup>10</sup> also failed to show a decrease in visual acuity with obliquely incident interference fringes.

In a separate experiment, Green<sup>9</sup> quantified the loss in contrast sensitivity with eccentric pupil entry for sinusoidal gratings produced on a CRT monitor. He found no loss in resolution with a pupil displacement parallel to the grating bars. However, there was a substantial loss in sensitivity when the pupil was displaced in a direction perpendicular to the bars of the grating, and that degradation occurred only at high spatial frequencies. Van Meeteren and Dunnewold<sup>11</sup> confirmed the loss of resolution with oblique incidence found by Green<sup>9</sup> and

Campbell.<sup>3</sup> Their modeling estimated that the modulation transfer function of the eye was diffraction limited for all conditions of their experiment, and they therefore suggested that the resolution losses were retinal in origin. Thibos's<sup>10</sup> experiments with a polychromatic interferometer, however, suggested that Green's decrement in CRT acuity<sup>9</sup> and van Meeteren and Dunnewold's effect<sup>11</sup> were due to ocular chromatic aberration and that this was the major factor responsible for the loss of acuity when polychromatic targets were viewed through a displaced aperture. Subsequent measurements with incoherent light and aberration modeling by Artal *et al.*<sup>12</sup> supported the conclusion that the Campbell effect was completely due to monochromatic and chromatic aberration for spatial frequencies up to 16 c/deg. These attempts to parcel out the contributions to decreased acuity with obliquely incident light are plagued by the problem of accurately modeling<sup>13</sup> or measuring the contribution of the anterior optics.

Chen and Makous<sup>14</sup> performed experiments similar to the interferometric condition of Green<sup>9</sup> with the goal of determining what fraction of obliquely incident light that escapes a given cone is recaptured by a neighboring cone. Interference fringe contrast sensitivity was measured with all beams equated for Stiles–Crawford brightness. They found a decrease in contrast sensitivity with oblique incidence, but only for high spatial frequencies. This result was in conflict with that of Green,<sup>9</sup> who found no decrease in contrast sensitivity at spatial frequencies as high as 47 c/deg. The decrease was slightly greater for point source displacements perpendicular to the grating bars. Quantitative analysis of their data suggested that when light entered through the pupil margin, over half of the light absorbed by cones had previously passed through other cones but that the spatial extent of the spreading was very small.

In 1998, Pask and Stacey<sup>15</sup> extended their earlier waveguide model of human foveal cones to make predictions about the Campbell effect for interference fringes. They calculated the proper intensity ratio between the interferometric point sources to achieve maximum fringe contrast for each direction of point source displacement. Their model of the interaction between light and the cone photoreceptor suggested that optimal fringe contrast required a physical equality of intensity between the two interferometric sources (rather than, for instance, an intensity ratio chosen to compensate for the Stiles–Crawford effect). This was because independent manipulation of the beam intensities would drastically alter the modal amplitudes and fundamentally change the field exciting the receptor. They modeled retinal resolution losses, with results consistent with the experimental findings using incoherent light: Moving the point sources from the center of the natural pupil led to a decrease in fringe contrast if the displacement was perpendicular to the bars of the grating but not if the displacement was parallel to the bars of the grating. However, this result was not consistent with the previous interferometric measurements of Green<sup>9</sup> or Chen and Makous.<sup>14</sup> Their prediction of the point source intensities required for maximum contrast was also inconsistent with experimental results of Makous and Schnapf,<sup>16,17</sup> who reported that when one point source entered through the center of the pupil and the

other eccentrically, the intensity of the eccentric beam had to be increased, and indeed had to be increased by much more than was necessary to make it equally visible (i.e., more intense than Stiles–Crawford equality), in order to yield fringes of maximum visibility.

The work reviewed above illustrates the range of theoretical and experimental findings regarding the source and extent of contrast losses when light passes through an eccentric pupil and is obliquely incident on the retina. Even the experiments that have isolated the retinal component with laser interferometry have produced inconsistent estimates of the amount of contrast loss attributable to the retina. In this paper we reexamine the extent to which vision with obliquely incident light is degraded by contrast losses originating in the retina. As in several of the previous studies, contrast losses due to blurring by the optics of the eye were avoided by forming interference fringes directly on the retina. A range of intensity ratios for the two interferometric point sources was used in each case, so as to determine by direct experiment both the optimal intensity ratio and the corresponding maximal contrast. Contrast-modulation flicker<sup>18</sup> was used as a psychophysical measure of contrast at the level of the photoreceptors. This technique provided two distinct advantages over previous techniques. First, it produced psychophysical measurements of the effective contrast at the level of the cone photoreceptors, without contamination by subsequent neural blurring. Second, it allowed measurement of the effective contrast for fringe patterns that are too fine to be subjectively resolved. By making measurements of effective fringe contrast at spatial frequencies that are comparable to the spacing between foveal cones, we were able to examine the fine spatial scale of the interaction between light and the cone mosaic more directly than was previously possible.

## 2. MATERIALS AND METHODS

### A. Stimuli

Stimuli were generated by a computer-controlled Argon laser interferometer. The filtered (514-nm) laser output was split into two equal beams by a beam splitter and directed through two acousto-optic modulators (AOMs). The AOMs chopped the light beams into a train of 480  $\mu$ s rectangular pulses separated by 1 ms. To vary the fringe contrast, the relative temporal phase of the pulses was manipulated by computer control of the AOMs. When the pulses from the two beams were presented simultaneously (with complete temporal overlap), they interfered and a grating of 100% Michelson contrast was produced. When the pulses were alternated, so that one was off whenever the other was on, interference was not possible and a zero contrast grating was formed.<sup>19</sup> This procedure allowed the contrast to be varied while maintaining a constant space-averaged retinal illuminance. The AOMs were also used to control the instantaneous light intensity of the two interferometric point sources during their “on” periods. This permitted us to measure the effective fringe contrast with different point source intensity ratios and also to measure, and adjust for, the Stiles–Crawford effect. The beam attenuation produced by the AOMs was proportional to their drive voltages. Desired

beam intensity values were converted to AOM drive voltages by a linearizing lookup table, and the required voltages were sent to the AOMs via a National Instruments digital-to-analog card.

Each channel's beam was expanded and spatially filtered, and the pinholes of the spatial filters were imaged as point sources in the pupil plane. The vertical position of the point source from one channel could be varied by computer control of an actuator attached to a mirror mount. The two point sources interfered with each other to produce a horizontally oriented sinusoidal intensity pattern on the retina. The fringe spatial frequency,  $f$  (c/deg), is proportional to the separation,  $d$  (mm), between the two point sources in the pupil plane and is represented by  $f = \pi d/180\lambda$ , where  $\lambda$  (mm) is the wavelength of the laser source. The subject's head was stabilized with a dental bite bar, which was attached to the optical table by a three-axis positioning device. The absolute  $x$ - $y$  position of the point sources in the pupil plane could be adjusted by manual positioning of the bite bar mount.

A field stop limited the field of view of the fringe to 0.9 deg of visual angle. The point sources in interferometric stimulators that have small circular fields are not ideal points but Airy disks, in our case with a radius (to the first zero) of approximately 20  $\mu\text{m}$ . This raises the possibility that high-order corneal aberrations within each Airy disk image might affect the interference pattern, a relevant concern since any optical degradation from this might well be anisotropic. Such aberrations will not, however, affect the contrast of the pattern. Full contrast requires only that destructive interference be complete. This is guaranteed so long as there are loci on the retina where the resultant waves from the two sources arrive in opposite temporal phase, with symmetrical waveforms that can cancel. Symmetry is given by the monochromatic (sinusoidal) nature of the source (which in the case of our laser, has a coherence length measured in inches rather than micrometers). Multiple phase-perturbed sine waves from such a source still give a temporal sine wave as their resultant, and the opposite-phase condition will be realized (somewhere) provided only that relative phase varies continuously across the retina. Continuity, in this sense, will not be affected by optical aberrations, and observation of low-spatial-frequency gratings confirms that it is maintained.

Other effects of aberrations were also not substantial. Aberrations occasionally brought the two fields out of register, but this was easily detected and compensated for with a correcting lens. Aberrations could change the shapes or intensity distributions of the fields, but no substantial effects of this sort were seen in observations of the separate fields as the point of entry moved within the pupil. In principle, aberrations could also perturb the local spatial frequency of the fringe pattern, but if this effect were important, it would be noticeable as a distortion of low-frequency gratings during head movement, and no such distortions could be observed. The wave-front-aberration data of Liang and Williams<sup>20</sup> also suggest that these effects, with the exception of the field misregistration, should be negligible under our conditions.

A computer controlled the stimulus presentation and data collection. This permitted the random ordering of

experimental conditions composed of various stimulus intensities, contrasts, and spatial frequencies.

## B. Observers

The authors, MM, a protanopic subject with normal acuity, and DM, a deuteranomalous subject with normal acuity, served as subjects.

## C. Measurement of the Stiles–Crawford Effect

To measure the Stiles–Crawford effect, the overlapping fields produced by the two point sources were alternated at 10 Hz, and the observer adjusted the intensity of the eccentric beam to minimize the percept of flicker. The Stiles–Crawford effect was measured over a vertical range of 7 mm centered on the horizontal extent of the dilated pupil.

## D. Measurement of Retinal Fringe Contrast

Contrast-modulation flicker was used as a psychophysical measure of contrast at the level of the photoreceptors.<sup>18</sup> In this technique, the Michelson contrast of a fine grating is altered between zero and 100% contrast at 12 Hz. Although the space-averaged illuminance remains constant, a low-level retinal nonlinearity generates a flicker signal equivalent to a full-field modulation of space-averaged intensity. Previous experiments have demonstrated that the nonlinearity is fed by individual cones and that the magnitude of the flicker is approximately proportional to the square of the fringe contrast.<sup>18</sup> Since the cones themselves can respond to spatial frequencies well above the limit of perceptual resolution, their summed flicker signal can be transmitted through subsequent stages of the visual system without the attenuation by neural spatial filtering that high spatial frequencies must undergo. In this way, contrast-modulation flicker makes it possible to assess optical attenuation of spatial frequencies too high to be perceptually resolved. This greatly enhances the precision with which optical contrast losses can be detected. Aliasing to low-frequency patterns could in principle provide another means of assessing the optical contrast of spatial frequencies that are not directly resolvable, but aliasing was not seen at all by our observers in the frequency range of interest here.

We determined the amplitude of the contrast modulation with a nulling method. A computer-generated luminance modulation was added on top of the contrast modulation. The phase of the luminance modulation was set to cancel the flicker generated by the contrast modulation. The observer adjusted the magnitude of the luminance modulation necessary to null the contrast-modulation flicker. Appendix A discusses the relationship between the nulling amplitude and the effective fringe contrast. This technique provides sensitive measurements of the effective fringe contrast at the level of the cone photoreceptors.<sup>18</sup>

The effective contrast of fringe patterns generated on the fovea was measured for various directions of incidence of the two interfering beams. Since the ratio of intensities that would yield maximal fringe contrast for a given pair of point sources was not known, a range of intensities was used, so as to determine both the optimal intensity

ratio and the corresponding maximal contrast (Experiment 1). The ratio of the point source intensities was changed over a 2-log-unit range, while their combined luminance was kept constant at the same value produced when they entered at the Stiles–Crawford peak. In addition, whenever the experiments called for the two point sources to be displaced together from the Stiles–Crawford peak, the intensities of both sources were increased to compensate for their decreased brightness, based on previous measurement of the subject's Stiles–Crawford effect.

### 3. RESULTS

#### A. Experiment 1. Determining the Optimal Point Source Intensity Ratio for Optimizing Fringe Contrast

Measurements were made of the effective contrast of an interference fringe generated on the fovea for various directions of incidence of the two interfering beams. The pupil entry points of the interfering beams fixed the direction of incidence at the retina, and their separation determined the fringe spatial frequency. Figure 1 shows the effective fringe contrast as a function of the intensity ratio of the two interfering beams for three conditions for subject MM. The first two panels show measurements made with a vertical point source separation of 1.5 mm, corresponding to a 51-c/deg grating. The center of the point sources was shifted 1.5 mm down from the Stiles–Crawford peak in Fig. 1(a) and 2.5 mm down in Fig. 1(b). Figure 1(c) shows measurements made with a 2.5-mm point source separation shifted down 1.0 mm from the Stiles–Crawford peak. Relative intensities are shown on a decimal log scale, with reference to the intensity ratio required for Stiles–Crawford equality for that condition's point source positions. Positive log (point source relative intensity) values correspond to intensities of the more eccentric point source that are greater than required for Stiles–Crawford equality. The small arrow pointing to the  $x$  axis in each plot marks the point source ratio for physical equality.

The data for each condition were fitted with a theoretical function for fringe contrast (see Appendix A). The function had two free parameters: the maximum contrast and the optimal intensity ratio. The Levenberg–Marquardt algorithm was used for fitting, and data were weighted by their standard error of the mean (SEM). Fringe contrast was maximal when the interfering beams were equal in perceived brightness, not when they were equal in physical intensity<sup>15</sup> nor when the eccentric beam was more intense than required for Stiles–Crawford equality.<sup>16,17</sup> The optimal point source log intensity ratios for the three panels in Fig. 1 were 0.06,  $-0.01$ , and 0.00 (plotted as a single solid diamond at the top of each panel). The error bars contain the 95% confidence interval of the parameter estimates, which were  $\pm 0.08$ ,  $\pm 0.13$ , and  $\pm 0.06$  for the three conditions in Fig. 1. None of the optimal point source intensity ratio estimates were statistically different from Stiles–Crawford equality.

Calculations were performed to estimate the expected effect of cone-pointing disarray on the optimal intensity ratio for peak contrast. We expected this to be relevant because in the presence of disarray, an obliquely incident

beam selectively stimulates cones oriented toward it, and the effectiveness of an interfering beam must depend on its stimulation of that subset of the cones. The intuitively expected effect was not, however, supported by the analysis given in Appendix B or by calculations based on the model outlined there. For a fixed point source separation (i.e., a fixed spatial frequency), increasing cone disarray resulted in a reduction in fringe contrast, but the reduction was slight. A generous estimate of pointing disarray ( $\sigma = 0.4$  mm, compare Ref. 21) resulted in a 0.01-log-unit decrease in contrast for a 68-c/deg grating with a 2.5-mm displaced pupil. Moreover, the optimal point source intensity ratio in the presence of disarray remained at the Stiles–Crawford equality setting; measurements of the optimal intensity ratio for maximizing fringe contrast may therefore reveal nothing about receptor disarray or about the acceptance angle of individual cones.

#### B. Experiment 2. Quantifying the Decrease in Effective Contrast with Oblique Incidence

To determine if there was a directional acuity effect, the pupil entry location was varied for a fixed spatial-frequency grating. The contrast was measured (1) with the point sources centered vertically on the Stiles–Crawford peak and horizontally aligned with the pupil center. Contrast was also measured for oblique incidence conditions produced (2) with the point sources displaced together temporally in the pupil (parallel to the bars of the grating), and (3) with the point sources displaced together downward in the pupil (perpendicular to the bars of the grating). The results are shown in Fig. 2 for spatial frequencies of 51 and 68 c/deg.

The first result to note is that there is a decrease in fringe contrast with oblique incidence. The effect is small, and it increases with more obliquely incident light. This can be seen by comparing observer MM's contrast loss for the 1.5-mm displacement [Fig. 2(a)] with his contrast loss for the 2.5-mm displacement [Fig. 2(b)].

A second result is that the decrease in fringe contrast is similar when the point sources are displaced parallel or perpendicular to the bars of the grating. This can be seen by comparing the parallel and perpendicular displacement conditions within each panel in Fig. 2. Because the precise location of the Stiles–Crawford peak in the horizontal dimension was not known, a control experiment was performed with subject MM to ensure that the pupil center was close to the Stiles–Crawford peak. In this experiment, a 2.5-mm nasal displacement from the pupil center produced an effective fringe contrast that was not statistically different from the contrast measured with a 2.5-mm temporal displacement. For observer DM at 68 c/deg, displacement of the point sources perpendicular to the grating bars may have produced a slightly smaller contrast decrement than displacement parallel to the grating bars for one condition [Fig. 2(d)], a result opposite to that of Campbell and Gregory<sup>4</sup> for spatial frequencies in the visible range.

Corneal birefringence can affect the polarization state of decentered entry beams. Since the beams are vertically polarized, corneal birefringence may rotate the polarization states of each beam in the temporally displaced condition in an opposite direction, resulting in a decrease

of fringe contrast. Displacement of the point sources in the vertical direction would not differentially affect the polarization states of the two beams, since in that condition the two displacements are in the same direction from the pupil center. Thus the net effect of birefringence is opposite to the one reported by Campbell.<sup>3</sup> The effect of corneal birefringence in the temporally displaced condition was calculated by using the data of Bour and Lopes Cardozo,<sup>22</sup> who measured a retardation of approximately 40 deg for light entering the eye 2.5 mm temporally from

the pupil center. The decrease in contrast due to this retardation was calculated to be 0.03 log unit for a 51-c/deg fringe pattern generated by 2.5-mm temporally displaced point sources. This calculation is in agreement with experimental results of Chen and Makous<sup>14</sup> showing a less than 0.03 log unit effect of birefringence on interference fringe contrast. Since this loss is only approximately 15% of the small loss shown in Fig. 2 for data gathered under these conditions, the losses of Fig. 2 are evidently of predominantly retinal origin. However, corneal bire-

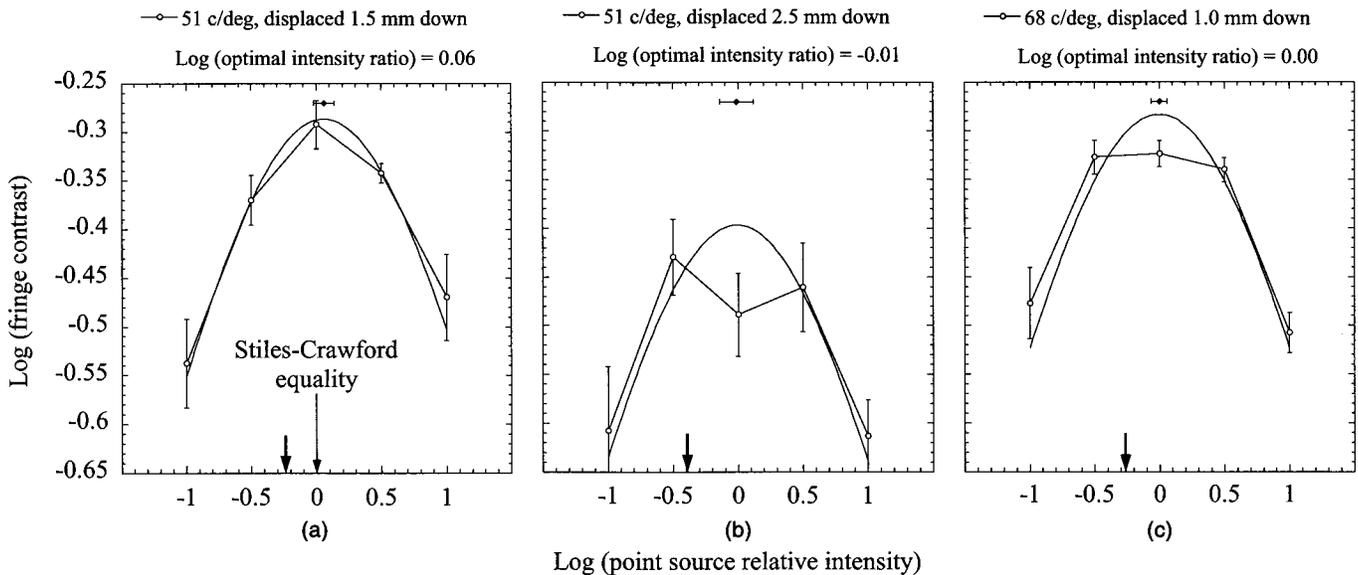


Fig. 1. Effective fringe contrast as a function of point source intensity ratio. Measurements of fringe contrast were made over a 2-log-unit range of point source intensity ratios to determine the optimal intensity ratio for maximizing fringe contrast. The 0 log (point source intensity ratio) denotes the *x* axis position that equates the beams for brightness, with a deviation from physical equality to compensate for the Stiles–Crawford effect. The black arrows pointing to the *x* axis mark the point source intensity ratio for physical equality. The smooth curves are theoretical fits to the measured contrast values (see Appendix A). Solid diamonds above the curves show the fitted optimal point source intensity ratio for maximum fringe contrast, with horizontal error bars enclosing the 95% confidence interval. All three conditions yielded maximum fringe contrast at a point source intensity value that was not statistically different from Stiles–Crawford equality.

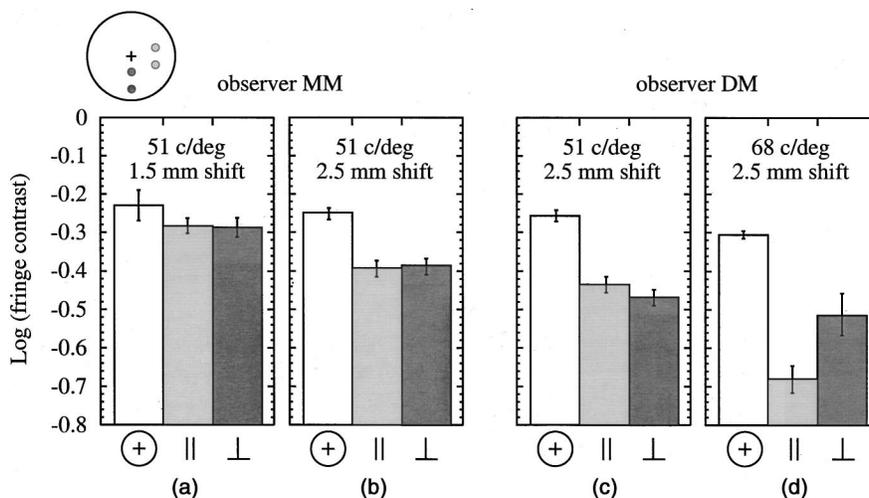


Fig. 2. Effect of oblique incidence on grating contrast. Each panel shows the measured fringe contrast for a 51-c/deg spatial-frequency grating (68 c/deg for panel (d)). White bars, point sources centered on the Stiles–Crawford peak. Light-gray bars, point sources displaced parallel to the bars of the grating. Dark-gray bars, point sources displaced perpendicular to the grating bars. The results demonstrate a small decrease in fringe contrast with oblique incidence. Unlike the original Campbell result,<sup>3</sup> the decrease in contrast was no greater for displacements perpendicular to the bars of the grating than for displacements parallel to the bars of the grating. A 2.5-mm displacement of the point sources [(b)] produced a larger decrease in fringe contrast than a 1.5-mm displacement [(a)]. Error bars represent  $\pm$ SEM.

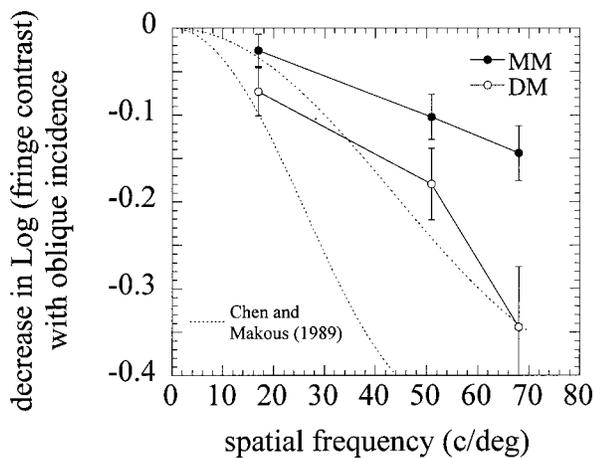


Fig. 3. Spatial-frequency dependence of the decreased contrast with oblique incidence. Data points represent the difference in log fringe contrast between centered point entry and a 2.5-mm temporal displacement parallel to the bars of the grating for that spatial frequency. This decrease in log fringe contrast with oblique incidence is measured as a function of spatial frequency for two observers, MM and DM. Error bars =  $\pm$ SEM. Also shown are Gaussian fits to the data from Chen and Makous.<sup>14</sup>

fringe may make a small contribution to the unexpected reversal of the Campbell effect at 68 c/deg for DM.

### C. Experiment 3. Dependence of the Loss of Effective Fringe Contrast with Oblique Incidence on Spatial Frequency

The decrease in fringe contrast with oblique incidence was measured by comparing (1) the effective fringe contrast obtained with centered point sources to (2) the fringe contrast with 2.5-mm temporally displaced point sources. The difference in log (effective fringe contrast) was measured for three spatial frequencies for observers MM and DM. Data for the six conditions for each observer were collected in random order. Data from similar conditions in Experiment 2 were not reused.

The results are shown in Fig. 3. The decrease in fringe contrast with oblique incidence is greater at higher spatial frequencies for both observers.

## 4. DISCUSSION

The experimental results can be discussed in relation to several simple models of light capture by human cones. The first two models predict no decrease in contrast with obliquely incident light. In the first model, light is always effectively contained by waveguiding (or in terms of ray optics, by total internal reflection) within the cone that it first encounters. This is illustrated in Fig. 4(a). If this were the case, obliquely incident light would not be less visually effective and would not decrease contrast by spreading from one cone to another. The second model, depicted in Fig. 4(b), proposes that this waveguiding fails to confine obliquely incident light to the outer segment. As a result, light “leaks” from the cone it first enters and is neither absorbed in the initially entered cone nor reabsorbed in another one. Although this model is commonly used to explain the Stiles–Crawford effect (the dramatic decrease in perceived brightness with obliquely incident

light<sup>8</sup>), it fails to predict the loss in contrast with obliquely incident light observed in our measurements.

A model that does predict a loss in contrast with oblique incidence is depicted in Fig. 4(c). In this scenario, oblique light escapes but is recaptured in the “wrong” cone. Chen and Makous<sup>14</sup> proposed this model to account for their interferometric data, calculating that over half of the light absorbed with oblique incidence has first passed through other cones. If light tracked straight through the cones, as this simple geometrical model suggests, then resolution should be impaired only when the incoming beam is displaced in a direction perpendicular to the bars of the grating, as in the original Campbell effect.<sup>3</sup> However, Chen and Makous,<sup>14</sup> as well as Enoch,<sup>5</sup> found that the contrast loss with oblique incidence depended only weakly on the orientation of the test grating. The data in Fig. 2, which show no difference between parallel and perpendicular displacements, provide further evidence against the simple directional model.

The magnitude of our contrast loss with oblique incidence is compared with that of Chen and Makous<sup>14</sup> in Fig. 3. The dotted curves represent the contrast loss with oblique incidence as a function of spatial frequency for two observers (see Fig. 7 of Ref. 14). The point sources were displaced 2.5 mm and 2.9 mm in the pupil for the two observers, parallel to the bars of the grating. There are large individual variations, but on the average the observers in the study by Chen and Makous showed larger contrast losses than those reported here. Our results are thus intermediate between those of Chen and Makous and those of the earlier studies of interference fringe contrast losses with oblique incidence<sup>9,10</sup> that found nothing attributable to the retina. Since the contrast-modulation flicker-detection mechanism is not affected by the observer’s steeply falling neural contrast-sensitivity function,

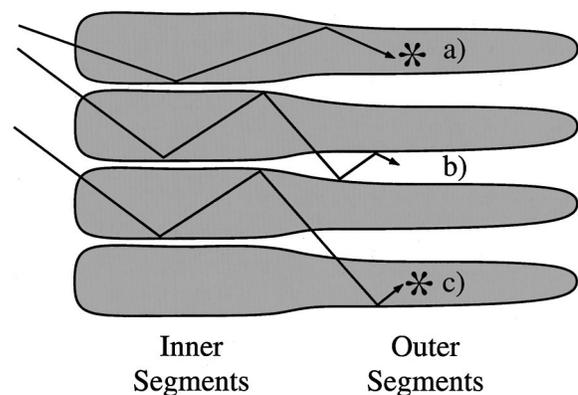


Fig. 4. Cone light-capture scenarios. Three simple cone light-capture models. In (a) light is perfectly waveguided by the cones. This model predicts no loss in resolution or sensitivity with oblique incidence. Model (b) proposes that obliquely incident light escapes from the cone and produces no visual effect. This type of model is often suggested to explain the large decrease in perceived brightness with obliquely incident light (the Stiles–Crawford effect). Model (c) proposes that some of the light that leaks from a cone is recaptured by a neighboring cone. This scenario results in a decrease in fringe contrast with oblique incidence. The simple case of this model, where light travels straight through a receptor, predicts a loss in resolution for grating oriented perpendicular to the pupil displacement, but not for parallel displacements.

we believe that our technique possesses a large advantage in sensitivity over previous ones. This is especially relevant for measurements at high spatial frequencies, where the retinal contribution is greatest. Individual differences, differences in technique, and wavelength differences must all be considered in evaluating any difference in results. But one important aspect of the results, common to all studies, is that retinal contrast losses due to oblique incidence have only minimal effects on the contrast sensitivity function, a point on which we elaborate below.

The spatial-frequency dependence of the contrast loss can be used to estimate the spatial extent of the spreading. In our analysis we approximate the point-spread function for obliquely incident light as the convolution of the spread function for a centered point source with a Gaussian blur function. If the effect of moving to oblique incidence is viewed as a convolution in the spatial domain then it can be represented as a multiplication in the frequency domain, and Fig. 3, which describes the loss in log contrast with oblique incidence, can be thought of as the frequency response of the blur process occasioned by oblique incidence. A Gaussian fit to the data in Fig. 3 was transformed to the spatial domain by taking the inverse Fourier transform. The resulting Gaussian spatial blurring profile is shown in Fig. 5, where its width is compared graphically with the cone outer segment length, width, and spacing ( $1\ \mu\text{m}$  width,  $40\ \mu\text{m}$  length, and  $2.3\ \mu\text{m}$  spacing). For comparison, the straight line in Fig. 5 illustrates the angle of incidence associated with a 2.5-mm shift from Stiles–Crawford peak in the plane of the pupil (approximately  $7^\circ$ ). The spatial blur function derived from our measurements demonstrates that the spatial extent of the blurring with oblique incidence is not large in comparison with the size of foveal cones. Even obliquely incident light is well contained within the single cone toward which it is directed, in that even the flanking nearest-neighbor cones absorb little of the incident energy. This conclusion from our results is consistent with color vision experiments in which the color change of monochromatic light at oblique incidence is well accounted for with a model postulating only self-screening (and not mutual screening) by the visual pigments.<sup>23,24</sup> Further, the reported chromatic deviations (notably, a desaturation of long-wavelength light) are not of the kind expected from mutual screening. It should be noted, however, that when the blurring associated with oblique incidence is modeled by a translation-invariant spread function as in Fig. 5, the spread function is wide enough that the light energy directed toward a point roughly midway between two cones may be captured equally by them both. If such spreading takes place before light enters the outer segment, it need not imply any mutual screening by the visual pigments.

Besides the partitioning of obliquely incident light between adjacent cones, two other potential contributions to the contrast reduction reflected in the finite width of the spread function in Fig. 5 warrant mention. First, the effective aperture of single cones might become greater with oblique incidence. The waveguide properties of the human photoreceptor array are complex, and the existing models are sensitive to small changes in a number of pa-

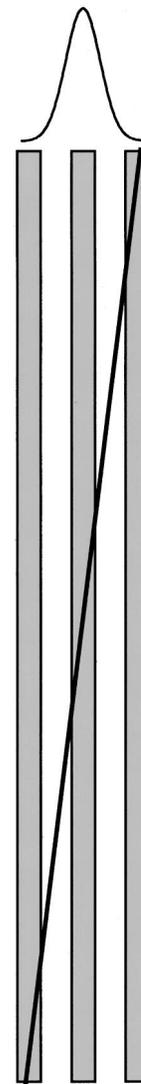


Fig. 5. Spatial extent of the retinal blurring produced by oblique incidence. The point-spread function for obliquely incident light was assumed to be the convolution of the spread function for a centered point source with a Gaussian blur function. The calculated Gaussian spatial blurring profile for oblique incidence is shown and is compared graphically with the cone outer segment length, width, and spacing ( $1\ \mu\text{m}$  width,  $40\ \mu\text{m}$  length, and  $2.3\ \mu\text{m}$  spacing). The straight line across the outer segments illustrates the angle of incidence associated with a 2.5-mm shift from Stiles–Crawford peak in the plane of the pupil (approximately  $7^\circ$ ). The spatial blur function derived from our measurements demonstrates that the blurring with oblique incidence is small in comparison with the size and spacing of foveal cones.

rameters, such as phase variations across cones; the index of refraction within cones and the interphotoreceptor matrix; and the dimensions of the cone length, width, and taper.<sup>25,26</sup> Therefore more sophisticated waveguide modeling of our results is unlikely to place strong constraints on any of the relevant physiological parameters. The anatomical dimensions of the cones, however, are small enough that this can hardly account for the full effect. Moreover, the even smaller estimates of the effective aperture of single photoreceptors obtained by MacLeod *et al.*<sup>27</sup> are based mainly on measurements with oblique incidence.

Second, some absorbed light may have undergone forward scatter in transit through the retina before entering the outer segments, and this light will be relatively more effective when the unscattered light loses the advantage of axial incidence. Van de Kraats *et al.*<sup>28</sup> measured the fundal reflection for two retinal angles of incidence: first, with an entrance pupil centered on the Stiles–Crawford peak and second, with it displaced 2.5 mm temporally. Their calculations showed that stray light in the fundal reflection greatly increases with oblique incidence. This suggests that light scattered by retinal structures and absorbed by adjacent cones may also play a role in decreasing contrast with oblique incidence, but the present results indicate that such scattering does not extend beyond the nearest-neighbor cone at an intensity sufficient to reduce the image contrast by a substantial factor. The directional sensitivity of cones must help to diminish the visual effectiveness of the scattered light observed in the fundal reflection with oblique incidence, and for this reason the extent of visually effective scatter is likely to be considerably less than the extent of scatter in light returned from the fundus.

What is the role of retinal contrast loss with oblique incidence under normal viewing conditions? The retinal component plays a large role only at high spatial frequencies (Fig. 3), where the human contrast sensitivity is dropping steeply as a result of the modulation transfer function of the human eye<sup>2</sup> and subsequent neural filtering.<sup>29</sup> Figure 6 shows CRT grating contrast sensitivity measured by Green<sup>9</sup> through a 2-mm artificial pupil. The curve represents the average of fits to his data gathered with the pupil displaced 2 mm and 3 mm from the center of the natural pupil. This steeply falling function reflects the combined influence of optical and retinal factors in decreasing contrast sensitivity with oblique incidence. The inset to Fig. 6 shows an expanded view of the spatial-frequency range near the resolution limit, which is 19.4 c/deg for the curve based on Green's experimental measurements. Our calculation of the retinal contribution to the loss in contrast sensitivity with oblique incidence (using the data of Fig. 3 for a 2.5-mm pupil eccentricity) was then subtracted from the contrast-sensitivity function measured by Green.<sup>9</sup> The inset to Fig. 6 shows that the resolution limit with the retinal contribution removed increases only by 0.1 c/deg to 19.5 c/deg. This minuscule increase in resolution implies that the decrease in fringe contrast with oblique incidence has a very small retinal component under normal visual conditions. Under these conditions, it is off-axis monochromatic and chromatic aberration that are responsible for the large decrease in contrast sensitivity observed with obliquely incidence light.<sup>10,12</sup> These factors obliterate all image contrast in the high-spatial-frequency range where retinal contrast losses are greatest.

It is also possible to calculate the decrease in contrast by using the simplest geometrical model, where light is not trapped within the photoreceptor waveguide at all but tracks straight through the cone outer segments [Fig. 4(c)], as illustrated by the heavy straight line in Fig. 5. The loss in resolution can be calculated by estimating the sampling aperture for obliquely incident light as the con-

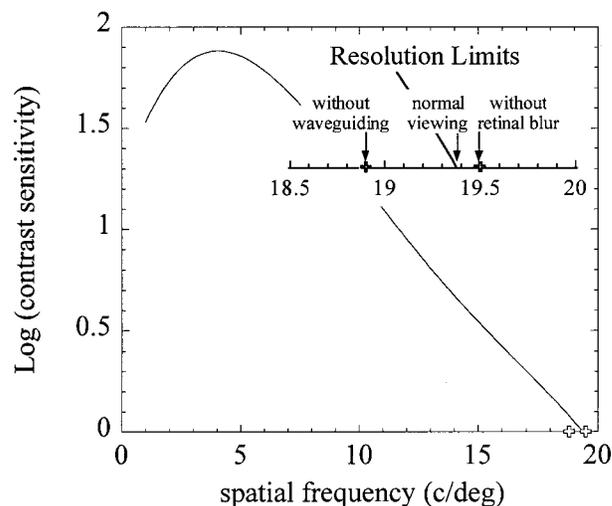


Fig. 6. Retinal contribution to loss of resolution with oblique incidence. The smooth curve shows CRT grating contrast sensitivity measured by Green<sup>9</sup> through a displaced, 2-mm artificial pupil. The inset shows an expanded view of the spatial-frequency range near the resolution limit, which is 19.4 c/deg for Green's measurements. The inset also shows the resolution limit calculated after removal of the retinal contribution: 19.5 c/deg. The loss in resolution based on the simple geometrical model in which light tracks straight through the cone outer segments [Figs. 4(c) and 5] is also shown. This loss in resolution is calculated by estimating the sampling aperture for obliquely incident light as the convolution of the sampling aperture for central entry with a rectangular function given by the lateral distance across the cone outer segments subtended by the obliquely incident ray. This simple model, which simulates a complete lack of waveguiding, would lower the resolution limit to 18.9 c/deg.

volution of the sampling aperture for central entry with a rectangular spread function having a width given by the lateral distance across the cone outer segments subtended by the obliquely incident ray (4.9  $\mu\text{m}$ , for a 7° angle and a 40- $\mu\text{m}$  outer segment length). The resulting loss in contrast is a sinc function of spatial frequency. The previously calculated resolution limit for a 2.5-mm displaced pupil under normal viewing, with the retinal blurring component removed, was 19.5 c/deg. The simple model described here, which simulates a complete lack of waveguiding, would lower the resolution limit to 18.9 c/deg (Fig. 6). This simple calculation provides a rough estimate of the benefit of waveguiding in preventing off-axis contrast losses in normal vision. The benefit is slight, but it is possible that even so small a benefit in resolution has significant adaptive value.

The measurements and calculations reported here suggest that the photoreceptors are fairly effective in trapping light within the cone first entered. Accordingly, the contribution of the retina to losses in contrast with oblique incidence is only minor. Indeed, it is certainly offset by a positive contribution of the retina to resolution. The directional sensitivity of the cones (Stiles–Crawford effect) greatly reduces the visual effectiveness of obliquely incident light, which is blurred by optical aberrations.<sup>30–32</sup> Thus light trapping and directional

sensitivity work together to minimize losses in contrast sensitivity with obliquely incident light or with large pupils.

## 5. CONCLUSION

There is a large decrease in grating contrast sensitivity with obliquely incident light under normal viewing conditions. This paper demonstrates that only a very small part of this decrease is attributable to contrast losses within the retina. This retinal contrast loss was greatest at high spatial frequencies and was similar whether the incident beams were displaced from the pupil center in a direction parallel or perpendicular to the grating bars.

### APPENDIX A: RELATIONSHIP BETWEEN LUMINANCE NULLING AMPLITUDE AND EFFECTIVE FRINGE CONTRAST

The following notation will be used in this appendix:

- $NA$ , luminance flicker nulling amplitude
- $C_E$ , effective fringe contrast
- $x = I_1/I_2$ , intensity ratio between the two point sources

From He and MacLeod,<sup>18</sup>

$$NA \propto (C_E)^2. \quad (\text{A1})$$

Born and Wolf<sup>33</sup> described the relationship between interference fringe contrast  $C$  and the intensities of the sources ( $I_1, I_2$ ):

$$C = \frac{2\sqrt{I_1 I_2}}{I_1 + I_2}. \quad (\text{A2})$$

So, for a point source intensity ratio  $x$ :

$$C = \frac{2\sqrt{x}}{x + 1}. \quad (\text{A3})$$

Substituting relation (A3) into relation (A1), we obtain

$$NA \propto \frac{4x}{(x + 1)^2}. \quad (\text{A4})$$

Data from Experiment 1 were fitted with the following equation:

$$\log(C_E) = k \left\{ m_1 + \log \left[ \frac{4 * 10^{(x-m_2)}}{(10^{(x-m_2)} + 1)^2} \right] \right\} / 2, \quad (\text{A5})$$

where  $m_1 = [\text{peak } \log(NA)]$ ,  $m_2 = (\text{optimal relative intensity})$ , and  $k = \text{constant}$ .

Because the proportionality constant  $k$  is not determined by our experiments, the absolute fringe contrast is not known. At the beginning of data collection, the log contrast of a 17-c/deg grating was estimated, with the point sources centered, for each subject. This produced a contrast value that was close to maximal, since it is known from previous work that the magnitude of contrast-modulation flicker decreases gradually with increasing spatial frequency.<sup>8</sup> All subsequent estimates of log contrast were subtracted from this reference level.

Using this difference in log contrast as a response measure cancels out the effect of the proportionality constant  $k$ .

### APPENDIX B: EFFECT OF CONE ANGULAR TUNING AND POINTING DISARRAY ON INTERFERENCE FRINGE CONTRAST

Receptor disarray could reduce the effective contrast of fringe patterns and thereby affect the results of the experiments of this paper, but its influence has never been quantitatively considered. If receptors are disarrayed, the effective amplitudes of two interfering wave fronts will be different for the differently oriented receptors in any given small retinal region. The amplitude ratio cannot then be optimal for all receptors, and a loss of fringe contrast will result. Here we evaluate this loss and show it to be slight and equal for all orientations.

The relative intensities required for best fringe contrast will also be affected by disarray. Intuition might suggest that when the two interfering beams both enter on the same side of the pupil center, the retinal response will be dominated by receptors oriented toward the two beams, making the optimal intensity ratio different from the one that compensates for the Stiles–Crawford effect. The following analysis, however, gives theoretical grounds for what we find experimentally: Even in the presence of disarray, contrast is optimized simply by compensating for the Stiles–Crawford effect. It follows that measurements of the intensity ratio required to optimize fringe contrast are not useful for estimating either receptor disarray or the acceptance angle of the individual photoreceptors.

We proceed on the standard assumption that photoreceptor sensitivity is a Gaussian function of the angle between the cone axis and the direction of incidence. This allows the problem to be reduced from a two- to a one-dimensional one, if the distribution of pupil intercepts is also a circular Gaussian.<sup>21</sup> On the line  $L$  containing the pupil entry points of the two interfering beams, we take the point of maximum sensitivity as the origin for pupil coordinates  $x$  along  $L$ , and  $y$  in the orthogonal direction. The tilt of a photoreceptor can be represented by the coordinates  $(x, y)$  of its “pupil intercept”: the point at which its axial ray meets the pupil plane.<sup>21</sup>

On the assumption of a circular Gaussian sensitivity profile, any deviation of a photoreceptor’s pupil intercept from the line  $L$  reduces the effective intensities of the two interfering beams by the same factor,  $\exp(-y^2/2s^2)$ , where  $s$  is the standard deviation of the Gaussian function for sensitivity of individual photoreceptors. So the effective contrast of the fringe pattern, as seen by an array of photoreceptors with a common pupil intercept  $(x, y)$ , is independent of  $y$ . And although variation in  $y$  does alter both effective intensity and pupil intercept density, it does so by a factor independent of  $x$ . We can therefore, for compactness, consider a population of photoreceptors with pupil intercepts  $(x, 0)$  all lying on the line  $L$ . The probability density function of the  $x$  coordinate of pupil intercepts is

$$f(x) = \frac{1}{\sigma\sqrt{2\pi}} \exp\left(\frac{-x^2}{2\sigma^2}\right), \quad (\text{B1})$$

where  $\sigma$  is the standard deviation of pupil intercepts.

Denote the intensities of the two interfering beams, entering the eye at  $x_1$  and  $x_2$  respectively, by  $I_1$  and  $I_2$ . The amplitudes are the square roots of these intensities. The peak intensity of the fringe pattern, where the wave fronts are in reinforcing phase, is  $(\sqrt{I_1} + \sqrt{I_2})^2$ ; the average intensity is  $(I_1 + I_2)$ , and the difference,  $\Delta I$ , is  $2\sqrt{I_1 I_2}$ . We now assume (perhaps too simply) that each intensity is scaled, for each cone, by a scaling factor that depends on the directional sensitivity and pupil intercept of the cone. The effective intensity of the beam at  $x_1$ , as seen by photoreceptors with pupil intercept  $x$ , then becomes

$$I_1(x) = I_1 \exp\left[\frac{-(x_1 - x)^2}{2s^2}\right], \quad (\text{B2})$$

where  $s$  is the standard deviation of the Gaussian representing photoreceptor sensitivity in the pupil plane, and similarly for  $I_2(x)$ . Considered as a function of the photoreceptor pupil intercept  $x$ , the difference between the peak effective local luminance and the average effective local luminance is therefore

$$\begin{aligned} \Delta I(x) &= 2\sqrt{I_1(x)I_2(x)} \\ &= 2\sqrt{I_1 I_2} \exp\left[-\frac{(x_1 - x)^2 + (x_2 - x)^2}{4s^2}\right]. \end{aligned} \quad (\text{B3})$$

We assume that the effective luminance profile for the photoreceptor matrix as a whole can be obtained by integrating over all cones, that is, by integrating with respect to the pupil intercept  $x$ , with a weighting coefficient equal to the probability density function of the pupil intercept. The effective Michelson contrast then becomes

$$C = \frac{\int f(x)\Delta I(x)dx}{\int f(x)I_1(x)dx + \int f(x)I_2(x)dx}. \quad (\text{B4})$$

The numerator here is the deviation of the peak intensity from the space average and according to Eq. (B3) is proportional to  $\sqrt{I_1 I_2}$ . The denominator represents the space-averaged effective intensity of the combined beams; each integral represents the effective intensity of one of the two beams. Each integral includes a Stiles–Crawford sensitivity factor that is a Gaussian function of its entry point, with a standard deviation equal to the Pythagorean sum of  $\sigma$  and  $s$ .<sup>21</sup> Thus for the beam at  $x_1$ , denoting the sensitivity by  $S(x_1)$ ,

$$\int f(x)I_1(x)dx = I_1 S(x_1) = I_1 \exp\left[\frac{-x_1^2}{2(s^2 + \sigma^2)}\right]. \quad (\text{B5})$$

The dependence of  $C$  on the intensities of the beams therefore has the form

$$C = \frac{k\sqrt{I_1 I_2}}{I_1 S(x_1) + I_2 S(x_2)}. \quad (\text{B6})$$

This is maximal when  $I_1 S(x_1) = I_2 S(x_2)$ , that is, when the intensities are adjusted to compensate for the Stiles–Crawford sensitivity loss.

The beam intensities (in arbitrary units) required to compensate for the Stiles–Crawford sensitivity loss are

$$I_1 = \exp\left[\frac{x_1^2}{2(s^2 + \sigma^2)}\right], \quad I_2 = \exp\left[\frac{x_2^2}{2(s^2 + \sigma^2)}\right]. \quad (\text{B7})$$

With contrast thus optimized, disarray still has an effect on contrast, which we investigate next. Substituting for Eq. (B7) in Eq. (B3) we have

$$\begin{aligned} \Delta I(x) &= 2 \exp\left[\frac{x_1^2 + x_2^2}{4(s^2 + \sigma^2)}\right] \\ &\times \exp\left[-\frac{x^2}{2s^2} + x\frac{(x_1 + x_2)}{2s^2} - \frac{(x_1^2 + x_2^2)}{4s^2}\right], \end{aligned}$$

and the integrand in the numerator of Eq. (B4),  $f(x)\Delta I(x)$ , becomes

$$\begin{aligned} \frac{\sqrt{2/\pi}}{\sigma} \exp\left[-x^2\frac{(s^2 + \sigma^2)}{2s^2\sigma^2} + x\frac{(x_1 + x_2)}{2s^2} \right. \\ \left. - (x_1^2 + x_2^2)\frac{\sigma^2}{4s^2(s^2 + \sigma^2)}\right]. \end{aligned}$$

This can be integrated by expressing it as the product of a Gaussian in  $x$  and a term not involving  $x$ :

$$\begin{aligned} \frac{\sqrt{2/\pi}}{\sigma} \exp\left\{-\left[x\sqrt{\frac{s^2 + \sigma^2}{2s^2\sigma^2}} - (x_1 + x_2)\sqrt{\frac{\sigma^2}{8s^2(s^2 + \sigma^2)}}\right]^2 \right. \\ \left. + (x_1 + x_2)^2\frac{\sigma^2}{8s^2(s^2 + \sigma^2)}\right\} \\ \times \exp\left[-(x_1^2 + x_2^2)\frac{\sigma^2}{4s^2(s^2 + \sigma^2)}\right], \end{aligned}$$

which yields for the numerator in Eq. (B4)

$$\begin{aligned} \int f(x)\Delta I(x)dx &= \frac{2s}{\sqrt{s^2 + \sigma^2}} \\ &\times \exp\left[-(x_1 - x_2)^2\frac{\sigma^2}{8s^2(s^2 + \sigma^2)}\right]. \end{aligned} \quad (\text{B8})$$

We finally show that the factor preceding the exponential here cancels with the denominator in Eq. (B4). Substituting for Eqs. (B7) and (B1) in Eq. (B2) yields expressions for the two components of the integrand in the denominator of Eq. (B4): for the beam at  $x_1$ ,

$$f(x)I_1(x) = \frac{1}{\sigma\sqrt{2\pi}} \exp\left(\frac{-x^2}{2\sigma^2}\right) \times \exp\left[\frac{x_1^2}{2(s^2 + \sigma^2)} - \frac{(x_1 - x)^2}{2s^2}\right],$$

which simplifies to a Gaussian in  $x$ :

$$f(x)I_1(x) = \frac{1}{\sigma\sqrt{2\pi}} \exp\left\{-\left[x\sqrt{\frac{s^2 + \sigma^2}{2s^2\sigma^2}} - \frac{x_1\sigma}{\sqrt{2s^2(s^2 + \sigma^2)}}\right]^2\right\}.$$

Each of the two components of the integral in the denominator of Eq. (B4) thus evaluates to  $s/(s^2 + \sigma^2)^{1/2}$ . Substituting for this and for Eq. (B8) in Eq. (B4), we obtain an equation relating the intensity-optimized effective contrast to the beam entry points, the single-photoreceptor directional sensitivity parameter  $s$ , and the disarray parameter  $\sigma$ :

$$C = \exp\left[-(x_1 - x_2)^2 \frac{\sigma^2}{8s^2(s^2 + \sigma^2)}\right]. \quad (\text{B9})$$

Since contrast here depends only on the pupil separation ( $x_1 - x_2$ ) and not on the relation between these entry points and the point of greatest sensitivity within the pupil, the contrast loss introduced by receptor disarray is independent of fringe orientation and would not generate a Campbell effect. Moreover, the loss of contrast implied by Eq. (B9) is expected to be slight. The disarray parameter is not known with precision, but if we adopt the values  $s = 1.56$  mm and  $\sigma = 0.32$  mm,<sup>21</sup> then the intensity-optimized effective contrast for a 2-mm separation between the interfering beams is greater than 99%.

## ACKNOWLEDGMENTS

This work was supported by National Institutes of Health grant EY01711 to D. I. A. MacLeod and by training grant GM08107 to M. J. McMahon. Part of this work was presented at the 2000 annual meeting of the Association for Research in Vision and Ophthalmology.<sup>34</sup>

Corresponding author M. J. McMahon can be reached by email at mm@mattmcmahon.com.

\*Present address, Department of Biological Structure, University of Washington, Box 357420, Seattle, Washington 98195-7420.

## REFERENCES

1. F. W. Campbell and D. G. Green, "Optical and retinal factors affecting visual resolution," *J. Physiol. (London)* **181**, 576–593 (1965).
2. D. R. Williams, D. H. Brainard, M. J. McMahon, and R. Navarro, "Double-pass and interferometric measures of the optical quality of the eye," *J. Opt. Soc. Am. A* **11**, 3123–3135 (1994).
3. F. W. Campbell, "A retinal acuity direction effect," *J. Physiol. (London)* **144**, 25P–26P (1958).
4. F. W. Campbell and A. H. Gregory, "The spatial resolving power of the human retina with oblique incidence," *J. Opt. Soc. Am.* **50**, 831 (1960).
5. J. M. Enoch, "Retinal directional resolution," in *Visual Science: Proceedings of the 1968 International Symposium*, J. R. Pierce and J. R. Levene, eds. (Indiana U. Press, Bloomington, Ind., 1971).
6. W. S. Stiles and B. H. Crawford, "The luminous efficiency of rays entering the eye pupil at different points," *Proc. R. Soc. London Ser. B* **112**, 428–450 (1933).
7. W. D. Wright and J. H. Nelson, "The relation between the apparent intensity of a beam of light and the angle at which the beam strikes the retina," *Proc. Phys. Soc. London* **48**, 401–405 (1936).
8. J. M. Enoch and F. L. Tobey, Jr., eds., *Vertebrate Photoreceptor Optics* (Springer-Verlag, Berlin, 1981).
9. D. G. Green, "Visual resolution when light enters the eye through different parts of the pupil," *J. Physiol. (London)* **190**, 583–593 (1967).
10. L. N. Thibos, A. Bradley, and D. L. Still, "Interferometric measurement of visual acuity and the effect of ocular chromatic aberration," *Appl. Opt.* **30**, 2079–2087 (1991).
11. A. van Meeteren and C. J. W. Dunnwald, "Image quality of the human eye for eccentric entrance pupils," *Vision Res.* **23**, 573–579 (1983).
12. P. Artal, S. Marcos, I. Iglesias, and D. G. Green, "Optical modulation transfer and contrast sensitivity with decentered small pupils in the human eye," *Vision Res.* **36**, 3575–3586 (1996).
13. G. Walsh and W. N. Charman, "The effect of pupil centration and diameter on ocular performance," *Vision Res.* **28**, 659–665 (1988).
14. B. Chen and W. Makous, "Light capture by human cones," *J. Physiol. (London)* **414**, 89–109 (1989).
15. C. Pask and A. Stacey, "Optical properties of retinal photoreceptors and the Campbell effect," *Vision Res.* **38**, 953–961 (1998).
16. W. Makous and J. Schnapf, "Two components of the Stiles–Crawford effect: cone aperture and disarray," presented at the annual meeting of the Association for Research in Vision and Ophthalmology, Sarasota, Fla., May 3–7, 1973.
17. J. Schnapf and W. Makous, "Individually adaptable optical channels in human retina," presented at the annual meeting of the Association for Research in Vision and Ophthalmology, Sarasota, Fla., April 25–29, 1974.
18. S. He and D. I. MacLeod, "Contrast-modulation flicker: dynamics and spatial resolution of the light adaptation process," *Vision Res.* **38**, 985–1000 (1998).
19. D. R. Williams, "Visibility of interference fringes near the resolution limit," *J. Opt. Soc. Am. A* **2**, 1087–1093 (1985).
20. J. Liang and D. R. Williams, "Aberrations and retinal image quality of the normal human eye," *J. Opt. Soc. Am. A* **14**, 2873–2883 (1997).
21. D. I. MacLeod, "Directionally selective light adaptation: a visual consequence of receptor disarray?" *Vision Res.* **14**, 369–378 (1974).
22. L. J. Bour and N. J. Lopes Cardozo, "On the birefringence of the living human eye," *Vision Res.* **21**, 1413–1421 (1981).
23. J. M. Enoch and W. S. Stiles, "The colour change of monochromatic light with retinal angle of incidence," *Opt. Acta (London)* **8**, 329–358 (1961).
24. M. Alpern, K. Kitahara, and R. Tamaki, "The dependence of the colour and brightness of a monochromatic light upon its angle of incidence on the retina," *J. Physiol. (London)* **338**, 651–668 (1983).
25. S. A. Klein, "Photoreceptor waveguides—a simple approach," in *Basic and Clinical Applications of Vision Science: The Professor Jay M. Enoch Festschrift Volume*, V. Lakshminarayanan, ed. (Kluwer Academic, Boston, Mass., 1997), pp. 37–41.

26. W. Wijngaard, "Theoretical consideration of optical interactions in an array of retinal receptors," in *Vertebrate Photoreceptor Optics*, J. M. Enoch and F. L. Tobey, Jr., eds. (Springer-Verlag, Berlin, 1981), pp. 301–323.
27. D. I. MacLeod, D. R. Williams, and W. Makous, "A visual nonlinearity fed by single cones," *Vision Res.* **32**, 347–363 (1992).
28. J. van de Kraats, T. T. Berendschot, and D. van Norren, "The pathways of light measured in fundus reflectometry," *Vision Res.* **36**, 2229–2247 (1996).
29. S. He and D. I. MacLeod, "Local luminance nonlinearity and receptor aliasing in the detection of high-frequency gratings," *J. Opt. Soc. Am. A* **13**, 1139–1151 (1996).
30. H. Metcalf, "Stiles–Crawford apodization," *J. Opt. Soc. Am.* **55**, 72–74 (1965).
31. P. Artal, "Incorporation of directional effects of the retina into computations of optical transfer functions of human eyes," *J. Opt. Soc. Am. A* **6**, 1941–1944 (1989).
32. A. Bradley and L. N. Thibos, "Modeling off-axis vision I: The optical effects of decentering visual targets or the eye's entrance pupil," in *Vision Models for Target Detection and Recognition: In Memory of Arthur Menendez*, A. R. Menendez and E. Peli, eds. (World Scientific, River Edge, N.J., 1995), pp. 313–337.
33. M. Born and E. Wolf, *Principles of Optics: Electromagnetic Theory of Propagation, Interference and Diffraction of Light*, 7th ed. (Cambridge U. Press, Cambridge, UK, 1999).
34. M. J. McMahon and D. I. A. MacLeod, "Visual resolution with obliquely incident light: retinal contrast losses," *Invest. Ophthalmol. Visual Sci. Suppl.* **41/4**, S100 (2000).