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Potential signal to accommodation from the Stiles–Crawford effect and ocular monochromatic aberrations

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Abstract

The purpose of this study is to determine if cues within the blurred retinal image due to the Stiles–Crawford (SC) effect and the eye's monochromatic aberrations can drive accommodation with a small pupil (3 mm) that is typical of bright photopic conditions.

The foveal, psychophysical SC function (17 min arc) and ocular monochromatic aberrations were measured in 21 visually normal adults. The retinal image of a 10.2 min arc disc was simulated for spherical defocus levels of –1 D, 0 D and +1 D in each of four conditions consisting of combinations of the presence or absence of the individual SC function and monochromatic aberrations with a 3 mm pupil. Accommodation was recorded in eleven participants as each viewed the simulations through a 0.75-mm pinhole.

The SC effect alone did not provide a significant cue to accommodation. Monochromatic aberrations provided a statistically significant but rather small cue to monocular accommodation.

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Keywords

ocular accommodation; Stiles–Crawford effect; cone photoreceptor; ocular aberration

1. Introduction

Human ocular accommodation responds to various aspects of the defocused retinal image (1). Blur from defocus alone carries no direct information about the required direction of accommodation, but it can be used to maximize image sharpness in a trial-and-error fashion (2). The low-frequency fluctuations of accommodation may be involved in extracting such a cue from the blurred retinal image (3). In addition, longitudinal chromatic aberration (LCA) provides an important signed cue to accommodation, which operates for stationary objects (4,5) and objects moving in depth (6,7). Kruger et al. (8) hypothesized the presence of a so-called ‘achromatic cue’, based on their finding that some individuals continue to accommodate in a Badal system even when prevented from using blur and LCA cues. In the present study, we consider two candidates for such a directional cue: the Stiles–Crawford effect and the monochromatic higher order aberrations.

Kruger et al. (9) proposed a geometrical optical model, based on an earlier model of Fincham’s (10), by which the Stiles–Crawford (SC) effect of the first kind (11,12) could provide a cue to accommodation (Figure 1). Kruger et al. (9) noted that the peak of the SC function is decentred from the entrance pupil centre in most eyes (13). Thus, rays that form opposite sides of the blur circle are absorbed more effectively or less effectively depending on their proximity in the entrance pupil plane to the peak of the SC function (Figure 1). This results in one side of the blur circle appearing brighter due to the decentred SC function (Figure 1). Importantly, the side that appears brighter changes between hyperopic and myopic defocus (Figure 1). Kruger et al. failed to show support for their model in a single-case experiment, but noted the need for more participants in future studies (9).

The natural monochromatic point spread function of the eye contains perceptual cues to focus direction (14). These cues could arise from ocular monochromatic aberrations (14). Experimental results (14–16) and theory (15) predict a role for the even aberration functions, but not the odd functions, in providing a directional cue. Even aberration functions are invariant under rotation of 180° about the eye’s line of sight. Examples are second-order defocus and spherical aberration. Odd functions are any functions that are not even. An example is coma. In the Zernike expansion, even Zernike orders contain only even functions and odd Zernike orders contain only odd functions. Recently, it has become possible to measure accommodation while manipulating or neutralizing experimentally the eye’s higher order aberrations. The earliest of these studies did not provide consensus on the role of higher order aberrations in accommodation (15,17,18), possibly due to small participant numbers. Recently, Chin et al. demonstrated that adaptive optics inversion of higher order aberrations could adversely effect accommodation, but that neutralization of aberrations had no significant effect (16).

Returning to the ‘achromatic cue’ of Kruger et al. (8), individuals who accommodated in that study in the absence of blur feedback and LCA cues, did so in the presence of a centred 3-mm artificial pupil. The effects of higher-order monochromatic aberrations on measures of visual performance are quite small for this pupil diameter (19,20), as are those of the SC effect (21, 22), tending to argue against a role for either cue. However, the key visual task for either cue, from monochromatic aberrations or the SC function, is to identify characteristic patterns in the retinal images of point objects and more complex objects (14). This task differs from a simple resolution or contrast detection task.

There is evidence (at high levels of defocus) for perceptibility of the SC effect in the point spread function (PSF) (23). In addition, humans have acute abilities to detect and recognize object asymmetries (24), including ones similar to those found in the PSF due to the SC function and the even aberration functions (25). Finally, directional cues in the natural PSF, possibly due to aberrations and the SC effect, provide a moderate level of perceptual discriminability between hyperopic and myopic defocus with a 3-mm pupil (14). This is true of both point and complex objects (14).

In the present study we tested the hypothesis that individual, characteristic changes in the intensity distribution of the blur-spread function due to the Stiles–Crawford effect and the monochromatic aberrations of the eye can, in isolation or unison, provide a signed cue to accommodation when the pupil is small (3 mm), typical of bright external viewing conditions.

2. Methods

2.1. Participants

Thirty-five individuals volunteered to participate in the study. Of these, nine were excluded due to poor corrected visual acuity in either eye. The remaining 26 individuals entered Stage 1 of the experiment to measure the SC function. They had no history of amblyopia, strabismus, or high uncorrected astigmatism as a child. They had no history of significant binocular vision anomalies, or of significant corneal injuries or surgery, or keratoconus.

Of those entering the SC function stage, one participant was excluded due to an unrelated red eye, and four participants dropped out of the study. Twenty-one participants completed the SC function stage of the study. Their characteristics are shown in Table 1, excluding visual acuity and objective refraction data for Participant 31, which were misplaced. Individuals then passed to Stage 2 of the study to measure accommodation.

Of those entering the accommodation stage, nine individuals dropped out. One was excluded due to accommodation spasm in the apparatus. Eleven subjects completed all stages of the study. Their characteristics are shown in Table 1.

This study followed the tenets of the Declaration of Helsinki. Informed consent was obtained from participants after an explanation of the nature of the study had been provided. Approval to conduct the study was given by the IRB of the SUNY State College of Optometry, the UHREC of Queensland University of Technology, and the IRB of the Southern California College of Optometry.

2.2. Design and overview

The foveal, psychophysical Stiles–Crawford function and the foveal higher order monochromatic aberrations were measured in each participant. These data were used within a finite schematic eye to simulate—for each participant individually the appearance of a foveal spot target with -1 D, 0 D, or $+1$ D of spherical defocus, in each of four conditions. Simulations were of an eye (1) with its SC effect and aberrations neutralized (control condition), (2) with the SC effect only, (3) with aberrations only, or (4) with the SC effect and aberrations present.

Subjects viewed these simulation images in a Badal optometer through a 0.75-mm pinhole pupil while their accommodation was monitored dynamically and objectively with an infrared recording optometer. The pinhole pupil ensures that the eye's natural SC function, aberrations, and accommodation response have negligible effects on the simulation target. The pinhole pupil also precludes trial-and-error feedback to accommodation. We have previously used this static open-loop method successfully to investigate the accommodation response to LCA cues (5). Some considerations in the use of this method, and arguments against the apodization filter

method (26) in this particular case, are discussed in a previous paper (27). Briefly, the apodization method uses an apodization filter, which is imaged optically at the entrance pupil to alter light transmittance by known amounts at each pupil location. In practice, inhomogeneities in the SC function across the retina, combined with miniature eye movements, make it difficult to provide complete correction of the SC function (27).

2.3. Apparatus

2.3.1. Stiles–Crawford apparatus—The Stiles–Crawford function was determined psychophysically with a custom Maxwellian view optical system (Figure 2). This system provides a 7.2° circular background field through Channel A, a superimposed flickering 17 minute arc test spot through Channel B, and a vernier target (3 min arc wide, with a central 84 min arc gap) to assist participant fixation through Channel C. The participant's view is shown in the inset of Figure 2. The background and test targets are illuminated with pseudomonochromatic light (552 nm, 12-nm bandwidth at half-height), obtained by filtering from radiometrically stabilized 100 W tungsten sources (Oriel Scientific, Bridgeport CT). The intensities of both targets can be changed using various filters in the light paths. A liquid crystal variable attenuator (Meadowlark Optics, Frederick CO) in Channel B was placed under computer control to allow psychometric determination of the flicker threshold, using custom software (28). Attenuation of light transmission by up to 3 log units was possible. The test spot was flickered as an 8 Hz temporal square wave and its exposure duration set to 2 sec by the variable attenuator.

The 0.47-mm diameter beam for the test spot passes through the centre of the eye's entrance pupil, but the location of the 0.52-mm diameter beam for the background field can be altered in the eye pupil using two calibrated motorized micro-positioning stages (Klinger Scientific, Garden City NY). This arrangement was chosen because in the alternative—in which the beam location of the test spot is altered—it could be argued that peripheral pupil aberrations affect the measured threshold of the spot because these aberrations manifest as small, lower-order defocus errors in the presence of a small artificial pupil (29).

The eye was illuminated with low-intensity infrared source (A1 in Figure 2; approximately 795–1000 nm) in Channel D. This source, in addition, provides a useful eye alignment landmark in the form of the Purkinje–Sanson I image. The eye's position is monitored using an infrared CCTV camera and monitor (Channel E). The participant rests at a chin and headrest mounted on a three-way stage. In a previous study using this stage, we found that eye alignment can be maintained within ± 0.06 mm during trials (30).

2.3.2. Aberrometer—The monochromatic aberrations of the eye were recorded with the COAS aberrometer (Wavefront Sciences Inc; Albuquerque, NM) (31). This instrument uses an infrared (850 nm) Hartmann–Shack wavefront sensor to sample the wavefront error in the entrance pupil at a period of 210 μ m, while the participant views an internal target. The COAS aberrometer was set to reference aberrations to the corneal vertex, and to correct longitudinal chromatic aberration with an arbitrary emmetropic wavelength of 552 nm. COAS software was set to fit Zernike polynomials (32) to each wavefront through the sixth Zernike order. Coefficients obtained with a natural pupil diameter larger than 4 mm were scaled mathematically to a standard aperture diameter of 4-mm, and an average of six readings obtained. (Later simulations with the schematic eye used these 4-mm data with a superimposed 3-mm entrance pupil.) COAS software provides conventional sphere, cylinder and axis from the wavefront using its 'Seidel method'; that is, by 'paraxial curvature matching' (33).

2.3.3. Badal optometer and infrared recording optometer—Targets were presented in non-Maxwellian view (34) within a Badal optometer (27), while accommodation was

recorded at 100 Hz with an infrared recording optometer (35). Both instruments have been described in detail previously, so only modifications are noted here. The Badal optometer was modified to allow direct imaging of the micro-mirror display of a modified Sharp Notevision projector (Mahwah, NJ) at the object plane of the Badal lens. Each pixel of the display subtends 0.46 min arc at the eye. Pseudo-monochromatic light of 552 nm (12-nm bandwidth) was provided in the main trials by an interference filter. The projector display initially exhibited a small spatial gradation of luminance across its full extent, which was corrected in software. In addition, a linear gamma function was obtained in software.

2.4. Procedures

In a preliminary session, a brief case history was gathered, and several tests were performed to assess the individual's suitability for participation in the study.

2.4.1. Monochromatic aberrations—An estimate of the left eye's objective refraction or objective contact lens over-refraction (for habitual contact lens wearers) was made with the COAS. Readings were made on the naked eye of habitual spectacle wearers and individuals who wore no correction. Readings were made with the contact lens in place for habitual contact lens wearers. The subject viewed a fixation target in the instrument and was instructed 'Look at the cross- target naturally, the same as you would if viewing it in a book or magazine. Look at various points near the centre of the target, but do not stare continuously in one place.' The COAS internal target was stepped distally in an attempt to relax accommodation, and then several readings of objective refraction were made. Readings with the most positive (least negative) sphere were taken as the objective refraction.

The internal COAS target was then set manually to provide an accommodative stimulus of 2 D. This level was chosen as a representative of a typical intermediate viewing distance (50 cm), such as when viewing a visual display terminal. We determined the eye's aberrations at a particular accommodation level because spherical aberration (Z_4^0) changes with accommodation (36). Changes in spherical aberration with accommodation did not invalidate the simulations because (1) the simulation represents the defocused image in the instant before accommodation has responded, and thus before spherical aberration has changed, and (2) the simulations were viewed through a pinhole pupil, and so were robust to changes in eye aberrations.

2.4.2. Stiles–Crawford function—Over several sessions (for a total of 8–12 hours), the two-dimensional SC function was sampled in the left eye using the custom Maxwellian apparatus. Spectacles and contact lenses were not worn in this stage of the study. The subject was first seated at the apparatus to locate the instrument on the eye's line of sight for a 3-mm pupil (32).

Measurements were made with the background target beam (nominal retinal illuminance of 2.86 log td) entering the pupil at each of 21 locations on a rectilinear 3 mm by 3 mm grid centred on the entrance pupil, with a period of 0.75 mm. (The points at the four corners of the grid were not tested.) In addition, trials were run for a central location of the background target beam in which the nominal background retinal illuminance was varied over a 0.98 log-unit range (2.18–3.16 log td). The order of conditions was randomized in blocks, with three repetitions of each condition. During each trial, the participant's task was to report the presence or absence of the flickering 8 Hz test spot (17 min arc), while the contrast of the spot was altered in a staircase (37). A 'free' trial (that is, target well above threshold) was provided every fourth trial, and the staircase continued for twelve reversals. Contrast stepped by 0.3 log units for the first four reversals, by 0.15 log units for the fifth and sixth reversals, and by 0.075 log units for the last six reversals. The threshold value was calculated from the last six reversals.

However, the calculated threshold was discarded if (1) the mean of the reversals differed from the median by greater than 0.08 log units, or (2) the psychometric function slope fell outside the range 2–16, or (3) the psychometric function lower asymptote, an indicator of false positives, was greater than 0.08.

Because all components of the target (background, test spot, fixation target) were imaged through pinhole pupils (Channel A, 0.52 mm; Channel B, 0.47 mm; Channel C, approx. 0.4 mm), the large depth of focus meant that accommodation was free to adopt its ‘pinhole-pupil’ open-loop state (38).

2.4.3. Psychometric analysis—The SC effect (η) at each point in the pupil was determined from the measured increment threshold. Our method of analysis is similar to that of Enoch and Hope’s (29), and a derivation is provided in the Appendix. Briefly, trials in which the background-target beam passed through the pupil centre were used to construct a threshold versus intensity (TVI) curve. Then, for any measured spot threshold, the corresponding perceived intensity of the background target could be determined using the TVI curve. This perceived background intensity is the nominal intensity weighted by the SC effect. Because the nominal intensity is known, then the SC effect at that point can be determined.

The experimental SC data were fit with a form that allows for axes of symmetry in the SC function at any meridian (39); namely,

$$\log \eta(x, y) = -\rho_1 x'^2 - \rho_2 y'^2 + z, \quad (1)$$

where x is the horizontal pupil location, y is the vertical pupil location, $x' = (x - x_0)\cos\alpha + (y - y_0)\sin\alpha$, and $y' = (y - y_0)\cos\alpha - (x - x_0)\sin\alpha$, and z is an arbitrary fitting constant. The centre of the SC function is located at point (x_0, y_0) . The base-10 directionalities (mm^{-2}) along the first and second principal meridians of the function are ρ_1 and ρ_2 , respectively. The angle (radians) by which the first principal meridian is rotated from the horizontal is α . Distances are measured in mm, and conventions for all distance and angles follow the ANSI standard (32). The function in Equation (1) was fit with the robust, iterative procedure described for the TVI function (Appendix). Points were discarded if their residuals were greater than three standard deviations from the mean. Points were also evaluated subjectively for their outlying status based on the spot threshold, SC function value, and the absolute size of the residual (in log units). Individual fits to Equation (1) were used as pupil apodizations in a finite eye to construct simulation targets for the accommodation trials (Section 2.4.4).

In addition to the form in Equation (1), we also fit a monomial form,

$$\log \eta = a + bx + cy + dx^2 + ey^2 + fxy, \quad (2)$$

to describe better the statistical properties of the SC function in the group. (Equation (1) has some undesirable properties, which are described in the Results section.) The function was fit with the robust, iterative procedure described for the TVI function, but outlier detection was different. Standardized residuals were calculated for each point in turn based on a fit to all other points but that one. Then, points with standardized residuals of 2.58 or greater were excluded.

2.4.4. Finite eye modelling—The current eye is based on the Indiana eye (40). Its paraxial power is +60 D, and its single refracting surface has a paraxial radius of curvature of +5.5713

mm. It is filled with the same refractive medium as the Indiana eye (40), but the axial length is altered to 22.238 mm so that the eye is emmetropic for the reference wavelength of 555 nm. The 3-mm aperture stop is placed at the vertex of the single refracting surface. The fovea is placed arbitrarily on the optical axis. The individual SC function is modelled as a pupil apodization (26); that is, the transmission of light at each point in the entrance pupil is described by the SC effect, rather than attempting to model the receptor waveguides in software. The individual monochromatic aberrations are modelled in software by advancing or retarding the wavefront by the correct amount across the exit pupil. For simplicity of modelling, only Zernike orders through the fifth (rather than the six collected) were used in the eye model. This number is adequate for a 3-mm pupil (20,41). In addition, the method of paraxial curvature matching (33) was used to simulate an eye fully corrected for its conventional ocular refraction. Thus, the current simulations preclude habitual, residual clinical astigmatism as a cue.

Numerical simulations were performed in the Zemax software (Zemax Development Corporation, Bellevue WA) to determine the on-axis PSF for 555-nm light. These simulations included diffractive effects, and were obtained by integration of Huygens wavelets. It is important to note that the finite eye was customized for the measured wavefront aberrations and SC function of each participant.

2.4.5. Accommodative stimulus construction—The target for simulations was a bright disc (183 td), 22 pixels in diameter, placed on a dark background. In the Badal system the disc subtends 10.2 min arc at the eye. The target was realized digitally as a bitmap image in 8-bit monochrome. Simulation targets were obtained by convolution of the disc target with the respective PSFs, using the ImageJ program (Wayne Rasband, National Institutes of Health).

A small disc target (10.2 min arc) was used to minimize known inhomogeneities in the SC effect across the foveal region (42–45). Importantly, dynamic accommodation in monochromatic light remains robust for spot targets down to 7–14 minutes arc (27).

A series of 12 animations were created in Director MX software (Macromedia, San Francisco) corresponding to the three defocus levels (that is, accommodative errors) of -1 D, 0 D, or $+1$ D. This was done for each of the four experimental conditions. Each 20.48 second animation consisted of an initial 10.24 seconds in which a fixation cross (4.6 min arc limb width, 40 td) appeared on a dark background, followed by one of the 12 simulation targets for the remaining 10.24 seconds. All animations were created at a secondary site, and coded by random names. In this way, the investigators at the primary site and the participants were masked to the identity of the stimuli.

2.4.6. Accommodation trials—If the participant habitually wore contact lenses, then these were worn during accommodation trials. Otherwise, refractive errors were corrected with trial lenses. The participant was seated in the apparatus, and the centre of their left-eye natural 3-mm entrance pupil aligned on the optical axis of the Badal system.

An individual calibration of infrared optometer (35) output (V) to accommodation (D) was obtained for each participant using bichromatic stigmatoscopy (5). Individuals were allowed to proceed with the remainder of the study only if they were able to perform the calibration procedure, and if their accommodative stimulus response function appeared normal. This function was required to display a monotonic increase in accommodation response as a function of accommodation stimulus, a slope greater than 0.5, and have values well fit by a linear equation ($r^2 > .9$).

In main trials, targets were viewed through a 552 nm interference filter (12-nm half-width), and through a 0.75-mm pupil conjugate, approximately, with the entrance pupil plane. This

pseudo-monochromatic light removes LCA as a cue to accommodation (46). The twelve 20.48-second animations were presented in blocked random order, for three trials per condition. Participants were told ‘concentrate your attention’ on the target, and were instructed to make small eye movements to different parts of the target. They were instructed to ‘keep the spot clear using the same amount of effort as when reading a book.’ Accommodation was recorded dynamically at 100 Hz.

Artefacts due to eye blinks were edited manually from the accommodation records (5). As in previous studies (5,30), the primary descriptor of the accommodation response to the simulations (denoted Δ) was calculated as the mean response to the simulation spot (final 10.24 seconds of animation) less the mean response to the fixation cross (first 10.24 seconds of animation). If the simulation is one of hyperopic defocus (posterior to the retina) indicating a need to increase accommodation, then an appropriate response is indicated by a positive value for Δ . If the simulation is one of myopic defocus (anterior to the retina) indicating a need to decrease accommodation, then an appropriate response is indicated by a negative value for Δ .

In each of the four conditions, the open loop pinhole-pupil gain of the response was calculated as the slope of Δ a function of simulated accommodation stimulus. The slopes were obtained in regression by minimizing the Huber function (47) rather than by least squares.

Planned comparisons were conducted between the control condition and each of the three other conditions. One-tailed tests were appropriate due to the directional hypothesis of a positive correlation between simulated stimulus and response. An unplanned comparison was made between the Aberration condition and SC and Aberration condition, using a two-tailed test.

3. Results

3.1. Stiles–Crawford function (Stage 1)

Twenty-one participants completed the first stage of the study to determine the foveal SC function. The statistical properties of the monomial coefficients of Equation (2) were first considered for their ability to provide simple summaries of the SC function in the population. The means and standard deviations of the coefficients are summarized in Table 2. Normality of each coefficient (a through f) could not be rejected with the Kolmogorov Smirnov test ($p > .2$) (48). The variance covariance matrix is provided in Table 3. (This matrix represents the variance of each variable, and the covariance between pairs of variables.) Of all the correlations between coefficients a through f , only two were significant; between c and e ($r = -.56$, $t = -2.96$, $p = .008$), and between d and e ($r = +.53$, $t = 2.73$, $p = .01$). Thus, the coefficients are not independent, but their interrelationships can be described by the variance covariance matrix. These properties allow for the construction of SC function pseudo-samples.

The monomial coefficients were converted to the intuitive parameters of Equation (1) for comparison to the literature, and to investigate their statistical properties. These are summarized in Table 4. The representation in Equation (1) has some unsatisfactory statistical properties. Generally, the SC function centre location (x_0 , y_0) becomes unstable as either or both directionality values (ρ_1 , ρ_2) approach zero. Accordingly, the observed x_0 and y_0 have very large ranges (Table 4), and neither is distributed normally by Kolmogorov–Smirnov test (x_0 , $D = 0.32$, $p < .05$; y_0 , $D = 0.35$, $p < .01$). Nevertheless, the other, linear parameters, z , ρ_1 , ρ_2 , and the mean rho-value, were normally distributed by Kolmogorov–Smirnov test ($p > .2$). Lack of normality of the x_0 and y_0 values makes the monomial form of Equation (2) more useful for describing the population.

The median location of the SC function centre is temporal and superior in the entrance pupil (Table 4). The current mean base-10 directionality of +0.032 is lower than found in the large

study by Applegate and Lakshminarayanan for a 4° central field (13), but is consistent with other reports of reduced directionality at the fovea (see Discussion).

Representative SC functions are shown in Figure 3. Interestingly, some foveal SC functions in the current study are quite flat, and some even have negative directionality values (Figure 3). These negative values form part of the respective normal distributions, and are not simply outliers (Figure 4). Based on the fitted distributions, 12% of mean ρ -values are negative, 33% of the ρ_1 values are negative, and 4% of the ρ_2 values are negative. (By convention here, ρ_2 is the more positive of the two ρ -values.) However, of the seven participants with negative rho-values, only one exhibited a SC function obviously different from the classical form (Figure 3, Participant 27); a toroid with areas of greater transmittance at the 2 and 7 o'clock positions. In other cases, the fitted rho-values seem to have captured flat functions (Participants 6, 9, 26), or graded functions with centres outside the pupil window (Participants 12, 20, 24).

The principal axis of the SC function, α , is not a linear variable but an axial circular variable (49). We wished to determine if this axis is distributed randomly in the population or perhaps has a tendency to lie along a particular meridian. The principal axis α has a circular mean of 1.02 rad (Table 4) (49), but the null hypothesis of a uniformly distributed circular distribution could not be rejected against the alternative of a distribution with a single mode ($Z = 0.645$, $p = .53$) (49). Thus, the principal axis of the SC function is distributed randomly in the population.

3.2. Accommodation responses (Stage 2)

3.2.1. Ocular monochromatic aberrations—Eleven participants completed both stages of the study. Zernike aberration coefficients for these individuals are listed in Table 5. The mean rms values were as follows: for all orders ($2 \leq n \leq 5$), 0.11 μm ; for the second order ($n = 2$), 0.08 μm ; for the higher orders ($3 \leq n \leq 5$), 0.07 μm ; for second order astigmatism ($n = 2$, $m \neq 0$), 0.02 μm ; for all even order terms except second-order defocus ($n = 2, 4$; excluding C_2^0), 0.03 μm ; for the even higher order (that is, for $n = 4$), 0.02 μm ; and for the odd higher orders ($n = 3, 5$), 0.06 μm .

3.2.2. Accommodation—The mean change in accommodation induced by each condition is summarized for the group in Figure 5. The responses in Figure 5 appear small. Only in the Aberration condition does a response appear, on visual inspection, to be in the correct direction to the simulations. The response level in the control condition provides an indication of response noise within the participant sample. The results of Figure 5 may be viewed in a condensed form by the open loop pinhole-pupil gain of the response, as shown in Figure 6.

The visual observations from Figures 5 and 6 were subjected to statistical analysis. Gain values in the SC condition were not significantly different from control ($t = -1.36$, $p = .10$). Gain values in the Aberration condition ($t = -2.08$, $p = .032$) and SC and Aberration condition ($t = -2.20$, $p = .026$) were significantly different from control, respectively. The responses in the Aberration condition and SC and Aberration were not significantly different ($t = 1.44$, $p = .18$). Together these results indicate that the SC effect does not provide a cue to accommodation, the monochromatic aberrations do provide a cue, and that the SC effect does not interact negatively with the cue provided by the aberrations.

Despite the statistically significant findings that were found, the differences in gain were rather small (Figure 6). Mean differences in gain were as follows: aberration condition less control condition, +0.14; SC and aberration condition less control condition, +0.06.

To determine whether individual variability in use of the putative SC cue was obscured by a group average in the t -test, a regression was performed on difference in accommodative gain

between control condition and SC condition as a function of pupil transmittance function (P) oddness. If the pupil transmittance function is even, then the SC effect cannot provide a cue to defocus direction. Greater oddness produces larger differences in the PSFs between myopic and hyperopic defocus (Figure 1). Perhaps individuals with very odd P respond to the simulations, while those with quite even P do not respond. Oddness was defined as the definite integral of $(P(x, y) - P(-x, -y))^2$ over the pupil area. Oddness of P did not predict the accommodation response to the SC condition ($r^2 = .001$, $F = 0.009$, $p = .92$).

To determine which, if any, of the monochromatic aberrations contributed most to the small, observed accommodation responses, the difference in gain between control condition and the aberration condition was regressed separately against various types of aberrations. Accommodation gain could not be predicted by total higher order rms aberration ($r^2 = .024$, $F = 0.22$, $p = .65$), higher order even rms aberration ($r^2 = .029$, $F = 0.27$, $p = .62$), higher order odd rms aberration ($r^2 = .016$, $F = 0.14$, $p = .71$), second-order astigmatism ($r^2 = .068$, $F = 0.66$, $p = .44$), or even rms aberration excluding second-order defocus ($r^2 = .007$, $F = 0.06$, $p = .81$).

4. Discussion

The main aim of the current study was to determine if either the SC function or the monochromatic aberrations of the eye can provide the ‘achromatic cue’ to accommodation postulated by Kruger et al. (8), which they found, empirically, to operate even with a 3-mm pupil. The current data do not support a role for the SC function at this pupil size. Even when considering individual differences in the potential strength of a cue from the SC function (as measured with SC function oddness), no role for the SC function emerged. However, monochromatic aberrations at a 3-mm pupil did provide a small but statistically significant cue to the accommodation response.

Gauging the practical significance of this study’s finding is not straightforward, as (1) the dependent measure is a pinhole-pupil ‘open loop’ ‘gain’ value that is specific to the particular static stimulus paradigm, and (2) because the relationship between open-loop and closed-loop gain is not linear. Nevertheless, some comparisons can be made with the cue provided by LCA in an earlier study of ours that used a similar stimulus paradigm (5).

Under closed-loop conditions, it is known that LCA provides an important stimulus to accommodation. Closed-loop gain to dynamic target motion typically falls by half when LCA is removed (6). In the study by Lee et al. (5), simulations of ± 1 D defocus in the presence of LCA led to pinhole-pupil ‘open-loop’ ‘gain’ values ranging between +0.04 and +0.84, with a mean of +0.41 gain units. By way of comparison, simulations of monochromatic aberrations in the present study led to ‘open-loop’ ‘gain’ values (in comparison to control) ranging between -0.22 and $+0.54$ with a mean of $+0.14$ gain units. By comparing these two studies, the ratio of mean monochromatic aberration gain to LCA gain is 0.34. Thus, the current study suggests a small role for monochromatic aberrations in the accommodation response even with a 3-mm pupil possibly providing a mechanism for Kruger et al.’s ‘achromatic cue’ (8). These findings augment an earlier one that monochromatic aberrations can provide a perceptual cue to defocus with a 3-mm pupil (14). However, the quantitative contribution of monochromatic aberrations to closed-loop gain cannot be ascertained from the current ‘open-loop’ design. The results from three closed-loop adaptive optics studies (16–18) suggest that neutralizing the monochromatic aberrations has no effect on accommodation in many individuals, but that reversing the aberrations leads to poor and misdirected accommodation responses.

Another advantage of closed-loop measures of accommodation with adaptive optics manipulation of aberrations is that it would be possible to use accommodative

microfluctuations as a further measure of the adequacy of the cues provided by monochromatic aberrations. This was not possible in the current 'open-loop' paradigm, because the small pupil (0.75 mm) itself leads to increases in the low frequency fluctuations of accommodation (50), and because the small pupil precludes normal negative feedback within the accommodative system. The adaptive optics method would allow such feedback, providing a way for low-frequency fluctuations in spherical defocus (3) to influence the response.

In the current study, we modelled the mean level of each monochromatic aberration term in an individual eye, but it is known that the aberrations exhibit fluctuations about the mean over time (51–53). Research is needed to determine how, in individual eyes, cues are extracted in the presence of aberrational temporal noise. In addition, the mean level of an aberration term may differ between eyes (54), and the temporal fluctuations of an aberration term may be poorly correlated between the two eyes (55). All studies to date (including the present one) were limited to monocular viewing. They cannot address how cues are combined binocularly in the presence of these inter-ocular differences.

The roles of the various types of monochromatic aberrations were not entirely as anticipated in the current study. Theoretical and experimental evidence favours the view that odd aberrations cannot provide a cue to accommodation (15), and supports a role for even aberrations (14–16). Nevertheless, we found that accommodation could not be predicted by the individual rms magnitudes of total higher order aberration, even higher order aberration, or odd higher order aberration. Perhaps, the perceptual cues to the sign of defocus are not well described by the gross metric of rms aberration. The ability to detect characteristic shapes in the blurred retinal image has more in character with letter or shape recognition. As suggested by Wilson et al. (14), current research on perception of azimuthal frequency patterns (25) may be helpful in this respect. (These patterns depart from a circle by the presence of lobes. For example, bi-lobed and tri-lobed azimuthal frequency patterns are similar to the PSFs in the presence of astigmatism and trefoil, respectively.)

In the current study, simulations were made to test Kruger et al.'s model (9) that characteristic changes in the photoreceptor representation of the *intensity distribution* of the PSF, due to the individual SC function, may provide a cue to accommodation. However, the current experimental results do not preclude other proposed models in which small groups of photoreceptors with waveguide properties extract information about the *wavefront vergence* at the retina (9).

The current study was limited to a 3-mm pupil, but could be repeated at other pupil sizes. Both the SC function and the monochromatic aberrations are more pronounced at larger pupils. In addition, the interactions between the two in producing particular shapes within the defocused PSF is likely to vary with pupil diameter, requiring continual adaptation of perceptual cue extraction.

It could be argued that the small effect sizes in the current study were not due to small or absent cues, but because of immediate down weighting of those cues in pinhole viewing. For example, from the study of depth perception it is known that visual and haptic cues are weighted adaptively by their individual reliability in a particular situation (56). Such processes can operate on time scales as short as the order of seconds (57,58). Along those lines, when an individual views a simulation of the effects the SC function or monochromatic aberrations in the current study, the pinhole viewing condition precludes the usual improvement in target clarity that occurs when a correct accommodation response is made. Perhaps, the individual learns quickly that responses to these cues are not helpful within the Badal optometer environment, and so adopts a largely tonic state of accommodation. Against this argument, LCA (an important cue in normal viewing) and monocular depth cues are both retained as cues

in pinhole-pupil viewing (5,59). Recently, Chin et al. used a closed loop adaptive optics paradigm which can address the issue of cue down weighting (16). Their trials were brief (4 s). Normal aberrations were always present in the first half of each trial, with adaptive optics manipulations introduced for the last half of each trial. In this way, the participant's exposure to the manipulated aberration environment was kept brief. While that study addresses cue weighting of aberrations, real-time correction of the SC function is a technological challenge due to the many inhomogeneities in the SC function across the fovea, combined with natural eye movements (27).

The current study provides the first large-sample description of the central foveal SC function to allow for principal axes other than at horizontal and vertical (39). The current data can be used to produce theoretical models of the SC function for future studies. Each described monomial coefficient (Table 2) is normally distributed. This, along with the variance covariance matrix of the coefficients (Table 3) allows for ready construction of SC function pseudo-samples. However, the current data were obtained over a 3-mm pupil, and should not be extrapolated to larger pupil sizes.

Although the current SC function directionality, for a 17-minute arc field, is lower than found in the large-sample study by Applegate and Lakshminarayanan for a 4° central field (13), it is consistent with other reports of reduced directionality at the central fovea (42,43,60,61). In addition, a novel finding of the current study is a significant minority of eyes with negative directionality values. These correspond to pupil efficiency that increases away from the centre of the function. These values are not simply outliers, as they form a significant portion of the normal distribution of each coefficient (Figure 4). The first explanation for these effects notes the small stimulus size of 17 min arc. Since individual cone photoreceptors at some retinal locations show disarray in their pointing directions (45), there may exist within the retinal image of a small target, small groups of cones. In this explanation, cones within a group have similar pointing directions, but adjacent groups have dissimilar pointing directions. This arrangement could produce a non-classical, bi-lobed SC function. However, disarray is thought to be minimal at the central fovea (60). A second explanation notes the combination of stimulus size, typical fixational eye movements, and known inhomogeneities in the location of the SC function peak over the central retina, particularly the radial inhomogeneity noted by Williams (44). In our previous analysis (27), we approximated Williams' (44) results as a 0.014 mm change in SC peak location per min arc diameter of retinal area covered by the target. For the current in-focus 17-min arc target, and for typical fixational eye movements traversing a diameter of 7.8–23.5 min arc, this inhomogeneity could account for a 0.35–0.57 mm change in peak location; insufficient to explain bi-lobed functions such as that of Participant 27 in Figure 3. A final explanation is based on visual analysis of the SC function plots (Figure 3). This suggests that negative rho- values may be capturing SC functions that are flat or have centres outside the 3-mm pupil diameter (Figure 3). Perhaps, these negative rho-values would not be observed with a larger pupil diameter. These speculations suggest that the aggregate, two-dimensional SC function could be revisited with finer sampling over a larger pupil to determine if other fitting functions can improve on the bivariate Gaussian form typically used for η .

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7. Appendix

We define the post-receptoral retinal illuminance (E') for any beam location in the pupil as the nominal retinal illuminance (E) weighted by the SC effect (η) at that point. Thus, for any target,

$$\log E'(x, y) = \log E + \log \eta(x, y). \quad (3)$$

Now initially, E can be known, but E' and η cannot. However, if at the pupil centre arbitrarily $\eta = 1.0$, then $\log E' = \log E$ for beams on the entrance pupil centre.

Interleaved randomly within the experimental trials, were trials in which both target beam and background beam passed through the entrance pupil centre, and for which the nominal background retinal illuminance (E) varied over a 0.98 log-unit range (2.18–3.16 log td). The purpose was to measure the Weber function for each individual. A *threshold versus intensity* (TVI) curve for flicker detection was obtained from these data, and fit by the form

$$\log \varepsilon'_s = \log a + \log(1 + 10^b), \quad (4)$$

with $b = \log E'_{BC} - \log k$. In these equations, ε'_s is the post-receptoral illuminance of the spot target at threshold, E'_{BC} is the post-receptoral illuminance of the background for a centred beam, a is the absolute threshold, and $\log k$ is the semi-saturation constant. This function approaches $\log a$ asymptotically as background illuminance decreases. As background illuminance increases, the instantaneous slope of the function approaches 1. This indicates Weber-like behaviour for the flicker detection task. The function was fit with an iterative procedure

(Generalized reduced gradient algorithm) embedded within a multi-start algorithm, and by minimizing the Huber function, a robust alternative to least squares minimization (47). Datum points with residuals greater than three standard deviations from the mean residual were discarded.

The TVI curve in Equation (4) may be expressed as a function of ε'_s with

$$\log E'_{BC} = \log[k(\varepsilon'_s - a)a^{-1}]. \quad (5)$$

If it can be shown that the TVI function of Equation (5) is independent of entry location of the background beam, then that function may be written in a general form as

$$\log E'_B(x, y) = \log[k(\varepsilon'_s(x, y) - a)a^{-1}]. \quad (6)$$

In a single participant, we tested this assumption by comparing the TVI at a central location of the background beam and at four other locations 1.5 mm above, below, nasal and temporal of the pupil centre. The slope of the TVI function did not vary significantly between these locations (p in the range 0.06–0.5). Finally, noting that $\varepsilon'_s = E_s$ (because the test beam is always centred) and substituting Equation (6) in Equation (3), the SC function at any point is given by

$$\log \eta(x, y) = \log\{k[\varepsilon'_s(x, y) - a]a^{-1}\} - \log E_B. \quad (7)$$

Figure 1.

Schematic representation of Kruger et al.'s model (9) of a cue to defocus from the Stiles–Crawford function. A left eye views a distant point object. Nasal (N) and temporal (T) directions are indicated. Myopic defocus is illustrated in panel (a) and hyperopic defocus in panel (b). The centre of the SC function is located nasally in the pupil at Point X. See the text for further explanation.

Figure 2.

Maxwellian view optical system for determination of Stiles–Crawford function. The five channels provide, respectively, the background target (a), the flickering test spot (b), a fixation target (c), infrared eye front illumination (d), eye front monitoring (e), and a calibrated pupil scale (g). The inset shows the participant's view of the target configuration, with a 1° scale bar. Key: **A1**, circular aperture (12.8 mm); **A2**, precision pinhole (600 μm); **A3**, pinhole aperture; **A4**, aperture (0.2 mm); **BS1–BS3**, pellicle beam splitter; **Ca**, infrared CCTV camera; **D1 D4**, diffuser; **F1, F3**, neutral density filter; **FP**, filter pair of infrared transmitting filter (795 nm cut on), and heat absorbing filter (trans. less than 1% beyond 1000 nm); **Gr**, precision graticule (1-mm spacing); **HM**, 45° hot mirror; **IF1, IF2**, interference filter 552 nm, 10 nm bandwidth; **L1, L6, L9**, condenser lenses in housings of light sources S1, SS1 and SS2, respectively; **L2**, lens; **L3**, precision achromatic lens (200 mm f. l.) as Badal lens; **L4, L5**, precision achromatic lens (+4.5 D); **L7**, precision achromatic lens; **L8**, precision achromatic lens (400 mm f.l.); **M1**, front surface mirror; **Mo**, CCTV video monitor; **S1, S2, S4**, incandescent light source; **SS1, SS2**, radiometrically stabilized 100 W tungsten source; **T1**, precision pinhole target (800 μm); **T2**, circular aperture target (25 mm); **T3**, vernier aperture target (0.18 mm wide, with 4.9 mm gap); **T4**, red green vernier target, made of 5 μm precision air slit, with Wratten filters described in Lee et al. (5); **VA**, liquid crystal variable attenuator; **xyS**, x–y precision stepping motor positioning stages; and **W2**, neutral density wheel.

Figure 3.

Examples of Stiles–Crawford functions. Each plot is for the left eye over a 3-mm diameter pupil. Each plot is normalized to 1.0 at its maximum. The contour increment is 0.05 transmittance, with a highest contour of 0.95. Circles indicate the function centre (where applicable), and the line indicates the principal axis of most negative (least positive) directionality. Participant 1 had the median of mean rho-values in the sample. Participant 7 had the maximum positive rho-value. Participants 6, 9, 12, 20, 24, 26 and 27 had negative rho-values in one or both principal axes.

Figure 4.
Cumulative frequency distributions of SC function base-10 directionality values, with respective best-fitting Gaussian distributions

Figure 5.

Mean change in accommodation induced by each simulation target for simulated defocus of -1 D, 0 D and +1 D ($N = 11$). Error bars indicate the standard error of the mean. See the text for details.

Figure 6.

Mean pinhole pupil 'open loop' accommodative 'gain' for each condition ($N = 11$). Error bars indicate the standard error of the mean. See the text for details.

Table 1

Subject characteristics

		Stage 1	Stage 2
		SC function	Accommodation
<i>N</i>		21	11
Source:		17	8
	Students		
	Investigators	4	3
Sex		Female, 16	Female, 8
		Male, 5	Male, 3
Age (years)		23.8 (21–29)	23.5 (21–29)
Visual acuity (log MAR)	RE	−0.03 (−0.10 – 0.00)	−0.03 (−0.10 – 0.00)
	LE	−0.02 (−0.10 – +0.02)	−0.02 (−0.10 – +0.02)
	Diff.	0.02 (0.00 – 0.10)	0.02 (0.00 – 0.10)
Objective refraction (LE)			
Best sphere (D)		−1.2 (−5.6 – +2.2)	−1.3 (−5.6 – +2.2)
Cylinder (D)		−0.4 (−1.7 – −0.1)	−0.4 (−1.0 – 0.1)

Listed are the mean and range of each parameter

Table 2

Coefficients of monomial description of the foveal Stiles–Crawford function

	<i>Coefficient</i>					
	<i>a</i>	<i>b</i>	<i>c</i>	<i>d</i>	<i>e</i>	<i>f</i>
Mean	+0.041 652	−0.029 962	+0.023 020	−0.032 809	−0.030 290	+0.010 259
Std. dev.	0.137 526	0.061 551	0.061 972	0.024 146	0.036 422	0.028 354

$N = 21$. The SC function was fit with the form of Equation (2); namely $\log \eta = a + bx + cy + dx^2 + ey^2 + fxy$. See the text for details.

Table 3

Variance covariance matrix ($\times 10^{-3}$) for coefficients of the monomial description of the foveal Stiles–Crawford function

<i>Coefficient</i>					
<i>a</i>	<i>b</i>	<i>c</i>	<i>d</i>	<i>e</i>	<i>f</i>
<i>a</i>	+18.013				
<i>b</i>	+2.468	+3.608			
<i>c</i>	+0.219	−1.511	+3.658		
<i>d</i>	−1.293	+0.079	−0.263	+0.555	
<i>e</i>	−1.589	+0.063	−1.209	+0.444	+1.263
<i>f</i>	−0.453	−0.520	+0.544	−0.003	−0.210
					+0.766

Details as for Table 1

Table 4
Coefficients of the ‘principal axes’ description of the foveal Stiles–Crawford function

<i>Coefficient</i>						
	<i>z</i>	<i>x</i> ₀	<i>y</i> ₀	<i>p</i> ₁	<i>p</i> ₂	<i>α</i> [*]
Mean	+0.042	−0.261	−2.015	+0.012	+0.051	+1.024
Std.						
dev.	0.138	5.802	7.914	0.028	0.028	1.230
Minimum	−0.212	−16.693	−34.411	−0.028	−0.003	
Quartile						
1	−0.022	−0.416	−0.465	−0.013	+0.028	
Median	+0.008	−0.138	+0.142	+0.018	+0.051	
Quartile						
3	+0.095	+0.456	+0.593	+0.028	+0.069	
Maximum	+0.505	+17.512	+4.619	+0.073	+0.100	

N = 21. The SC function was fit with the form of Equation (1). See the text for details.

* Given for *α* are the circular mean and circular standard deviation (49).

Table 5

Zernike aberration coefficients for a 3-mm pupil after pseudo-subjective refraction

Coefficient (n, m)	Aberration Mean	(μm)
		Std.
		dev.
2, -2	-0.004	0.012
2, 0	-0.070	0.063
2, +2	-0.002	0.019
3, -3	-0.024	0.033
3, -1	+0.013	0.035
3, +1	-0.008	0.024
3, +3	-0.004	0.027
4, -4	-0.000	0.005
4, -2	-0.001	0.003
4, 0	-0.018	0.016
4, +2	-0.000	0.005
4, +4	-0.001	0.004
5, -5	-0.000	0.003
5, -3	+0.001	0.003
5, -1	-0.000	0.003
5, +1	+0.001	0.002
5, +3	-0.000	0.002
5, +5	+0.001	0.002

$N = 11$. Clinical spherical and cylindrical refractive errors were set to zero by the method of paraxial curvature matching (33).