Accommodation to wavefront vergence: adapting ‘averse channels’

by

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ABSTRACT

Purpose: Accommodation responds to wavefront vergence, but the mechanisms for vergence detection are unknown. One possibility is that accommodation responds to the angle of incidence of light at edges blurred by defocus. ‘Averse channels’ that sample light from opposite sides of the pupil were hypothesized by Makous (1968, 1977). Makous named the phenomenon a “transient” Stiles-Crawford effect because he found that there was a reduction in sensitivity to light entering one side of the pupil that lasts for a short period of time. Such ‘averse channels’ that sample modulation across the pupil are a possible mechanism for detecting the sign of defocus. The purpose of the present experiment is to determine whether such ‘averse channels’ can operate separately of each other to specify the sign of defocus for accommodation.

Method: Accommodation was monitored continuously while subjects viewed a vertical monochromatic (548nm) luminance edge (1.0 contrast) that stepped either to a far or near direction in a Badal optometer. Various levels of adapting field were used to reduce the contrast of the edge (0.48, 0.36, 0.26, or 0.17 contrast) to determine the contrast threshold for accommodation. In a final experiment, an adapting field entered the eye through the nasal or temporal side of the pupil, to selectively adapt nasally or temporally tuned ‘channels’, while the target stepped randomly toward or away from the eye. The orientation of the vertical edge was either bright on the right side or bright on the left.

Results: In a preliminary experiment, only five out of twenty-six subjects showed reliable and consistent responses, with gains >0.5 for both positive and negative step change in vergence. The contrast threshold for accommodation to step changes in target vergence was approximately 26%. Data from three subjects who accommodated reliably to both directions of step changes in vergence do not support the claim that ‘channels’ sample light separately from opposite sides of the pupil to determine the sign of defocus.

Conclusion: Potential factors that account for the poor accommodative responses in the present study include: 1) the target was illuminated with monochromatic light, 2) the target was a simplified stimulus in which the blur was in only one direction (one spatial phase), 3) the target was viewed monocularly, 4) the 3mm artificial pupil increased depth-of-focus and removed the normal dynamic behavior of the pupil, 5) our subjects were untrained. The negative results suggest alternate hypotheses: 1) ‘averse channels’ work in conjunction with each other, not separately, to detect vergence, 2) ‘averse channels’ can function separately to detect vergence, but the signal was undetectable using the current method, and 3) ‘averse channels’ do not mediate vergence detection.

Key words: accommodation, averse channels, blur, defocus, wavefront vergence
INTRODUCTION

Accommodation refers to the temporary change in the refractive state of the eye that provides clear focused vision of objects at different distances. The basic drive for accommodation is the blur of the out-of-focus image (defocus-blur) due to the changes of the vergence of the incident light. This response of the accommodative mechanism to the changes of the vergence of the incident light occurs automatically without conscious awareness of the blur (Fincham, 1951). Research on the “reflexive” accommodation response to defocus has centered on determining which aspects of a defocused retinal image provides the direction of defocus to drive the accommodation response.

Fincham (1951) was the first to propose that odd-error stimuli derived from longitudinal chromatic aberration (LCA) and the angle of incidence of light provide directional cues for accommodation. As a result of LCA short-wavelength light (e.g. 420nm) comes to focus further forward in the eye than long-wavelength light (e.g. 580nm) and the difference in the refractive states of these two wavelengths is approximately 1.33D (Bedford and Wyszecki, 1957). When the image is out-of-focus, LCA produces color fringes at the edges of the image, especially for spatial frequencies above 1 cycle per degree.

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Figure 1 shows that under-accommodation is characterized by higher contrast for short-wavelength components of the retinal image than the long-wavelength components, which produces a red fringe; whereas over-accommodation is characterized by higher contrast for long-wavelength component than short-wavelength component, which produces a blue fringe. Thus
the relative contrast of wavelength components of the retinal image specifies focus behind or in front of the retina, and this acts as a directional cue for accommodation, and a signal for perception of relative depth order (Nguyen, Howard & Allison, 2007).

Longitudinal chromatic aberration is not the only stimulus for accommodation, since blur of the out-of-focus retinal image can drive accommodation in the absence of LCA. However defocus-blur is an “even-error” signal, which has only magnitude but no sign, thus feedback from changes in accommodation is essential in this standard model of accommodation (Stark and Takahashi, 1965). Nevertheless, subjects can accommodate without feedback from changes in blur in the absence of LCA (Kruger, Mathews, Katz, Aggarwala, and Nowbosting, 1997) and this indicates the presence of an unknown odd-error achromatic signal to accommodation. Such a signal is potentially provided by blur from asymmetric monochromatic aberrations of the eye or from cone receptor directionality.

Monochromatic aberrations that exist in the human eye give rise to different appearances of the point spread functions (PSF) or blur circles, depending on whether the defocus is positive or negative (Wilson, Decker, and Austin, 2002). Even-order aberrations like astigmatism and spherical aberration give rise to odd-error blur cues when combined with defocus, which indicate whether the light is focused in front of or behind the retina. The ability to discriminate the differences in shape or skewing of the PSF for myopic and hyperopic defocus varies among individuals, but in general discrimination increases as the monochromatic aberrations increase (Wilson et al., 2002). Nevertheless, three recent investigations suggest that most subjects do not use higher-order monochromatic aberrations to determine the sign of defocus for accommodation (Chen, Kruger, Hofer, Singer, and Williams, 2006; Lopez-Gil, Rucker, Stark, Badar, Borgovan, Burke, and Kruger, 2006; Stark, Kruger, Rucker, Schmidt, Rutman, Borgovan, Burke, Badar,
and Shah, ARVO 2007). So blur of the retinal image might not be the only source of the signed vergence signal.

Cone receptors in human eyes generally all point towards the center of the entrance pupil. Light rays that enter near the center of the pupil are parallel to the axes of the retinal receptors, and are more effective than rays entering near the margin of the pupil (Stiles and Crawford, 1933). Studies have shown that the peak of the Stiles-Crawford function is often decentered towards one side of the pupil by a small amount (0.5mm), usually the nasal side (Stiles and Crawford, 1933; Enoch, 1957; Applegate, Meade, and Sorenson, 1987; Gorrand and Delori, 1995), and such an effect results in asymmetry in the retinal (neural) representation of blurred points and edges.

In figure 2 all the cone receptors are facing the left side of the pupil (dotted lines) and the blurred PSF on the retina is symmetrical. The symmetrical blur circle or PSF can be modeled as a Gaussian distribution of light. However, the retinal representation of the PSF (after including the Stiles-Crawford effect) has the peak of the PSF skewed to the left side for under-accommodation and to the right side for over-accommodation. The direction of asymmetrical PSFs specifies the direction of the defocus. However two recent experiments suggest that such decenteration of the Stiles-Crawford effect does not provide the sign of defocus for accommodation (Kruger, Lopez-Gil, and Stark, 2001; Stark et al., 2007).

Another potential mechanism for detecting the sign of defocus may be separate ‘channels’ or ‘pools’ that sample light from opposite sides of the pupil. Markous (1968; 1977)
described a transient Stiles-Crawford effect and suggested that ‘averse channels’ sample light from opposite sides of the pupil. He named this phenomenon ‘transient’ Stiles-Crawford effect because he found that there was a reduction in sensitivity to light entering one side of the pupil that lasts for a short period of time. The adaptation of the ‘channel’ that samples from one side of the pupil is transient in that the adaptation lasts for only a short period of time. Theoretical analysis by Sansbury, Zacks, and Nachmias (1974) supported Makous’ conclusions. By sampling light from opposite sides of the pupil as blurred edges move across the retina, such ‘averse channels’ could detect the vergence of light, and thus provide a directional cue to accommodation. However this hypothesis has never been tested. In this study, theoretical nasally or temporally tuned ‘channels’ will be adapted selectively with an adapting field entering the eye either through nasal or temporal side of the pupil, and the accommodation target will step randomly towards or away from the eye. If the ‘channels’ operate somewhat separately from each other to detect the angle of incidence of light at blurred edges, an adapting field from one side of the pupil should reduce the ability of the system to detect either positive or negative vergence depending on the orientation of the blurred edge (bright on the right or bright on the left) and the angle of incidence of the adapting field (nasal or temporal).

---------- Insert Figure 3 approximately here ----------

Figure 3 (left) illustrates that the marginal rays from the edges of the pupil reach the retina uncrossed in hyperopic defocus. For viewing a bright left blurred edge (bright on the left side and dark on the right), light entering the nasal side of the pupil forms the dark nasal margin of the blurred edge spread-function on the retina (solid ray). Light entering the temporal side of
the pupil does not contribute to the dark margin of the blurred edge (dashed ray). Conversely the rays cross before reaching the retina in myopic defocus, so that light entering the temporal side of the pupil forms the dark margin of the blur (solid ray). Figure 3 illustrates that the angle of incidence of light forming the blurred margin of the edge together with the spatial phase of the edge (dark/bright or bright/dark) specifies the sign of defocus. In the present experiment a fiber-optic light source and a small artificial pupil are imaged in the plane of the subject’s natural pupil to provide an adapting field for channels tuned to the nasal or temporal side of pupil (see figure 4a).

--------------- Insert Figure 4a approximately here ------------

An adapting field entering one side of pupil should reduce the sensitivity of the channel tuned to the corresponding side of the pupil, but not the channel tuned to the opposite side of the pupil. For the bright left target orientation illustrated in figure 3, an adapting field entering the temporal side of the pupil should impair the accommodation response in hyperopic defocus but not in myopic defocus. By taking into account the target orientation and the angle of incidence of the adapting field, it should be possible to predict whether or not the adapting field would reduce sensitivity to myopic or hyperopic defocus and impair the accommodation responses.

**METHODS**

**Apparatus**

The apparatus included an infrared recording optometer and associated Badal stimulus system. The infrared optometer measured dynamic changes in the power (spherical wavefront
curvature or refractive state) across the vertical meridian of the eye (Kruger, 1979). The optometer is sensitive to accommodative changes over a range of 6 D, resolution is better than one-tenth of a diopter, and the cut-off frequency is 10 Hz. Position of the subject was maintained during trials with an adjustable chin and headrest while alignment of the subject’s pupil to the axis of the Badal system was monitored continuously by the investigator viewing an image of the pupil and Purkinje image 1 with an infrared camera and video monitor.

The Badal optical system allowed the dioptric stimulus for accommodation (wavefront vergence) to be varied in steps without changing the visual angle subtended by the target (Ogle, 1968). The twin-channel optical system included a target channel with a video projector that provided the target, and an adapting channel with a fiber-optic source that provided a uniform adapting field of light that covered the entire target. The adapting field provided a “veiling luminance” that reduced the contrast of the target. Figure 4 is a schematic of the Badal stimulus optometer, including a modified Sharp M20X video projector for providing the target, and a moveable fiber-optic light source for providing the adapting field or “wash.”

---------- Insert Figure 4b approximately here ----------

The target was a vertical monochromatic luminance edge displayed from computer on the digital micro-mirror display (DMD) in a video projector. Light from the projector was filtered by neutral density filters and an interference filter (548nm with 10 nm bandwidth), then reflected by a front surface mirror and collimated by lens 1. Collimated light from the target passed through a 3mm artificial pupil and was focused by lens 2 in the focal plane of Badal lens 3. Motion of prism 1 (as shown by the arrow) moved the target image towards or away from lens 3, thus
altering the dioptric stimulus to accommodation. The subject viewed the image of the target in Badal lens 3. A blurred field stop (not shown) was positioned beyond optical infinity and reduced the field of view to 4 degrees. The blurred field of view and vertical edge (bright on left and bright on right side) are shown at the top of figure 4b.

The fiber-optic light source could be moved laterally to provide an adapting field or “wash” that could be superimposed over the target image to reduce the contrast of the edge. Light from the fiber-optic source (dashed rays) was diffused (ground glass) and filtered (interference filter; 548 nm), collimated by lens L2 and focused in the pupil plane by lens L3. The diameter of the adapting source was 0.75 mm when imaged in the subject’s pupil plane. Maximum retinal illumination from the adapting field was a uniform 322 trolands covering the entire target. Neutral density filters were used to adjust the retinal illumination provided by the adapting field, thus producing various levels of target contrast. The fiber-optic source could be moved laterally to position the image of the small adapting source at the center of the subject’s pupil, or 1.5 mm nasal or 1.5 mm temporal to the pupil center. Thus the adapting field entered the pupil through a small “artificial pupil” positioned centrally, nasally or temporally while light from the target (edge) entered through a larger 3 mm artificial pupil. The bottom of figure 4b shows the blurred field of view and vertical edge when the "wash" was superimposed on the bipartite field.

The 3 mm artificial pupil minimized higher order monochromatic aberrations of the eye (Liang and Williams, 1997). The target was illuminated with monochromatic light to eliminate chromatic cues for accommodation from longitudinal chromatic aberration. The accommodation stimulus (wavefront vergence) was controlled by computer software that moved prism 1 along the optical axis of the Badal system, as shown by the arrows in Figure 4a.
Photometry

The target was a high-contrast vertical luminance edge. The edge bisected a circular visual field that subtended 4 degrees at the eye. Photometry was performed through the Badal stimulus system using Westheimer’s method and a Pritchard photometer and to match the luminance of the target to the luminance of the wash. The bright and dark sides of the target provided retinal illumination of 135 and zero trolands. Neutral density filters were applied to the fiber-optic source to provide adapting fields with approximately one times, two times, three times, or four times the retinal illumination of the bright side of the target edge. Resulting Michelson contrasts \( \frac{L_{\text{max}} - L_{\text{min}}}{L_{\text{max}} + L_{\text{min}}} \) for the target edge were 100%, 48.3%, 36.3%, 25.8%, and 17.4%.

Subjects

In the present experiment, monochromatic light was used to eliminate chromatic cues for accommodation from longitudinal chromatic aberration. However some subjects accommodate poorly and some cannot accommodate at all in monochromatic light (Fincham, 1951; Kruger, Mathews, Aggarwala, and Sanchez, 1993). Therefore a “preliminary experiment” was run to determine each subject’s ability to accommodate in monochromatic light. Twenty eight subjects, students from SUNY State College of Optometry presented and only four subjects (S10, S18, S24, and S28) showed reliable accommodation responses to both near and far step changes in target distance under the conditions of the experiment. These four subjects participated in a second “contrast threshold experiment” to determine the threshold spatial contrast needed for a step change in accommodation. Finally three of these subjects participated in a third “averse channels experiment.” The subjects ranged in age from 24 to 27 years old. For subjects who
showed refractive errors, spherical refractive error ranged from -2.50D to -7.50D and astigmatism ranged from -0.37D to -1.75D. Subjects with spectacle or ocular corrections had 20/20 Snellen visual acuity, they were free of ocular pathology, had sufficient amplitude of accommodation for the experiment and normal color vision (Nagel anomaloscope). All subjects gave informed consent and were paid for participation. The study was approved by the Institutional Review Board of SUNY College of Optometry (IRB).
**Procedures**

Calibration

Each subject’s eye was calibrated by measuring accommodative responses subjectively and objectively at the same time over a range of stimulus distances. For the subjective measurements, the subject viewed red (642 nm) and blue-green (500 nm) vernier lines superimposed on a back-illuminated, high contrast, white Maltese cross at several different accommodative stimulus levels (e.g. 1.00, 2.00, 3.00, and 4.00 D). At each stimulus level, the subject adjusted the distance of the red and blue lines until both appeared equally blurred. An objective measurement of optometer voltage output was recorded simultaneously. During the objective measurement, the subject was instructed to keep the center of the white Maltese cross clear while the cross was positioned at 0, 1, 2, 3, and 4 D of accommodative demand. A linear equation relating accommodation response to infrared optometer output over the range measured was computed with principle axis regression (Sokal and Rohlf, 1981). All 28 subjects showed linear regression above 0.9 and were enrolled in Part I of the experiment.

Part I – Preliminary experiment

The subject’s left eye was tested and the right eye was patched. Trial lenses were placed in front of the left eye to correct for ametropia. Ten trials were run to examine subjects’ accommodation responses to step stimuli. The target was a vertical monochromatic (548nm) luminance edge in a “bright-left” orientation (bright on the left side of a vertical border, and dark on the right side). The subject was instructed to fixate at the center of the vertical edge and to “keep the vertical edge clear with about as much effort as if you are reading a book.” The room
was darkened and the subject was unable to see the surrounding environment while viewing the target during each trial. The trial lasted 10.24 s (see Fig 5).

---------- Insert Figure 5 approximately here ----------

The target remained stationary at -2 D (50 cms from the eye) for the first 5.12 s of the trial and then stepped +1 D or -1 D randomly towards or away from the eye and remained stationary for the final 5.12 s. Standard signal processing procedures were used to remove artifacts as a result of blinking in each 10.24 seconds trial (Lee et al., 1999). Two 2.56 s periods, before and after the step, were used to calculate the response gain (see Figure 5). Gain is stimulus step amplitude (1 D) divided by accommodative response amplitude. An average gain of 0.5 was used as the cut-off point for including subjects in the next part of the study. For some subjects, trials were repeated with a white Maltese cross target to examine the effects of chromatic aberration and target form.

Part II – Contrast Control Experiment

Previous experiments show that accommodative gain decreases when the contrast is reduced to between 5% and 20% (Bour, 1987; Ciuffreda and Rumpf, 1985; Mathews and Kruger, 1989), however the contrast threshold for accommodation to step changes in target vergence in monochromatic light is not clear. This experiment aims to determine the threshold contrast for accommodation to step changes in target distance, so that the threshold luminance of the wash can be selected for the subsequent experiment. The target, step stimulus, trial length, and procedures were the same as Part I. In addition, the fiber-optic source was used to
superimpose different wash luminances over the entire vertical edge target to reduce the edge contrast from 100% to 48%, 36%, 26%, and 17%. The ‘veiling luminance’ from the fiber-optic source entered the eye through a moveable pinhole pupil (0.75 mm diameter) that was positioned at the center of the subject’s natural pupil. There were ten conditions and six trials of each condition performed in six separate blocks. Conditions were randomized and there was a minimum of one minute of rest between trials during which subjects were allowed to look around in the dark room. Two 2.56 s periods, before and after the step, were used to calculate gain, which was plotted as a function of target contrast.

Part III- Averse Channels Experiment

In the previous experiment (above), subjects had the tendency to over-accommodate when the adapting field was introduced. This initial over-accommodation to the appearance of the wash lasted for several seconds, and could give a misconception that the subject actually accommodated to the step stimuli. To solve this problem, trial duration was doubled from 10.24 sec to 20.48 sec. The target remained stationary at 2 D for the first 15.36 sec of the trial and then stepped 1 D randomly towards or away from the eye and remained stationary for the final 5.12 sec. From the results of previous experiment, the minimum contrast for accommodation to step changes in target distance was estimated to be approximately 26%. Thus the target contrast was reduced to 26% for the final adaptation trials. The adapting field entered at the nasal or temporal side of the pupil to adapt one of the proposed ‘averse channels.’ There also were control trials in which there was no adapting field and where contrast was 100%. The vertical target edge was presented in two orientations: bright left (bright on the left side) and bright right (bright on the right side). Two defocus conditions (myopic or hyperopic), three adaptation conditions (nasal,
temporal, or none), and two target orientations (bright left or bright right) gave 12 conditions overall. There were six trials of each condition performed in six separate blocks. Conditions were randomized and there was a minimum of one minute of rest between trials during which subjects were allowed to look around in the dark room. For each trial, 2.56 sec periods before the step (12.80 to 15.36 sec) and after the step (17.92 to 20.48 sec) were used to calculate the response gain.

Stiles-Crawford effect measurements

The threshold for detecting light varies as a function of pupil entry position, producing the Stiles-Crawford effect of the first kind. The peak position of the Stiles-Crawford effect usually is decentered nasally by a small amount (0.5 mm) but in some subjects the peak is decentered temporally. Thus a decentered Stiles-Crawford effect (either nasal or temporal) might influence the effect of the adapting source in the “averse channels” experiment. To avoid the problem, each subject’s Stiles-Crawford function (Type 1) was measured, and neutral density filters were used to compensate for any asymmetry in sensitivity to nasally and temporally entering light (Kruger, Stark, Swanson, Rutman, Hu, Borgovan, Burke, and Shah, ARVO 2007).

A twin-channel Maxwellian view optical system was used to measure the threshold luminance of a small target on a background field. The target was a flickering spot (548 nm with 12 nm bandwidth; 10 min arc; 8 Hz) superimposed on a larger uniform circular field (548 nm with 12 nm bandwidth; 7 deg). During measurements of threshold, the beam for the flickering target always passed through the center of the subject’s entrance pupil. The beam for the background passed through each of 21 pupil locations on a square sampling grid with a period of 0.75 mm. A two-alternative temporal forced choice procedure was used to find the threshold for
detecting the target against the background. Three threshold measures were made at each pupillary position giving 75 measures per eye. Data were fit with the numerically stable monomial form \( \log_{10} h = a + bx + cy + dx^2 + ey^2 + fxy \), where \( h \) is the pupil transmittance, and \( x \) and \( y \) are the pupil coordinates.

The measurements of thresholds that were made 1.5 mm nasal and 1.5 mm temporal to the pupil center were used in the final experiment to “correct” for the subject’s S-C function. During some trials, neutral density filters were placed in front of the fiber-optic source to reduce the luminance of the wash and thus compensate for any asymmetry of the subject’s S-C function.

**Data Analysis**

Blinks were edited manually from the accommodation records before analysis, and replaced with a linear interpolation between pre- and post-blink points. Trials were excluded from analysis if they contained more than 12% of blink affected data. Gains were calculated for accommodation to the step targets in the three experiments. Gain is the amplitude of the response divided by the stimulus amplitude.

Univariate analysis of variance for repeated measures ANOVA with systematic permutation was run on the gain data for the three subjects who completed the Averse Channels Experiment (Edgington, 1995). These powerful non-parametric procedures are valid for use in single subject designs (Edgington, 1995). For each subject four comparisons were made. For each combination of step stimulus (myopic or hyperopic defocus) and target orientation (bright-left or bright-right) a comparison was made between no wash, nasal wash, and temporal wash conditions.
RESULTS

Part I-Preliminary Experiment

Figure 6 shows the accommodation traces from two trials for S10 illustrating the sort of responses to step changes that we were looking for in the study. In figure 6b, S10 under-accommodated initially, but then accommodated accurately to the stimulus after two seconds of the trial and correctly decreased her accommodation when the target stepped to the far position. Figure 7 shows mean accommodation gains for the preliminary trials for twenty-six subjects.

Most subjects showed differences in accommodation behavior between trials, resulting in high standard deviations. Negative gains indicate that the subjects accommodated to the opposite direction from the stimulus. An average cut-off gain of 0.5 was used for including subjects in the subsequent experiment. Twenty-six subjects presented and five had gains >0.5 for both near and far steps. S3, S10, S18, S23, and S24, indicated with asterisks in the figure 7, showed gains higher than 0.5 to both step stimuli and they were recruited for the subsequent contrast control experiment (below). S18 accommodated accurately to the far step in four out of five trials, but accommodated in the wrong direction in one trial, and this unusual response reduced her averaged gain below 0.5. Since she showed consistent and stable responses to step far stimulus in four out of five trials, she was included in the study. Notice the averaged gains of S11, S14,
and S15 met the cut-off gain criterion, but they were excluded from the study due to their unstable accommodation. Figure 8 demonstrates the time courses of accommodation responses for S11, S15, and S16.

In figure 8a, S11 showed an initial over-accommodation that resulted in a gain higher than 0.5 and an incorrect impression of the subject’s ability to respond to step changes. Figure 8b and 8c illustrate that the data from both S15 and S16 were noisy with low frequency oscillations of accommodation.

Many subjects showed highly variable accommodation responses between trials. To minimize the effect of unusual responses, median gains were computed (Figure 9) instead of means (Figure 7). S18 had consistent gains in four out of five trials and a median gain to the far step that is higher than 0.5 (Figure 9) while the mean gain is lower (Figure 7). In figure 9, S7 had median gains to both step changes that were higher than the cut-off. But when the data trace of each individual trial was examined, no response to the far step stimulus was evident. Figure 10 shows the traces of two trials for this subject (S7).
It is clear that S7 showed very different behaviors of accommodation between trials; she over accommodated in figure 10a, but under-accommodated initially in figure 10b. And in figure 10b, accommodation increased before the target stepped near. Thus the gains in figures 7 and 9 can be misleading, and S7 was not included in the final experiment.

Part II – Contrast Control Experiment

Although S3 showed fairly reliable responses to step changes in the preliminary experiment, in the contrast control experiment, she over-accommodated substantially (1 to 5D) in the conditions without an adapting field (figure 11a), and when the ‘wash’ was applied to reduce the contrast of the vertical edge, S3 over-accommodated significantly beyond the target distance (figure 11b) particularly at the lower contrasts. Thus S3 was excluded due to unstable and excessive over-accommodation.

Figure 12 showed the results of contrast control experiment for Subjects S10, 18, 23, and 24. For S10, decreased target contrast did not affect the accommodative gains for step far stimuli. But the increased standard deviation indicated that the accommodative responses became more variable when the target contrast was decreased down to 26% and 17% (see figure 12a).
For step near stimulus, S10’s accommodative gains were greatly affected when the target contrast was reduced to 36% and lower (figure 12a).

S18 showed accommodative gains above 0.5 to both step far and step near stimuli when the target contrast was 48% (see figure 12b). The accommodative gain to step near stimulus was reduced to less than 0.5 when target contrast was reduced to 26%. Her accommodative responses to step far stimulus fluctuated a lot with decreased target contrast. Therefore no specific target contrast threshold was clearly indicated for step far stimulus for S18.

For S23, the averaged accommodative gains to step near stimulus were greatly reduced with 26% contrast and lower (see figure 12c). For step far stimulus, S23’s accommodative responses were decreased when contrast was reduced to 36%, compared to 100% and 48% target contrast. But for some unclear reasons, the accommodative responses increased with target contrasts of 26% and 18%.

S24 showed reduced accommodative gains to both step far and step near stimuli when target contrast was reduced to 26% and 17% (see figure 12d). Overall, the contrast control experiments on subjects S10, 18, 23, and 24 suggest that the minimum contrast for accommodation to step changes in target distance is approximately 26%. Thus the contrast of the target was reduced to 26% in the adaptation conditions of the subsequent Averse Channels Experiment.
Figure 13 shows the Stiles-Crawford function for S10, S18, and S23. S10 has the peak of the S-C function pointed towards nasal side of the pupil (see figure 13a), and ND filters (0.2 ND) were needed in front the fiber-optic source to compensate in the experimental trials in which the wash entered nasally. However, no ND filters were used for this subject when the wash entered temporally. In contrast S23 has the peak of the S-C function pointed towards temporal side of the pupil (see figure 13c). Thus ND filters (0.1 ND) were placed in front the fiber-optics source during the experimental trials that used a temporal adapting field. The Stiles-Crawford function for S18 is decentered down and slightly temporal (figure 13b), but relative luminous efficiency is very similar at the nasal and temporal entry positions for the adapting source (1.5 mm nasal and 1.5 mm temporal) thus no compensating neutral density filter was used for this subject.

Four subjects from the previous experiment were enrolled, but one (S24) could not complete the trials and was excluded. Data for the remaining three subjects are shown in figure 14. Among all three subjects, S23 was the only subject who accommodated in the correct direction under all twelve conditions (see figure 14c).
For each combination of target orientation and defocus condition, subjects’ accommodation responses were compared between the three adaptation conditions. Negative accommodation gains indicate that the subjects accommodated in the opposite direction from the stimuli.

F-tests were run on the data for each subject for each combination of target orientation and defocus condition between the three adaptation conditions, to compare any differences in accommodative gain between wash conditions. The results are summarized in table 1.

For all three subjects, the F-tests were not significant between each adaptation condition (no wash, nasal wash, and temporal wash) for all combinations of target orientation and defocus condition. Overall, the results do not support the hypothesis that separate “channels” sample light from opposite sides of the pupil to determine the sign of defocus.

**DISCUSSION**

Part I-Preliminary Experiment

The results of the “preliminary experiment” showed large individual differences in subject’s accommodation gain to step changes in wavefront vergence (see figures 7 and 9). Only five out of twenty-six subjects showed accommodative gains greater 0.5 for both near and far steps. The high standard deviations in majority of subjects’ accommodation gains indicated highly variable accommodation responses between trials (see figure 7). It was difficult to find subjects who accommodated reliably to step changes in both directions. Twenty-one subjects were excluded from the subsequent experiments due to their low gains to the step changes in one
or both directions. Reliable responses were necessary to distinguish between a weak response in monochromatic light and a reduction in response when the adaptive field was applied to the target for the subsequent experiments. There are several factors that may account for the poor response in monochromatic light.

Longitudinal chromatic aberration (LGA) of the eye produces “color fringes” at the edges which specify the direction of the focus, and Fincham (1951) concluded these chromatic effects were important for accommodation. Fincham found that most subjects accommodated appropriately to the step changes in lens power introduced in front of the eyes in polychromatic “white” light. But 60% of these subjects had difficulty accommodating or they could not accommodate at all in monochromatic light. Some studies after Fincham also showed that subjects demonstrated a great variability in response to monochromatic targets (Kruger et al., 1993; Lee, Stark, Cohen, and Kruger, 1999). Kruger et al. (1993) suggested that “achromatic” and “chromatic” mechanisms complement each other in the ‘reflexive’ focusing system. In some individuals the achromatic system is rather slow and inefficient on its own, but with the supplement by the chromatic system, there is much finer control of accommodation and a more accurate and effective response. This type of accommodation behavior was also observed in some subjects in our study.

The target used in the study was a single vertical edge, which could also be a factor causing the difficulty for some subjects to accommodate accurately. This target was a simplified stimulus in which blur faced only one direction. Some studies have also examined accommodation under monochromatic light, but the targets used were a Maltese cross or gratings, which had blur facing multiple directions or two directions, respectively (Chen, Kruger, Hofer, Singer, and Williams, 2005; Rucker and Kruger, 2004). This vertical edge target provided
very limited information about the blur thus the subjects had more difficulties accommodating to step changes as compared to the Maltese cross or grating target. For some subjects who showed no responses to the step changes in monochromatic light, we also examined their responses to step changes to a white Maltese cross. S21 showed no responses to step changes when the target was vertical edge illuminated with monochromatic light, but she showed very accurate accommodation responses to step changes when the target was the white Maltese cross. It is clear that S21 needed the chromatic signals and/or a more complex target to accommodate accurately to the step changes.

Most subjects in the study showed no or low accommodation responses to step changes under monochromatic green light since it was not a natural stimulus to the accommodation system and subjects were not familiar with it. Charman & Tucker (1978) demonstrated that subjects with adequate training showed an equally accurate response in monochromatic light as in white light. We suspected that these subjects might exert voluntary accommodation under monochromatic light after the training. In our study subjects were untrained to ensure the accommodation responses were “reflexive” and not voluntary.

There were a few other minor factors which may explain for low, variable, and inconsistent responses to step changes in some subjects. Accommodation may be more unstable when it is operated under monocular than binocular conditions, and thus viewing the target monocularly may be a problem for some subjects to accommodate accurately to the stimulus. A 3mm artificial pupil was used to minimize monochromatic aberrations, but on the other hand it increased the depth-of-focus for subjects who naturally had pupils larger than 3mm. With 3mm pupil, subjects might not respond to the blur as strongly as with their natural pupils, thus reducing the signal to accommodation. Moreover natural pupils dilate and constrict while
responding to defocus and this dynamic response of the pupil may assist for accurate accommodation in some individuals. However in the present study pupil size was fixed at 3mm so the dynamic response of natural pupils had no effect in the experiment.

Part II-Contrast Control Experiment

The effect of target contrast on accommodation has been investigated previously by several studies. Bour (1981) measured the dynamic accommodation as a function of the contrast of the sine-wave target. He found that accommodation was most stable and accurate when the contrasts were somewhat lower than 100%. In general, the accommodative response decreased slightly and regularly as contrast was initially reduced from 0 to -4dB, and then continued to decrease, as contrast was reduced further. The accommodative response approached the tonic accommodation level when contrast was reduced to -10dB. Bour listed several cues that the observer could have been used to obtain about the position of the target or state of accommodation. These cues included chromatic aberration, feeling the effort of the observer’s own accommodation, and hearing the movement of optical components, which could not be eliminated in the experiment. The observer could have consciously or unconsciously used these cues to focus on the target. But when the contrast of the target was markedly decreased, a reduction or even errors in the response of the accommodative system occurred. This suggested that other cues besides retinal image contrast did not play such an important role in the accommodative task.

Ciuffreda and Rumpf (1985) also investigated the effects of contrast on steady-state accommodation in visually-normal subjects and amblyopes. The targets used were sinusoidal and square-wave grating. Visually-normal subjects showed relatively robust accommodation to
targets with substantial decreases in contrast. The accommodation remained relatively constant as grating contrast was reduced by as much as 70%. The contrast cut off values were found to be 8% to 1.7% (-20 to -35 dB) for a 4 cycles per degree sine grating, and 25% to 14% (-10 to -15 dB) for an 8 cycles per degree sine grating. The cut-off values were similar for both sine and square wave gratings. These cut-off values were even further reduced in amblyopic subjects. In conclusion, Ciuffreda and Rumpf showed comparable results to Bour, that accommodative accuracy was relatively unchanged until contrast was markedly reduced. In these experiments the target was stationary and voluntary accommodation may have played a role.

Mathews and Kruger (1989) monitored accommodation continuously with a dynamic infrared optometer. The target was a 3 cycles per degree sine wave grating over a range of contrasts from 5% to 50%. Dioptric vergence changed sinusoidally between 1 and 3 diopters at 0.2 Hz. Accommodative gain decreased linearly between 20% and 5% contrast. In conclusion, these three studies together show that accommodative gain decreases when the contrast is reduced, and the contrast threshold for the sine wave grating with intermediate spatial frequency (3-4 cycles per degree) was about 5-8%.

All of the previous studies mentioned above used chromatic (“white”) sine wave gratings as their targets. The contrast threshold for accommodation to step changes in target vergence in monochromatic light is not clearly established. In the present “contrast control” experiment, the minimum contrast for accommodation to step changes in vergence was estimated to be approximately 26%. Most subjects maintained good accommodative gain when contrast was reduced from 100% to 48% for both step far and step near target vergences. Some subjects started to show either reduced accommodative gains or highly variable accommodative
responses between trials when contrast was reduced to 36%. The clear cut off value for both target vergences in all four subjects was approximately 26%.

The contrast threshold for accommodation in the present study (26%) was higher than the contrast threshold established by previous studies mentioned above (5-20%). Previous studies used chromatic sine wave gratings as their target, which provides a stronger accommodative stimulus. Chromatic sine wave grating provide chromatic signals and blur facing two directions as accommodative cues. Conversely the single vertical edge in monochromatic light used in the present study, provided very limited information about the blur for accurate accommodation. Despite 100% target contrast, many subjects already showed rather variable accommodative responses between trials to this simplified stimulus. When target contrast was reduced, observers showed more difficulty in maintaining the correct accommodation level and made more errors in the choice of the direction.

Part III-Averse Channel Experiment

The hypothesis of the current experiment was based on the following two assumptions: the angle of incidence of light at blurred edges provides the sign of defocus, and “averse channels” sample light separately from opposite sides of pupil (Makous 1968, 1977).

------- Insert Figure 15 approximately here -------

First we consider the possibility that the angle of incidence of light at blurred edges provides the sign of defocus. Ray diagrams at the top of figure 15 illustrate that light from a distant point comes to focus in front of the retina in myopic defocus (figure 15a) and behind the
retina in hyperopic defocus (figure 15b). In myopic defocus, light rays cross in front of the retina, thus the nasal and temporal sides of the blur circles are formed by light from the temporal and nasal sides of the pupil respectively. Conversely in hyperopic defocus, light rays cross behind the retina, thus the nasal and temporal sides of the blur circle come from the corresponding sides of the pupil. The angle of incidence of rays at the margins of blurred image points provides the sign of defocus, either myopic or hyperopic defocus.

At blurred edges, blur circles from adjacent points overlap each other at edges to form blurred edge spread-functions on the retina (figure 15c and 15d). At blurred bright-dark edges that are out of focus, blur circles originating from bright points at the border in object space extend beyond the bright-dark border in image space by half the diameter of the blur circle. The overlapping half of the blur circles on the retina comes from only one side of the pupil. The darker side of the blurred edge-spread function comes from temporal side of the pupil in myopic defocus, but from nasal side of the pupil in hyperopic defocus. As a result of the many adjacent overlapping blur circles that contribute to the blurred edges, the darker half of the edge-spread function, and most of the brighter half as well, comes from only one side of the pupil.

------- Insert Figure 16 and 17 approximately here -------

Figure 16 shows the retinal image of the edge for the left eye viewing a dark-bright border in myopic defocus. The retinal image of the edge is blurred by defocus. In figure 17, the location of the ray source in the exit pupil is plotted as a function of location on the retina for a single geometrical-optical blur circle in an eye with myopic defocus. Note that light on the nasal side of the blur circle arrives from the temporal side of the exit pupil, and light on the temporal side of
the blur circle arrives from the nasal side of the exit pupil. On the bottom diagram which shows six blur circles in an eye with myopic defocus, note that all the overlapping blur circles are placed temporal of the initial blur circle. These blur circles correspond to the images of point objects that are nasal in object space. Note that the dark side of the dark-bright edge, which is temporal in object space, has no object points, and thus does not produce blur circles on the nasal side of the image border.

--------- Insert Figure 18 approximately here ---------

Figure 18 is extended in figure 18 to represent an infinite number of overlapping blur circles. The grey shaded area indicates how the contribution of light from each point in the pupil changes across the blurred edge, and the heavy dashed line indicates the average location of ray sources in the pupil. On the nasal side of blurred edge, which corresponds to the darker side of the blur spread function, light arrives only from the temporal side of the exit pupil. At the extreme temporal side of the blurred edge, which corresponds to the brightest margin of the blur spread function, light arrives from all directions in the pupil, with an average direction that is neither nasal nor temporal.

The bottom diagram of figure 18 represents an infinite number of overlapping blur circles in hyperopic defocus. At the darkest margin of the edge-spread function, the light arrives from only the nasal side of the pupil. These frequency density diagrams show that light is eliminated progressively starting on one side of the pupil and extending to the opposite side of the pupil, as a function of position across the blurred edge. The direction of such “vignetting” of light (contrast or modulation of intensity) across the pupil provides the sign of defocus.
Experiments by Makous (1968; 1977) and Sansbury et al. (1974) suggest a transient Stiles-Crawford effect, which he attributed to “channels” that sample light from opposite sides of the pupil. Makous described the existence of two sets of photopigment molecules, which he referred as ‘channels’ or ‘pools.’ These two ‘channels’ are not coherently oriented, thus they are called ‘averse channels.’ The pair of ‘channels’ represents a theoretical vergence detector located in one or more retinal cones. Makous (1968) suggested that cones have slightly different orientation, and photopigment molecules in the cone are differentially sensitive to light incident on the retina at different angles. Thus two channels might coexist in a single cone although this possibility is not our main focus.

Our hypothesis assumes that if only one of the averse channels is needed to detect the angle of incidence at edges, it might be possible to disable one channel with adapting field while keeping the other channel intact. As discussed earlier, because the margin of the defocused blur spread-function comes from one side of the pupil in myopic defocus, but the opposite side of the pupil in hyperopic defocus, it should be possible to predict whether the adapting field would reduce sensitivity to myopic or hyperopic defocus, taking into account of the orientation of the target. For instance, a nasally entering adapting field should reduce subject’s accommodative gain when the dark margin comes from the nasal side of the pupil (myopic defocus while viewing a bright-dark blurred edge or hyperopic defocus while viewing a dark-bright blurred edge). On the other hand a temporal entering adapting field should reduce subject’s accommodative gain when the dark margin comes from the nasal side of the pupil. The results of current experiment did not confirm the hypothesis; the negative results suggest alternate hypotheses.
First, the angle of incidence of light may be detected by averse channels in a way that was not tapped by the present experimental design. Based on Makous’ proposal, the pair of channels in each individual cone works separately to sample light from opposite sides of pupil. Thus when we introduced the adapting field from either nasal or temporal entry in the experiment, we expected to selectively adapt either one of the channels, and test the ability of the other channel to detect the angle of incidence of light. Yet the proposition that averse channels work separately to sample light from opposite sides of the pupil was never confirmed experimentally. Therefore it is possible that these channels could work in conjunction with each other, instead of working separately, to measure wavefront vergence across the pupil. If this is indeed how “averse channels” function, then we actually may have disabled both channels by applying the adapting field either from nasal or temporal entry. The negative results suggest that the pair of channels might not work separately, as we assumed.

Another possible explanation for the negative finding is that ‘averse channels’ simply do not exist, and the accommodative system of an eye does not measure vergence of incidence of light at the retina. Nevertheless this explanation is unlikely the case. Kruger et al. (1997) demonstrated that accommodative system of an eye responds to sign of vergence. In the experiment, accommodation was monitored continuously under open-loop conditions (without normal feedback) while subjects viewed a sinusoidally oscillating sine-wave grating in a Badal optometer. The target was illuminated by monochromatic light or white light with longitudinal chromatic aberration normal, double, neutralized and reversed. Subjects’ accommodative gains were reduced when the longitudinal chromatic aberration was neutralized and reversed but subjects continued to accommodate effectively in monochromatic light, albeit with reduced gain.
The results suggest that accommodation responds to changes in the vergence of light, perhaps as a modulation of light across the pupil, in conjunction with modulation across the retina.

As mentioned earlier, many of our subjects recruited in the preliminary experiment could not accommodate to step changes in an edge border in a monochromatic light. For subjects who could accommodate to the stimuli correctly, the signal was low even without adapting field. With the adapting field, the accommodative responses became further reduced and more variable. The current method to test the ability of averse channels to detect angle of vergence required the detection of a small signal in noisy data. Adverse channels could possibly function separately to detect angle of vergence just as we predicted, but the signal was just undetectable with the current method.

A major limitation to the current method was the small pool of subjects who could accommodate to a single edge target in monochromatic green light. In addition to the small pool of subjects, there were large individual differences between subjects and variability within each subject. Thus any future experimental investigations of the ‘averse channels’ would need to recruit a larger pool of subjects to compensate for these disadvantages.

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Table 1.

Results of the F-test by a randomization procedure for each combination of target and defocus condition between the three adaptation conditions.

<table>
<thead>
<tr>
<th>S#</th>
<th>Myopic defocus WB orientation</th>
<th>Myopic defocus BW orientation</th>
<th>Hyperopic defocus WB orientation</th>
<th>Hyperopic defocus BW orientation</th>
</tr>
</thead>
<tbody>
<tr>
<td>10</td>
<td>F = 1.94, p = 0.2188</td>
<td>F = 2.83, p = 0.25</td>
<td>F = 0.26, p = 0.7188</td>
<td>F = 1.33, p = 0.25</td>
</tr>
<tr>
<td>18</td>
<td>F = 0.23, p = 0.609</td>
<td>F = 2.48, p = 0.156</td>
<td>F = 0.12, p = 0.765</td>
<td>F = 0.38, p = 0.625</td>
</tr>
<tr>
<td>28</td>
<td>F = 0.25, p = 0.8750</td>
<td>F = 0.12, p = 0.8125</td>
<td>F = 0.97, p = 0.4063</td>
<td>F = 0.01, p = 1.0000</td>
</tr>
</tbody>
</table>
Figure Captions

Figure 1.
Illustration of directional signals from longitudinal chromatic aberration (LCA) for accommodation. Long wavelength red light (solid rays) is refracted less than short wavelength blue light (dashed rays). Myopic defocus is characterized by a blue fringe, and hyperopic defocus is characterized by a red fringe.

Figure 2.
Illustration of potential directional signals for accommodation from decentered Stiles-Crawford functions. The blur circles (point spread functions) on the retina are modeled as symmetrical gaussian distributions of light. The neural representation of point spread function after the decentered Stiles-Crawford effect is skewed to one side. “N” indicates the nasal side of the pupil and “T” indicates the temporal side of the pupil.

Figure 3.
Illustration of optical principles and proposed mechanism for channels that sample light from the opposite sides of the pupil to detect the vergence of light in hyperopic and myopic eyes. Solid rays form the margins of the blurred retinal image, and the angle of incidence specifies the sign of defocus. Dashed rays do not form the margins of the blurred edges.

Figure 4a.
Badal stimulus system for presenting stepping targets away or towards the eye. Movable fiberoptic source provides adapting field to the nasal or temporal entry of the artificial pupil. Top right is the schematic drawing of the position of the 3mm artificial pupil. Arrows point to the nasal or temporal entry for adapting field.

Figure 4b.
Stimulus. Vertical luminance edges (bright on left side and bright on right side) are shown in focus at the top of the figure, blurred without wash at the middle of the figure, and blurred with wash superimposed at the bottom of the figure.
Figure 5.
Time course for a 10.24 s trial. The target steps randomly from 2.00 to 1.00D or 2.00 to 3.00D after the first 5.12 s of the trial (dashed lines). Horizontal arrows indicate the two 2.56s periods that were used to calculate the response gain before and after the step.

Figure 6.
Time course of two trials of accommodation responses for S10.
(a) response to step far stimulus. (b) response to step near stimulus.

Figure 7.
Averaged gains of accommodation for Part I “Preliminary Experiment” for twenty-six subjects. Subjects who were included in Part II “Contrast Control Experiment” are indicated with asterisks. Negative gains are responses in the wrong direction.

Figure 8.
Graphs are the accommodation responses for S11, S15, and S16 who were excluded from the study due to their variable and noisy responses. The rapid, transient changes are blinks.

Figure 9.
Median gains of accommodation for Part I “Preliminary Experiment” for twenty-six subjects. Subjects who were included in Part II “Contrast Control Experiment” are indicated with asterisks.

Figure 10.
Graphs show accommodation responses for S7.
(a) response to the step far stimulus. (b) response to the step near stimulus.

Figure 11.
Graphs show the accommodation responses for S3 in the contrast threshold experiment. (a) accommodation response without any ‘wash’ applied to the vertical edge. (b) accommodation response when the contrast was 17.4%.
Averaged gains of accommodation to 100%, 48%, 36%, 26% and 17% of target contrast for Contrast Control Experiment for Subject S10, S18, S23, and S24.

Stiles Crawford (S-C) functions for left eye S10, S18, and S23. Color scale is log optical density.
(a) S10 has the peak of the S-C function pointed towards the nasal side of the pupil and superior.
(b) S18 has the peak of the S-C function decentered down and slightly nasal. S-C measurements are essentially the same 1.5 mm nasal and 1.5 mm temporal for this eye. (c) S23 has the peak of the S-C function pointed towards the temporal side of the pupil. Measurements at 1.5 mm nasal and 1.5 mm temporal to the pupil center were used in the final experiment to determine the density of filters needed to compensate for an off-center S-C effect.

Averaged accommodation gains for each combination of target orientation (Bright Left and Bright Right) and defocus condition (step far and step near) between the three adaptation conditions (no wash, nasal wash, and temporal wash) for Subjects S10, S18, and S23.

Blur circles on the retina are projections of the pupil. In myopic defocus, the light rays come into focus in front the retina, and the blur circle is an inverted projection of the pupil (top to bottom and left to right). In hyperopic defocus, the light rays come into focus behind the retina, and the blur circle is a direct projection of the pupil.

Blur circles at edges overlap the edge by half the diameter of the blur circle. Blur circles from adjacent points on the bright side of the border overlap each other. As a result, light from only one side of the pupil forms the dark margin of the edge spread-function, and light from the opposite side of the pupil increases from zero at the center of the spread-function to 50% at the brightest margin of the blurred edge.
Figure 16.
Illustration of a left eye viewing a dark-bright border in myopic defocus (dark on the left side of the border and bright on the right side). The dark portion is temporal in object space and nasal on the retina because the retinal image is inverted. The bright portion is nasal in object space and temporal on the retina. The sharp object edge is blurred by the optics of the eye.

Figure 17.
Top panel
The location of the ray source in the exit pupil is plotted as a function of location on the retina for a single geometrical-optical blur disc. This is a geometrical-optical approximation. This schematic plot confirms that light on the nasal and temporal sides of the blur circle arrives from the temporal and nasal side of the exit pupil, respectively.

Lower panel
The location of the ray source in the exit pupil is plotted as a function of location on the retina for six blur circles. Note that they are all placed temporal of the initial blur disc. With reference to the myopic eye, note how the discs correspond to the images of point objects that are nasal in object space. Note that the dark part of the target, which is temporal in object space, has no object points and so cannot produce blur discs on the nasal side of the image border.

Figure 18.
Top panel
Schematic plot represents an infinite number of blur circles in myopic defocus. The grey shaded area indicates how the contribution of light from each point in the pupil changes across the blurred edge, and the heavy dashed line indicates the average location of ray sources in the pupil. Note that in the nasal portion of the blurred edge, light always arrives from the temporal side of the exit pupil. On the temporal portion of the blurred edge, light arrives from all direction in the pupil, with an average direction that is neither nasal nor temporal.
Lower panel

Lower panel represents repeated schematic plot, but for hyperopic defocus. In hyperopic defocus, the tendency is for light in the darker side of the blurred edge to arrive from the nasal side of the pupil.
References


Figure 1.

Hyperopic Defocus  Myopic Defocus

Red Fringe  Blue Fringe
Figure 3.
Figure 4a.
Figure 4b.
Figure 5.
Figure 6.

(a)

(b)
Figure 7.
Figure 8.

(a) S11

(b) S15

(c) S16
Figure 9.
Figure 10.
Figure 11.
Figure 12.
(a) S10

(b) S18
Figure 13.

(a) S10

(b) S18

(c) S23
Figure 14.
(a) S10

(b) S18
Figure 15.
Figure 16.
Figure 17.
Figure 18.