Accommodation to wavefront vergence and chromatic aberration: color normal and deutan observers.

by

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M.S. RESEARCH PAPER

In partial satisfaction of the requirements for the degree of

Master of Science
In
Vision Science

State University of New York
State College of Optometry

March 2009

Approved by M.S. Research Committee:

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Abstract:

Purpose: Longitudinal chromatic aberration (LCA) provides a cue to accommodation with small pupils. However, large pupils increase monochromatic aberrations, which may obscure chromatic blur (McLellan, Marcos, Prieto, & Burns, 2002). We examined the effect of pupil size and LCA on accommodation in color normal and deutan observers.

Methods: Participants were nine normal trichromats, three deuteranomalous trichromats, and two deuteranopic dichromats (anomaloscope and D-15). Accommodation was recorded by infrared optometer (100 Hz) and pupil by video-camera (30 frames/s) while observers viewed a sinusoidally moving Maltese cross target (1-3 D at .2 Hz) in a Badal stimulus system. There were two illumination conditions: white (3000 K; 20 cd/m^2) and monochromatic (550 nm with 10 nm bandwidth; 20 cd/m^2) and two artificial pupil conditions (3 mm and 5.7 mm). Separately, static measurements of wavefront aberration were made with the eye accommodating to targets between zero and 4 D (COAS, Wavefront Sciences).

Results: Dynamic gain to vergence modulation increased significantly with pupil size in monochromatic (p=.005) but not white light (p=.12), and gain increased significantly with addition of LCA at both pupil sizes (5.7 mm, p=.004; 3 mm, p=.02). Mean RMS higher order aberration increased from .23 μm with small pupils (3 mm) to .48 μm with large pupils (5.7 mm). There were no significant differences in dynamic accommodation between color normal and deutan individuals for any condition (.68≤p≤.96). Normals and deutan observers showed large individual differences in dynamic gain to both vergence and LCA. Mean responses also varied among individuals, but deuteranomalous observers over-accommodated compared to color normal observers (.06≤p≤.12).

Conclusions: Large individual differences in accommodation to wavefront vergence and to LCA are a hallmark of accommodation in normal and deutan observers. LCA continues to provide a signal at large pupil sizes despite higher levels of monochromatic aberrations. Monochromatic aberrations may defend against chromatic blur at high spatial frequencies, but accommodation responds best at 3 c/deg where blur from higher order aberrations is less (Mathews, 1998; Mathews & Kruger, 1994).

Key words: accommodation, blur, longitudinal chromatic aberration, wavefront

aberration, color vision

1. Introduction

Stimulus to reflex accommodation: vergence, defocus & chromatic aberration

The conventional view of reflex (blur-driven) accommodation control is that luminance contrast of the retinal image provides an even-error stimulus without directional information. The eye accommodates to reduce myopic or hyperopic defocus blur and maximize luminance contrast of the retinal image, and in this systems control model, negative feedback from changes in luminance contrast is essential. However, Fincham (1951) found that more than 90% of subjects could accommodate without trial-and-error focusing behaviors, and contrary to the conventional view, he proposed odd-error signed stimuli for accommodation including an achromatic signal from wavefront vergence extracted by the Stiles–Crawford effect and a chromatic signal from the effect of longitudinal chromatic aberration (LCA).

At spatial frequencies above approximately 0.5 cycles per degree (c/deg), longitudinal chromatic aberration (LCA) of the eye from the dispersion of white light by the ocular media alters ocular focus as a function of wavelength. Short wavelength light focuses much further forward in the eye than long wavelength light, producing approximately 2 diopters (D) chromatic difference of focus between 400 and 700 nm (Bedford & Wyszecki, 1957; Howarth & Bradley, 1986; Wald & Griffin, 1947) and significantly different contrasts for spectral waveband components of the retinal image (Kruger, Mathews, Aggarwala, Yager, & Kruger, 1995; Marimont & Wandell, 1994). Thus when the eye is over-accommodated, the red (long-wavelength) component of the image is in focus on the retina with high contrast, and the image of a white target has a blue fringe; and when the eye is under-accommodated, the blue (short-wavelength) component is in focus on the retina with high contrast, and the image has a red fringe. Fincham (1951) proposed that most subjects used the color fringes from LCA to determine the direction of defocus. He found that 60% of subjects showed weak or no accommodation reaction when LCA was eliminated by using monochromatic light to illuminate the target. Fincham suggested that the 40% of subjects who could still accommodate normally in the absence of LCA use an achromatic directional signal extracted from Stiles–Crawford effect. To this day, LCA has been substantially proved to provide an important directional stimulus to the reflex accommodation. Studies suggest that the signal from LCA is analyzed by comparing long-wavelength sensitive cone (L-cone) contrast and middle-wavelength sensitive cone (M-cone) contrast (Aggarwala, Kruger, Mathews, & Kruger, 1995; Aggarwala, Nowbotsing, & Kruger, 1995; Crane, 1966; Flitcroft, 1990; Kotulak, Morse, & Billock, 1995; Kruger, Mathews *et a*l., 1995; Rucker &

Kruger, 2004; Rucker & Osorio, 2008; Rucker & Wallman, 2008).

However, the eye can accommodate in the absence of chromatic and higher-order aberrations and without feedback from defocus-blur (Kruger, Mathews *et a*l., 1995, Chen, Kruger, Hofer, Singer, & Williams, 2006, Stark *et al.*, 2009) which suggests that blur on the retina image is not sufficient to control accommodation even in polychromatic light. Apparently something more than blur specifies the sign and amplitude of defocus. One theory is that eye monitors wavefront vergence (Zernike defocus) directly. Wavefront vergence is the radius of spherical curvature of the wavefront measured at the eye, and is specified by the changes of the angular incidence of the light as a function of location across blurred edges. In addition, LCA alters wavefront spherical curvature (vergence) as a function of wavelength (Marcos, Burns, Moreno-Barriusop, & Navarro, 1999) so that the ratio of cone contrasts measured separately by cone type (L-cones, M-cones & S-cones) specifies wavefront vergence and drives accommodation.

Effect of higher order wavefront aberrations on accommodation

Besides defocus and chromatic aberration, monochromatic higher-order aberrations of eyes affect retinal image quality and interact with chromatic aberrations and might provide an odd-error signal to accommodation (Buehren, Collins, & Carney, 2005; Chen *et a*l., 2006; Fernandez & Artal, 2005; Lo´pez-Gil *et a*l., 2007; Wilson, Decker, & Roorda, 2002). McLellan *et al.* (2002) used the modulation transfer function (MTF) of the eye to evaluate retinal image quality for a model eye with LCA but no other aberrations, and also for real eyes with both LCA and monochromatic wavefront aberrations. For the model eye with LCA alone, MTF was degraded distinctly for 450 nm light, which is defocused substantially as a result of LCA, compared with the MTF for 550 nm light which is in focus on the retina. On the other hand, for a real eye with both LCA and monochromatic aberrations, the MTF is very similar for 450 nm and 550 nm light. This result suggests that monochromatic aberrations decrease the difference in MTF across wavelengths that results from LCA alone. The MTF for L-cones, M-cones, and S-cones computed separately in real eyes are more similar to each other than in the model eye with LCA alone. While monochromatic wavefront aberrations degrade the retinal image at a single wavelength, McLellan *et al.* (2002) concluded that monochromatic aberrations also attenuate the effects of LCA and thus help the eye defend against chromatic blur.

Previous experiments in our lab show that LCA increases dynamic accommodation gain significantly for normal subjects, suggesting that LCA provides an effective directional signal that specifies wavefront vergence (Aggarwala, Kruger *et a*l., 1995; Aggarwala, Nowbotsing *et a*l., 1995; Kruger, Aggarwala, Bean, & Mathews, 1997; Kruger, Mathews, Aggarwala, & Sanchez, 1993; Kruger, Mathews *et a*l., 1995; Kruger, Mathews, Katz, Aggarwala, & Nowbotsing, 1997; Kruger, Nowbotsing, Aggarwala, & Mathews, 1995; Kruger & Pola, 1986; Lee, Stark, Cohen, & Kruger, 1999; Rucker & Kruger, 2004; Stark, Lee, Kruger, Rucker, & Fan, 2002). The previous experiments all used 3 mm artificial pupils to minimize higher-order wavefront aberrations of the eye, since at the pupil size of 3 mm, the monochromatic aberrations of the eye have minimal effects on the retinal image quality (Liang & Williams, 1997; Walsh & Charman, 1985). Thus the relatively small pupil size may have influenced the previous results. Following McLellan *et al.* (2002), the increase in monochromatic aberrations at large pupil sizes may obscure the effects of LCA, and thus dynamic accommodation gain should decrease.

Accommodation of subjects with color deficiency

Our previous studies on the effect of LCA on accommodation used subjects with normal trichromatic color vision. However, it is not clear whether subjects with red-green color vision defects use the color signal derived from LCA for accommodation. Dichromats (protanopes and deuteranopes) lack one of the retinal photopigments, and have the same photopigment in both L-cones and M-cones, while anomalous trichromats (deuteranomalous and protanomalous trichromats) have one cone photopigment with a displaced absorption spectrum.

Thus both dichromats and anomalous trichromats have impaired color vision, but the impairment is more severe for dichromats. Fincham (1953) examined the accommodation reflex in subjects with color deficiency, including two anomalous trichromats and fifteen dichromats. Fincham used two light sources to illuminate the target in his study: monochromatic yellow sodium light (590 nm) and a heterochromatic mixture of red (644 nm) and green (546 nm) light that matched the appearance of the monochromatic yellow light. Fincham tested the effectiveness of the chromatic and monochromatic stimuli for accommodation in color normal and deficient subjects by comparing the minimum target size needed for accommodation in the two illumination conditions. Subjects who accommodated effectively to both heterochromatic and monochromatic stimuli, responded to smaller targets (approximately 3 arc min) in heterochromatic light than in monochromatic light (approximately 6 arc min). For the two anomalous trichromats that were examined (1 deuteranomalous and 1 protanomalous) the minimum effective target size was smaller in heterochromatic light than in monochromatic light, indicating LCA provides a directional signal to accommodation in anomalous trichromats as well as normal trichromats. Fincham also found seven of fifteen dichromats (4 deuteranopes and 3 protanopes) who showed no accommodation response at all to changes in target vergence under both illumination conditions. The minimum effective target size for the two illumination conditions was the same for the eight dichromats who did accommodate effectively (6 deuteranopes and 2 protanopes) which suggested that their accommodation response was not affected by LCA.

To examine the effect of pupil size and higher-order aberrations on accommodation, we compared dynamic gain with and without the normal LCA of the eye in observers while they viewed through 3 mm and 5.7 mm diameter artificial pupils. Color normal and deutan observers were included in the experiment which used more sensitive methods than were available to Fincham (1953).

2. Methods

Subjects

Twenty volunteers (subjects) were involved in this Institutional Review Board (IRB) approved study. All subjects gave informed consent. Three were investigators and the others were naive to the purpose of the study. All subjects were visually normal and had no history of strabismus, amblyopia, binocular vision problems, or significant ocular injury, surgery, or disease. Refractive errors were corrected by the subjects' own contact lenses or by trial lenses. Distance refractive states and near point of accommodation were measured for all subjects. Two subjects were excluded for poor accommodation to a stationary target during the optometer calibration procedure (described below). One subject was excluded for accommodative spasm (severe over-accommodation) and three for excessive blinking during trials. Thus, fourteen subjects ranging from 21 to 33 years of age participated in this study, including nine normal trichromats, three deuteranomalous trichromats, and two deuteranopic dichromats.

Apparatus

Dynamic accommodation was monitored continuously (100 Hz) with a high-speed infrared optometer (Kruger, 1979) and the pupil was monitored by video-camera (30 frames/s) while the subject viewed a high contrast Maltese cross target in a Badal stimulus system. The Badal optical system keeps the visual angle subtended by the target constant despite changes in target distance (Kruger *et al*., 1993). Figure 1 is a schematic illustration of the apparatus used in the experiment.

------------“Insert Figure 1 approximately here”----------

Measurements of accommodation are recorded along the vertical meridian of the eye from a fixed 3 mm diameter area at the center of the subject’s natural pupil. The recording optometer is insensitive to changes in pupil size for pupil diameters that are 3 mm or larger, and the optometer is insensitive to small eye movements up to 3 deg from the center of the target. The output voltage of the optometer is proportional to the accommodative response and is linear over a 6 D range (Kruger, 1979). After analog-to-digital conversion, data are recorded to computer using Asyst Scientific software (Metrabyte Corporation).

The Badal stimulus system includes an illumination system illustrated by dashed lines and a superimposed target system illustrated by solid lines (Kruger *et al*., 1993). All lenses are computer optimized achromatic doublets (Melles Griot). In the illumination system, “white” light from a tungsten halogen source (S) is focused by a condensing lens (CL1) and then filtered by either a 550 nm interference filter (IF) to provide quasi-monochromatic green light (10 nm bandwidth; 20 cd/m^2) or 1.2 log units of neutral density filters to provide broadband “white” light luminance (3000 K; 20 cd/m^2). After filtering, the light is diffused by an opal diffuser (D1), an integrating bar (IB), and a second opal diffuser (D2) to provide a uniform field of diffused light. Light from diffuser D2 is collimated by lens L1 and reflected by front-surface mirror M to illuminate the target T (35 mm photographic transparency) from behind. Lens L2 focuses the diffused light in the plane of an artificial pupil (A) and lens L3 collimates the light again. After reflection at the mirror-coated surfaces of right-angled prisms P1 and P2, light is focused by lens L4 in the pupil of the subject’s eye.

Target T is a high-contrast Maltese cross, illuminated from behind by collimated light. Light from the target is collimated by lens L2, and focused by lens L3 at T' after reflection by prisms P1 and P2. The image of the target (T') is formed in the focal plane of Badal lens L4 so that collimated light reaches the subject's eye. An image of the target is formed on the retina of the subject's emmetropic unaccommodated eye (E). Prism P2 can move as shown by the arrow, to move the image of the target (T') toward and away from lens L4 and this alters the dioptric stimulus to accommodation. The artificial pupil (A) is imaged at the center of the subject's natural pupil. Two artificial pupils (3 mm and 5.7 mm diameter) were used in the experiment.

Procedures

Preliminary examinations

During a preliminary session, case histories and Snellen acuities were measured for each subject, and color vision was tested by Nagel anomaloscope (mean of five measurements) and Farnsworth D-15. Monochromatic wavefront aberration and distance refractive error were measured by clinical aberrometer (COAS, Wavefront Sciences). The subject was directed to focus on a stationary white "ships wheel" target in the aberrometer positioned at 5 stimulus levels between zero and 4 D while wavefront aberration was measured. The subject's refractive state was measured with the eye accommodating for a far distance. These measurements were taken with subjects' natural (large) pupils in a dark room. Near point of accommodation was measured monocularly by standard push-up technique.

Subjects' calibration

During the accommodation trials, the subject was positioned in front of the apparatus on a chin and forehead rest, which kept the subject still. Left eye of each subject was tested and the right eye was patched. The subject's refractive error was corrected by the subject's own contact lenses or by trial lenses. Trial lenses were placed in front of the left eye to compensate the refractive error, and the room was kept dark. The subject's pupil was monitored by video-camera (30 frames/s) and the image of the pupil was viewed on a video display so that the investigators could adjust the position of the subject's eye continuously during the experiment. The center of the subject's pupil was aligned with the optical axis of the stimulus system using the first Purkinje image as a reference point.

The IR optometer was calibrated for each subject's eye using a method of bichromatic stigmatoscopy (Lee *et al*., 1999) that includes both objective and subjective measurements of accommodation at five stimulus levels: 0, 1, 2, 3, and 4 D. Computer software correlated the subjective measurement of accommodative response calculated from the stigmatoscopy and the objective infrared optometer voltage output using principal axis regression. Figure 2 shows calibration results from a typical color normal subject. Most of the normal subjects over-accommodated for the farthest distance and showed a lag of accommodation (under-accommodation) at near target distances.

------------“Insert Figure 2 approximately here”----------

Experimental trials

During experimental trials, the Maltese cross target moved sinusoidally toward and away from the subject’s eye between 1 D and 3 D at 0.2 Hz with a mean level of 2 D. The subject was instructed to “concentrate on the center of the target and to keep the target clear using the same amount of effort as reading a book”. There were two illumination conditions: white light (3000 K; 20 cd/m^2) to include normal chromatic aberration of the eye, and monochromatic green light (550 nm with 10 nm bandwidth; 20 cd/m^2) to eliminate chromatic aberration. There were two artificial pupil diameters: 3 mm and 5.7 mm. Thus there were 4 conditions in total (2 illumination conditions and 2 pupil conditions), as shown in Table 1. For each subject, six trials were conducted for each condition randomized in blocks, giving 24 trials in total. To limit subject fatigue, the 24 trials were run separately in two experimental sessions. Each trial lasted 40.96 s with a break of approximately 1 min between trials.

------------“Insert Table 1 approximately here”----------

Analysis

Data were analyzed using custom software written in Asyst programming language. Blinks were removed manually from each accommodation trial before analysis. Trials with more than 14.65% blinks were discarded (Kruger, Stark, & Nguyen, 2004). Data were scaled according to the subject’s calibration and analyzed using a fast Fourier transform to extract dynamic gain and temporal phase-lag at the stimulus frequency (0.2 Hz). Data from the six trials for each condition were vector averaged to determine mean gain and temporal phase-lag of accommodation for each condition. In addition, mean accommodation response was calculated for each trial, and means for the six trials were averaged for each condition. For each of the three subject groups (normal trichromats, deuteranomalous trichromats and dichromats) mean gains and temporal phase-lags were vector averaged to determine the group average dynamic gain and phase-lag for each condition, and mean responses were averaged to find the group average mean response for each condition.

The geometrical test, a powerful non-parametric alternative to multivariate analysis of variance for distribution-free sampled populations, was used in the statistical analysis (Stark, 2000). To determine whether chromatic aberration and monochromatic higher-order wavefront aberration improve or impair the accommodative response, comparisons were made between the accommodation responses in the two illumination conditions and also between the accommodation responses to the two pupil size conditions for normal subjects. Since one of the two dichromatic subjects did not respond to the dynamic target, a single case analysis was performed for the dichromatic subject who did respond. Data also were compared between normal trichromatic subjects and deutan subjects for each condition to determine whether use of chromatic aberration is impaired in deutan subjects.

For each subject root-mean-square (RMS) higher-order aberrations were calculated by the aberrometer for 3 mm and 5.7 mm pupil diameters (COAS, Wavefront Sciences). For these measurements the aberrometer target was moved to a near distance so that the subject was accommodating approximately the same amount as the mean accommodation level measured during the dynamic accommodation trials (white light, large pupil condition). RMS higher-order aberrations for two pupil diameters were compared for each subject.

3. Results

Large variation in accommodation to wavefront vergence and LCA

------------"Insert Table 2 and Figure 3 approximately here"----------

Each subject's mean dynamic gains and phase-lags for the four conditions are summarized in Table 2 and Figure 3. Mean gain varied widely among the normal and deutan observers for the four conditions, indicating large individual differences in the sensitivity to vergence and LCA among normal and deutan subjects. Among the normal subjects, some had very low dynamic gains such as subject 1 (S1) whose mean gains were 0.14, 0.26, 0.03, and 0.01 for the four conditions. Others like subjects like S3 had very high gains, which were all above 1 for the four conditions. Out of the five deutan subjects, two (S11 and S13) had gains below 0.1 for all four conditions, which are close to the level of noise. Although the dynamic response of these two subjects was very poor, they accommodated quite well to the static (stationary) target during the calibration procedure (Figure 4). On the contrary, S12 had high gains of 1.06, 0.68, 1.06, and 0.75 for the four conditions.

------------"Insert Figure 4 approximately here"----------

Mean accommodation response levels are summarized in Table 3 and Figure 5. Mean responses varied widely among the 14 subjects. Since the mean target position was at 2 D, accurate accommodation should approximate 2 D. Color normal subjects' mean accommodation responses were close to 2 D, but deutan observers especially those with deuteranomaly, over-accommodated substantially compared to color normal observers ($.06 \le p \le .12$).

------------"Insert Table 3 and Figure 5 approximately here"----------

Effect of chromatic aberration and pupil size on accommodation

Out of the nine normal subjects, eight showed reduced dynamic gains in monochromatic light at both small and big pupil sizes. Only one (S3) had slightly decreased accommodative responses in white light compared with monochromatic light with a small pupil, and gains were approximately the same in white and monochromatic light with the big pupil. This suggests that the normal subjects (except S3) were sensitive to the effect of LCA.

------------"Insert Figure 6 approximately here"----------

Figure 6 shows data from a typical color-normal subject under each of the four experimental conditions. The top trace is the stimulus and the four traces below are the responses in each condition. The amplitude of response increased in white light for both pupil sizes, and the amplitude of response increased with pupil size in both white and monochromatic light. Among the three deutan subjects who had robust dynamic accommodative responses, one deuteranomalous (S10) and one dichromat (S14) showed reduced responses in monochromatic light at both pupil sizes (like most of the color-normal subjects), but the response of one deuteranomalous subject (S12) was the same in monochromatic and white light.

------------“Insert Figure 7 approximately here”----------

To investigate the effect of chromatic aberration and pupil size on accommodation for the color normal subjects, gain ratios were calculated for each subject for two pupil sizes (3 mm pupil/5.7 mm pupil) and for two illumination conditions (monochromatic/white), and box plots of the gain ratios were used to summarize the distribution of the gain ratios among the normal subjects. Figure 7 shows the box plots of the normal subjects' gain ratios for different conditions. The top figure shows the ratio of gain in monochromatic light to gain in white light for two pupil sizes. For both pupil sizes, most subjects' gain ratios are less than 1, which means their gains in monochromatic light are less than gains in white light. The bottom figure plots the ratio of the gain with small pupil to the gain with big pupil in white and monochromatic light. In monochromatic light, most subjects' gain ratios are less than 1, which means their gains are reduced with small pupils. However, in white light the gain ratios do not follow this pattern. In agreement with the box plots, statistical analysis (geometric test) shows: (1) dynamic accommodation improved significantly in white light at both 5.7 mm ($p = 0.004$) and 3 mm ($p = 0.02$) pupil sizes; (2) no significant difference between the ratios of gain in monochromatic light to gain in white light for the two pupil sizes ($p = 0.0746$); (3) in normal subjects, dynamic gain increased significantly with larger pupils in monochromatic light ($p = 0.005$), but the pupil size had no significant effect on dynamic accommodation in white light ($p = 0.12$). Thus, LCA still provides a useful signal to accommodation at large pupil sizes, and the presence of higher order monochromatic aberrations does not attenuate the effect of LCA. Geometrical test results showed no significant differences in dynamic accommodation between color normal and deutan individuals for any condition ($0.68 \le p \le 0.96$).

A single case analysis was conducted for the one dichromat (S14) who accommodated well. Dynamic gain increased significantly with the larger pupil in both monochromatic ($p = 0.03$) and white light ($p = 0.03$), and the increase in white light approached significance at both pupil sizes (5.7 mm pupil; $p = 0.06$ and 3 mm pupil; $p = 0.0635$). This suggests that this dichromat uses chromatic aberration as a directional signal to accommodation.

Effect of pupil size on RMS higher-order aberrations

------------“Insert Figure 8 approximately here”----------

Figure 8 shows the RMS higher order aberrations (HO) for 13 subjects with two pupil sizes (data were not obtained for one of the dichromats). RMS higher-order aberrations increased with pupil size for all 13 subjects (0.23 μm for 3 mm pupil and 0.48 μm for 5.7 mm pupil), and for the group HO doubled with the larger pupil.

4. Discussion

The present results show that LCA continues to provide a directional signal for accommodation at large pupil sizes despite higher levels of monochromatic aberrations. The results also show that large individual differences in accommodation to wavefront vergence and to LCA are a hallmark of accommodation in normal trichromats and deutan observers, which agrees with previous findings.

In the present study we used sinusoidally moving targets instead of stationary targets to minimize voluntary accommodation. Voluntary accommodation can mask the effects of spatial frequency, contrast, chromatic aberration and defocus when the target is stationary (Kruger *et al*., 1993). In addition, we instructed the subjects to “concentrate on the center of the target and to keep the target clear using the same amount of effort as when reading a book” rather than to “focus the target as hard as you can” or “use as much effort as you can”. This type of instruction in conjunction with the moving target can isolate reflex blur-driven accommodation by minimizing voluntary accommodation.

Individual differences among color normal and deutan observers

In the current experiment, we found that normal and deutan observers showed large individual differences in dynamic gain to both wavefront vergence and LCA (Figure 2). This confirms the results of previous accommodation experiments that wide variation among individuals in sensitivity to both vergence and LCA is typical (Fincham, 1951; Kruger, Aggarwala *et a*l., 1997; Kruger *et a*l., 1993; Kruger, Mathews *et a*l., 1995; Kruger, Mathews *et a*l., 1997; Kruger, Nowbotsing *et a*l., 1995; Lee *et a*l., 1999; Rucker & Kruger, 2001, 2004; Stark *et* *a*l., 2002). All the normal subjects except S1 used LCA as a directional cue for reflex accommodation. This confirms that most normal subjects are sensitive to LCA and individuals like S1 are unusual (Kruge*r et al*., 1993). Mean responses also varied among individuals, but the deutan observers especially deuteranomalous observers over-accommodated substantially compared to color normal observers. We also found that during the calibration procedure all five deutan observers over-accommodated for the static (stationary) target. In deuteranopes the M-cone photopigment (chlorolabe) is completely absent and is replaced by the L-cone photopigment (erythrolabe) in both L-cones and M-cones, while deuteranomalous trichromats have an abnormal M-cone photopigment (chlorolabe) with an absorption spectrum that is displaced toward longer wavelengths. Thus deutan observers may over-accommodate in an attempt to bring longer wavelength light into focus on the retina.

The peaks of L-cone and M-cone photopigment absorption spectra are separated by approximately 0.3 D, which is similar to amount of over-accommodation of the two dichromats (S13 and S14). However three anomalous observers (S10-12) over-accommodated much more substantially, with average responses for the group of 3.5 D and >5 D for S10 (Figure 5). Despite the presence of substantial defocus-blur from over-accommodation S10 and S12 responded with high dynamic gain to vergence modulating at 0.2 Hz. This behavior does not support the standard model of accommodation as a contrast-maximizing negative feedback system. Instead these deuteranomalous observers respond with high gain to temporal modulations of optical vergence despite the presence of substantial blur from over-accommodation. Some normal trichromats also over-accommodate this way and respond with high dynamic gain under open-loop conditions where feedback from blur is absent (Kruger, Mathews *et a*l., 1997). This suggests that normal and deuteranomalous trichromats accommodate to change in angle of incidence of light at edges in conjunction with polychromatic blur of the retinal image.

Fincham (1953) found that two anomalous trichromats (1 deuteranomalous and 1 protanomalous) were able to use the effects of LCA as a directional cue to accommodation as effectively as color normal subjects. He also found that 50% of dichromats showed no accommodation response at all, while the other 50% of dichromats were able to accommodate, but they could not use chromatic aberration to improve accommodation. In agreement with Fincham (1953) we found that one deutanomalous observer showed increased gain in white light suggesting the ability to use LCA as a directional stimulus for accommodation, and one of the two dichromats in the present study could not accommodate at all to the moving target. However, different from Fincham (1953) we found that the second dichromat did use LCA to increase dynamic gain. In Fincham's experiment, a heterochromatic mixture of red and green light was used to provide a yellow illumination condition that included the effects of chromatic aberration. Thus Fincham's heterochromatic condition stimulated L- and M-cones, but not S-cones, which only respond to short-wavelength light below approximately 520 nm. In the present experiment we use broadband white light (tungsten-halogen source; 3000K) to stimulate all three cone types (L, M, S). Since dichromatic observers lack one of the retinal photopigments and the same photopigment is found in both L-cones and M-cones, they cannot compare long- and middle-wavelength cone contrasts which specify the sign of ocular defocus for color-normal observers. To explain our result we hypothesize that some dichromats use a second color-opponent mechanism (S-[L+M]) to compare S-cone contrast and luminance contrast (L+M) and thus provide a signed signal to accommodation.

Pupil size and higher-order aberrations

We found that LCA continued to provide a useful signal to accommodation at large pupil sizes despite the increased monochromatic aberrations. Yet McLellan *et al.* (2002) concluded that monochromatic aberrations attenuate the effects of LCA and help the eye defend against chromatic blur. While monochromatic aberrations may defend against chromatic blur at high spatial frequencies, the effects of LCA are most effective for reflex accommodation at intermediate spatial frequencies between 3 and 5 c/deg (Mathews, 1998; Mathews & Kruger, 1994; Stone, Mathews, & Kruger, 1993). Defocus and other aberrations of the eye reduce retinal image contrast as a function of spatial frequency. The effect is most prominent at high spatial frequencies (> 30 c/deg) and minimum at very low spatial frequencies (< 0.3 c/deg). But at intermediate spatial frequencies (0.5-8 c/deg) defocus and LCA have moderate effects on image contrast, and dynamic accommodation responds best around 3 c/deg. At 3 c/deg higher order aberrations have minimal effect on contrast of the retinal image and defocus and LCA are the principal cause of retinal blur. The target in the present experiment was a Maltese cross with broadband spatial frequency content. Thus higher order aberrations may defend against chromatic blur at high spatial frequencies (McLellan *et a*l., 2002) but they do not attenuate the effects of LCA when the target includes intermediate spatial frequencies even at large pupil sizes.

The present findings support the view that blur from defocus and chromatic aberration specifies optical vergence at intermediate spatial frequencies for accommodation, emmetropization and depth perception (Fincham, 1951, 1953; Nguyen, Howard, & Allison, 2005; Rucker & Osorio, 2008; Rucker & Wallman, 2008).

Acknowledgements:

The research was supported by grants from the National Eye Institute of NIH (2R01-EYO5901) to Philip B. Kruger, and Minnie Flaura Turner Memorial Fund for Impaired Vision Research to Yinan Wang. I thank Lawrence Stark for helping with experimental design and statistical analysis.

Figure Legends

Figure 1.

Badal stimulus system. The illumination system is in dashed lines and the target system in solid lines.

Figure 2.

Calibration plot of a typical normal subject. The crosses show the subject's accommodative responses (Y-axis) to the stimuli (X-axis). The diagonal line represents the unit ratio line showing equal units of accommodative stimulus and response.

Figure 3.

Mean gain for fourteen subjects under four stimulus conditions. 1-9 are normal subjects, 10-12 are deuteranomalous subjects, and 13-14 are dichromatic subjects.

Figure 4.

Calibration plots of Subject 11 (deuteranomalous trichromat) and Subject 13 (deuteranopic dichromat). The crosses show the subject's accommodative responses (Y-axis) to the stimuli (X-axis). The diagonal line represents the unit ratio line showing equal units of accommodative stimulus and response.

Figure 5

Mean accommodation responses of the three different subject groups for four conditions. Single-hatched bars represent the normal observer group, dotted bars represents the deuteranomalous observer group, and grey bars represent the dichromatic observer group. Error bars are one SE.

Figure 6.

Typical accommodation data from one normal subject for four stimulus conditions. The top trace is the accommodative stimulus and the four traces below are the accommodative responses for each of the four conditions. Each trace is for one 40-sec trial.

Figure 7.

Box plots of gain ratios (monochromatic / white) for two pupil sizes (top) and gain ratios (3 mm pupil / 5.7 mm pupil) for two illumination conditions (bottom). Gain ratios are given on the y-axis, and different conditions on the x-axis. The boxes represent the inter-quartile range. The upper and lower edges of the boxes indicate the 75th and 25th percentile. The horizontal line in the box represents the median value. The ends of the vertical lines indicate the minimum and maximum values. The box and the whiskers together indicate the area within which all data are found.

Figure 8.

RMS higher order aberrations for 13 subjects for two different pupil analysis sizes. Gray bars are for 3mm pupil and hatched bars are for 5.7mm pupil. 1-9 are normal subjects, 10-12 are deuteranomalous subjects, and 13 is a dichromatic subject.

Table Legends

Table 1.

Four experimental conditions.

Table 2.

Each subject's mean dynamic gains and mean phase-lags for the four conditions. Bold letters are the averages of all subjects' mean gains and mean phase-lags in each of the three subject groups.

Table 3.

Each subject's mean accommodation responses for the four conditions. Bold letters are the averages of all subjects' mean accommodation responses in each of the three subject groups.

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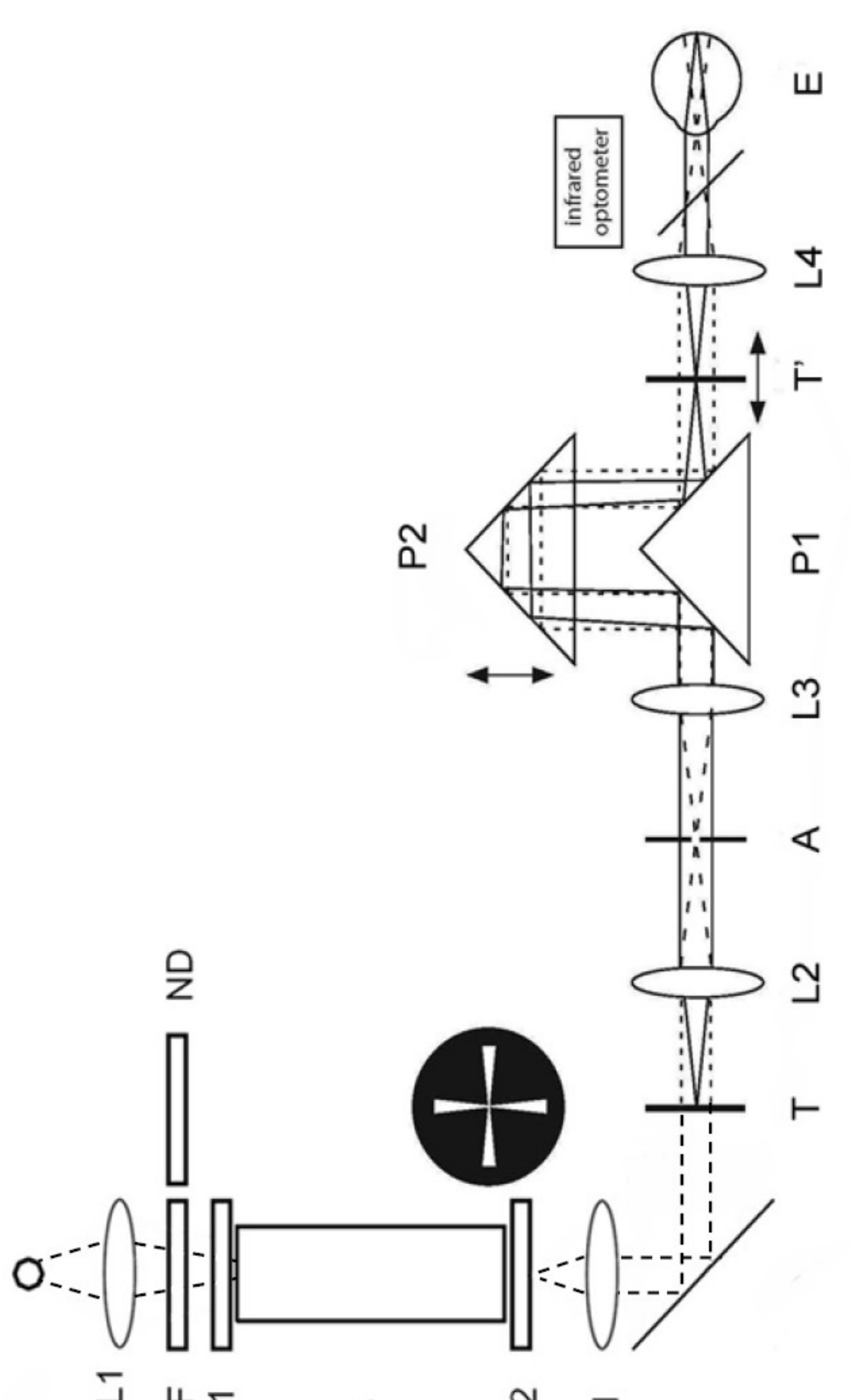


Fig. 1

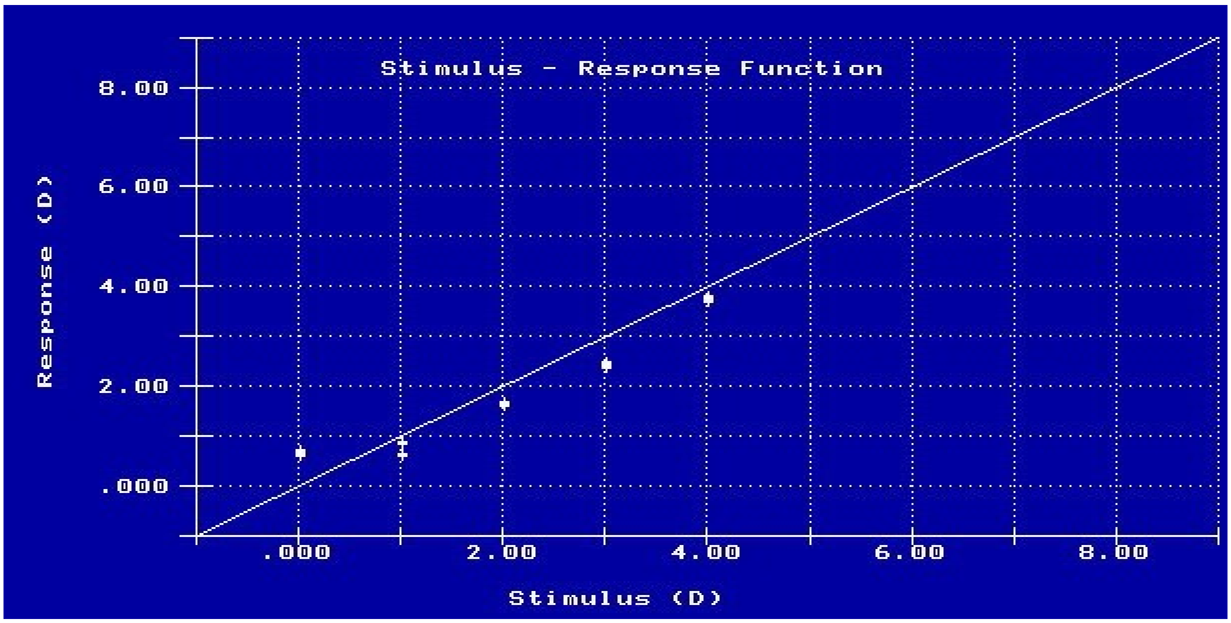

Stimulus - Response Function
8.00
6.00
4.00
2.00
.000
Response (D)
.000
2.00
4.00
6.00
8.00
Stimulus (D)

Fig. 2

Conditions	Illumination	Artificial pupil size
1	White light (3000 K; 20 cd/m^2)	5.7 mm
2	White light (3000 K; 20 cd/m^2)	3 mm
3	Monochromatic light (550 nm with 10 nm bandwidth; 20 cd/m^2)	5.7 mm
4	Monochromatic light (550 nm with 10 nm bandwidth; 20 cd/m^2)	3 mm

Table 1

Subject	White + 5.7mm		White + 3mm		Mono + 5.7mm		Mono + 3mm	
	mean gain	mean phase lag	mean gain	mean phase lag	mean gain	mean phase lag	mean gain	mean phase lag
1	0.14	-59.89	0.26	-56.43	0.03	-76.58	0.01	-4.03
2	0.45	-36.60	0.36	-46.61	0.36	-60.20	0.12	-74.58
3	1.26	-23.65	1.01	-32.39	1.23	-32.56	1.10	-40.48
4	0.73	-41.77	0.58	-49.04	0.59	-48.98	0.50	-56.63
5	0.15	-55.90	0.17	-59.50	0.05	-49.82	0.01	12.07
6	0.26	-63.59	0.16	-69.81	0.11	-71.80	0.09	-83.79
7	0.52	-91.70	0.63	-127.87	0.42	-109.85	0.44	-140.89
8	0.41	-68.85	0.53	-62.71	0.34	-91.77	0.21	-86.91
9	0.33	-63.99	0.27	-65.56	0.17	-84.30	0.04	-62.00
Average	**0.44**	**-48.41**	**0.38**	**-59.71**	**0.32**	**-58.28**	**0.23**	**-65.03**
10*	0.63	-52.61	0.41	-80.49	0.46	-64.79	0.28	-62.35
11*	0.02	-32.54	0.02	-167.32	0.02	-69.01	0.01	147.97
12*	1.06	-38.80	0.68	-55.07	1.06	-38.60	0.75	-50.63
Average	**0.56**	**-43.82**	**0.35**	**-65.70**	**0.50**	**-46.71**	**0.34**	**-53.98**
13†	0.06	131.56	0.05	115.86	0.05	124.12	0.01	114.83
14†	0.73	-54.66	0.55	-50.82	0.53	-59.97	0.26	-62.67
Average	**0.34**	**-55.18**	**0.25**	**-49.57**	**0.24**	**-60.36**	**0.12**	**-62.52**

* Deuteranomalous trichromats

† Deuteranopic dichromats

Table 2

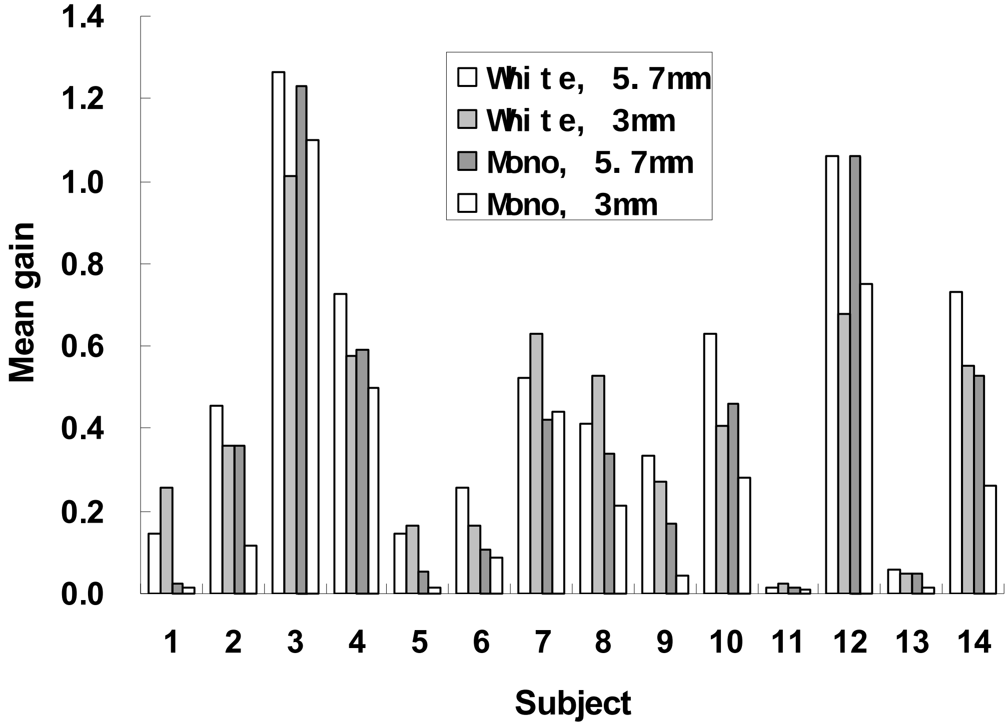
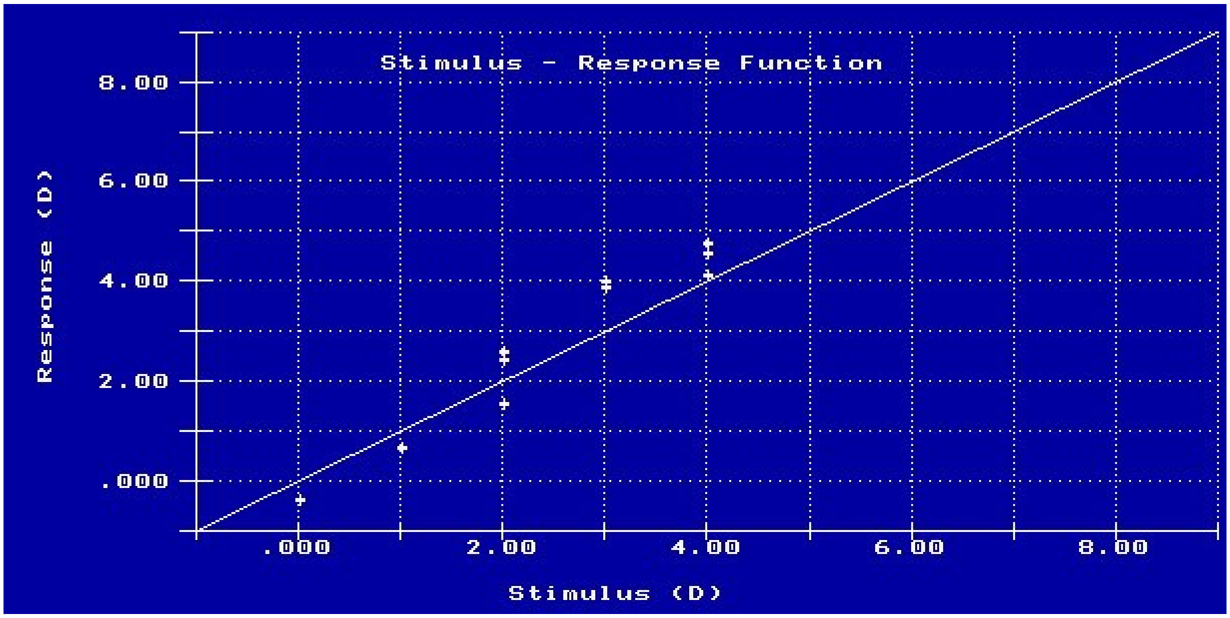

1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
Mean gain
White, 5.7mm
White, 3mm
Mono, 5.7mm
Mono, 3mm
1
2
3
4
5
6
7
8
9
10
11
12
13
14
Subject

Fig. 3


Stimulus - Response Function
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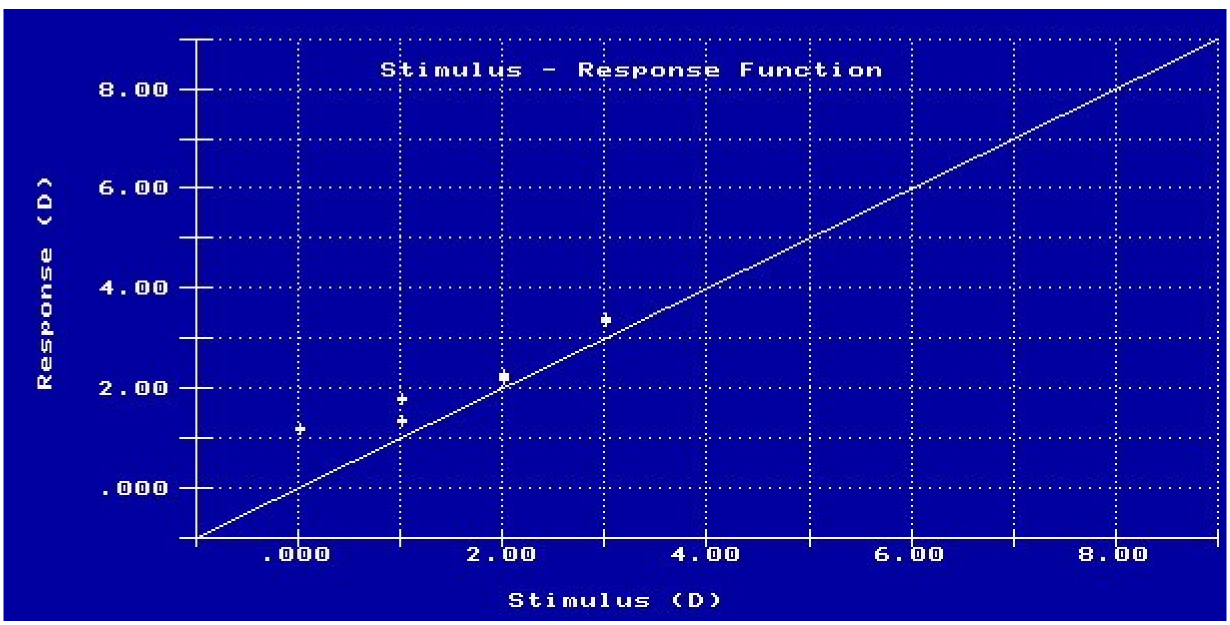
6.00
4.00
2.00
.000
Response (D)
.000
2.00
4.00
6.00
8.00
Stimulus (D)

S 11


Stimulus - Response Function
8.00
6.00
4.00
2.00
.000
Response (D)
.000
2.00
4.00
6.00
8.00
Stimulus (D)

S 13

Fig. 4

Subject	White + 5.7mm	White + 3mm	Mono + 5.7mm	Mono + 3mm
	mean AR	mean AR	mean AR	mean AR
1	2.55	2.38	2.34	2.47
2	2.34	2.28	2.50	2.46
3	1.15	1.32	0.99	0.62
4	0.98	0.99	1.02	0.93
5	2.61	2.20	2.31	2.44
6	2.02	1.69	1.87	1.81
7	3.72	3.52	3.83	2.63
8	2.60	2.62	2.95	3.10
9	2.30	1.84	2.38	2.21
Average	**2.25**	**2.09**	**2.24**	**2.07**
10*	5.11	4.73	3.94	4.04
11*	2.93	2.93	2.99	2.89
12*	3.93	2.99	3.49	3.06
Average	**3.99**	**3.55**	**3.47**	**3.33**
13†	2.04	2.09	2.09	2.02
14†	3.04	2.95	2.66	2.60
Average	**2.54**	**2.52**	**2.38**	**2.31**

* Deuteranomalous trichromats

† Deuteranopic dichromats

Table 3

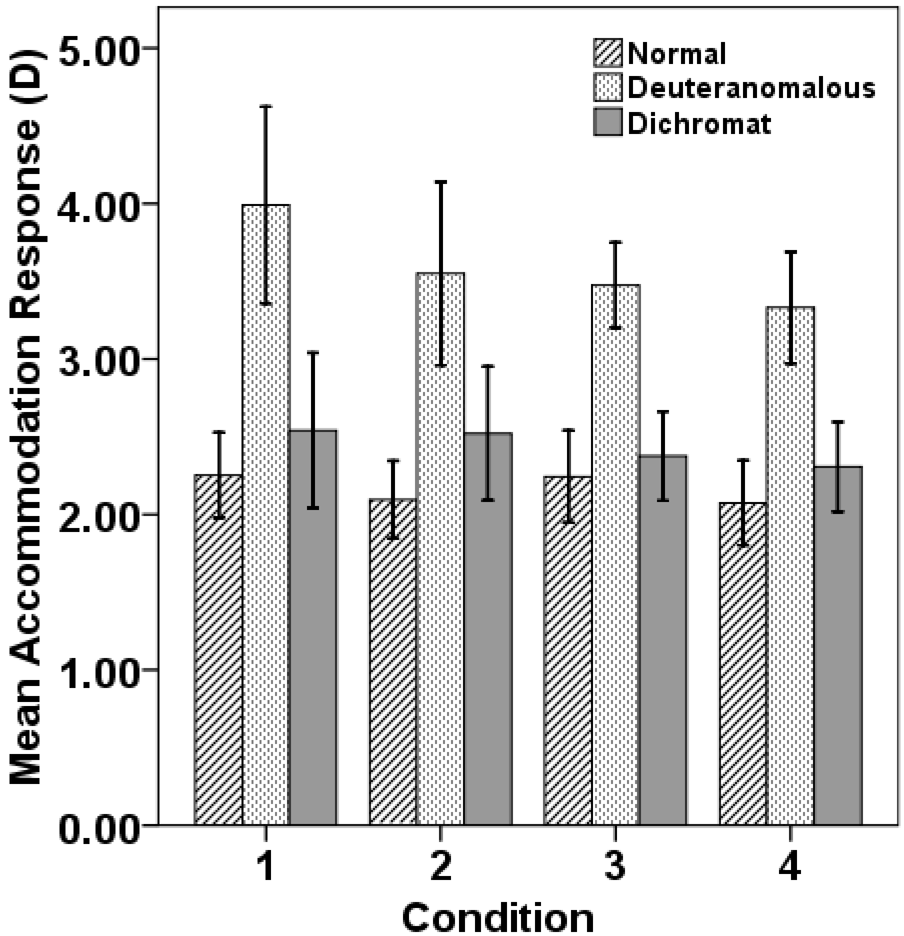

Mean Accommodation Response (D)
5.00
4.00
3.00
2.00
1.00
0.00
Normal
Deuteranomalous
Dichromat
1
2
3
4
Condition

Fig. 5

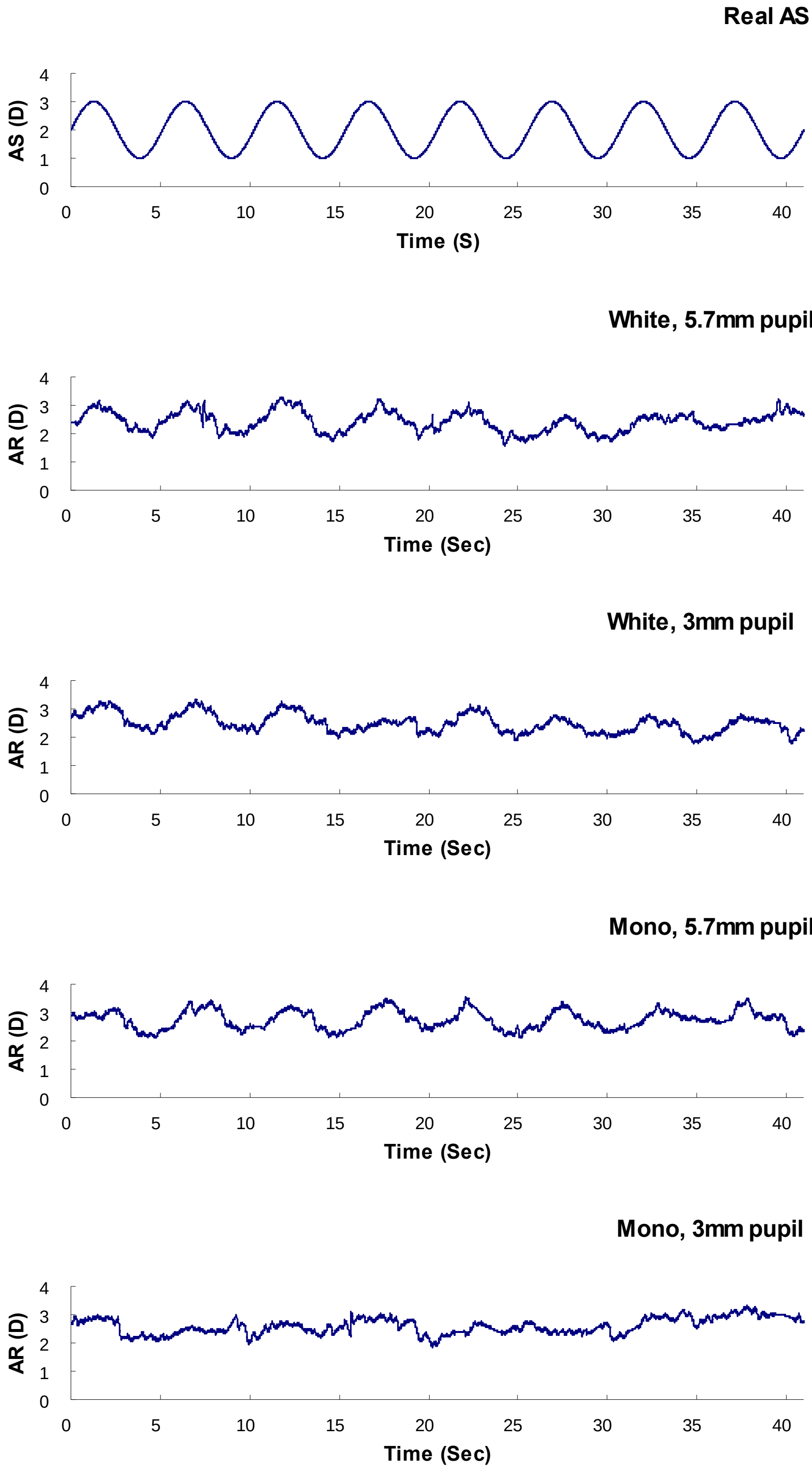

Real AS
AS (D)
4
3
2
1
0
0
5
10
15
20
25
30
35
40
Time (S)
White, 5.7mm pupil
AR (D)
Time (Sec)
White, 3mm pupil
AR (D)
Time (Sec)
Mono, 5.7mm pupil
AR (D)
Time (Sec)
Mono, 3mm pupil
AR (D)
Time (Sec)

Fig. 6

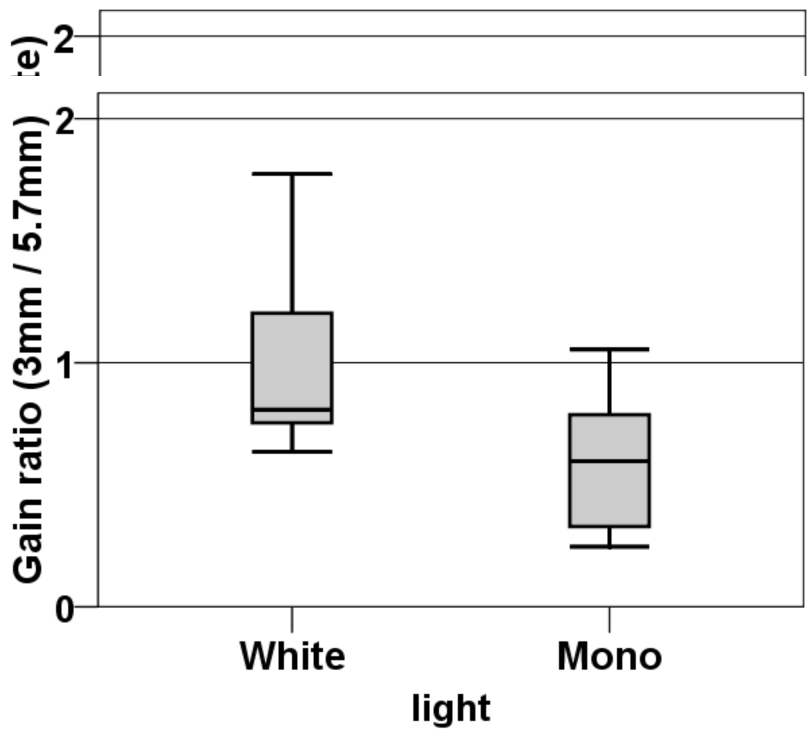


Fig. 7

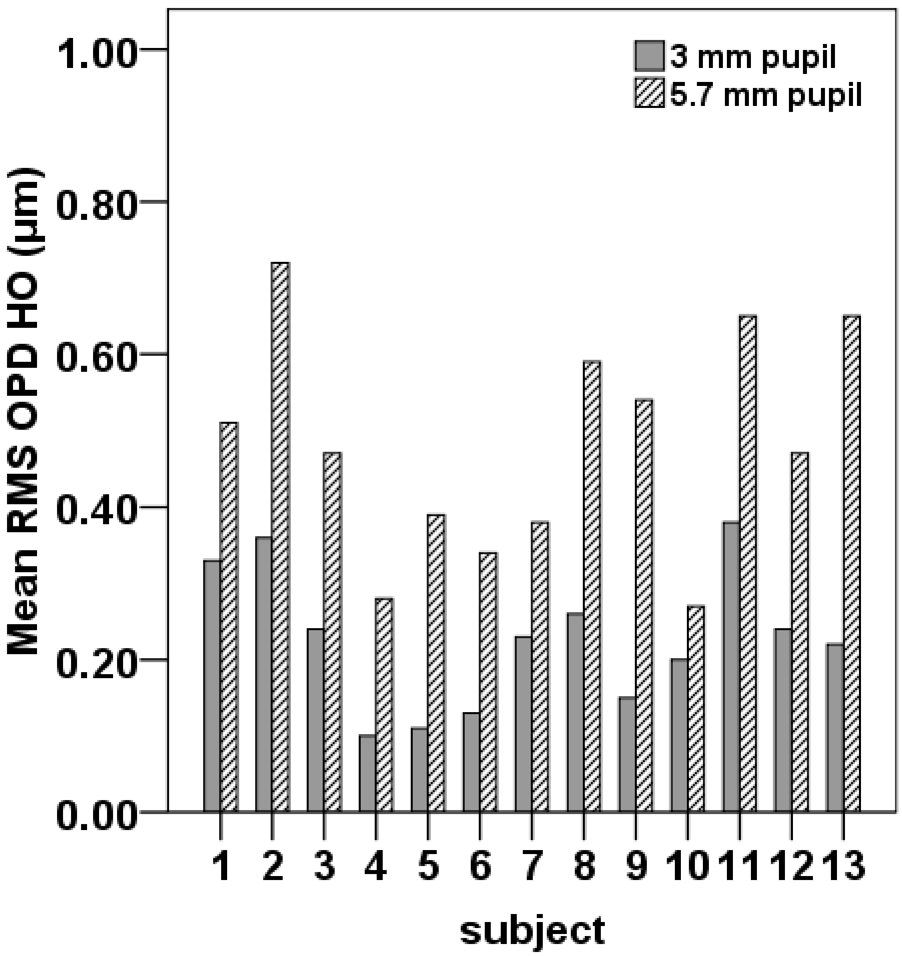

3 mm pupil
5.7 mm pupil
Mean RMS OPD HO (µm)
1.00
0.80
0.60
0.40
0.20
0.00
1
2
3
4
5
6
7
8
9
10
11
12
13
subject

Fig. 8