

Accommodation with and without short-wavelength-sensitive cones and chromatic aberration

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Abstract

Accommodation was monitored while observers (23) viewed a square-wave grating (2.2 cycles/deg; 0.53 contrast) in a Badal optometer. The grating moved sinusoidally (0.2 Hz) to provide a stimulus between -1.00 D and -3.00 D during trials lasting 40.96 s. There were three illumination conditions: 1. Monochromatic 550 nm light to stimulate long-wavelength-sensitive cones (L-cones) and medium-wavelength-sensitive cones (M-cones) without chromatic aberration; 2. Monochromatic 550 nm light + 420 nm light to stimulate long-, medium- and short-wavelength-sensitive cones (S-cones) with longitudinal chromatic aberration (LCA); 3. Monochromatic 550 nm light + 420 nm light to stimulate L-, M- and S-cones viewed through an achromatizing lens. In the presence of LCA mean dynamic gain decreased ($p = 0.0003$; ANOVA) and mean accommodation level was reduced ($p = 0.001$; ANOVA). The reduction in gain and increased lag of accommodation in the presence of LCA could result from a blue-yellow chromatic signal or from a larger depth-of-focus.

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1. Introduction

The standard view of accommodation control is that luminance contrast provides the stimulus (Bobier, Campbell, & Hinch, 1992; Charman & Tucker, 1978; Heath, 1956; Phillips & Stark, 1977; Stark & Takahashi, 1965; Troelstra, Zuber, Miller, & Stark, 1964; Wolfe & Owens, 1981). Since blur from defocus reduces luminance contrast both for myopic and hyperopic defocus, the stimulus from defocus blur is an “even-error” signal without directional quality, and feedback from changes in defocus is an essential part of the accommodative process. However, several lines of evidence suggest that

“odd-error” signals provide the sign of defocus for accommodation (Fincham, 1951; Flitcroft, 1990; Kruger, Mathews, Katz, Aggarwala, & Nowbotsing, 1997b; Lee, Stark, Cohen, & Kruger, 1999; Rucker & Kruger, 2004a; Smithline, 1974; Stark, Lee, Kruger, Rucker, & Fan, 2002b). Similarly experiments on animals show that signed error signals control the coordinated growth and development of axial length and optical components of the eye (Park, Winawer, & Wallman, 2003; Schaeffel & Diether, 1999; Smith & Hung, 1999; Smith, Hung, & Harwerth, 1994; Wildsoet & Schmid, 2001; Wildsoet & Wallman, 1995). We propose that the signed signals that control emmetropization also could control accommodation (Rucker & Kruger, 2001).

Fincham (1951) was the first to show that a chromatic signal from the longitudinal chromatic aberration

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(LCA) of the eye provides the sign of defocus for accommodation. He also suggested that a luminance signal from the angle of incidence of light reaching the retina distinguishes myopic from hyperopic defocus (Fincham, 1951). One possibility is that the directional sensitivity of cones (Stiles–Crawford effect Type 1) extracts the sign of defocus (Fincham, 1951; Kruger, López-Gil, & Stark, 2001; Kruger, Stark, & Nguyen, 2004; Stark, Kruger, & Atchison, 2002a) and monochromatic aberrations of the eye also could play a role (Chen, Kruger, & Williams, 2002; Fernandez & Artal, 2002; Wilson, Decker, & Roorda, 2002).

Most investigators have agreed with Fincham's findings regarding the chromatic signal from LCA (Aggarwala, Kruger, Mathews, & Kruger, 1995a; Aggarwala, Nowbotsing, & Kruger, 1995b; Flitcroft, 1990; Kotulak, Morse, & Billock, 1995; Kruger, Mathews, Aggarwala, & Sanchez, 1993; Kruger, Aggarwala, Bean, & Mathews, 1997a; Kruger, Mathews, Aggarwala, Yager, & Kruger, 1995a; Kruger, Nowbotsing, Aggarwala, & Mathews, 1995b; Kruger & Pola, 1986; Lee et al., 1999; Rucker & Kruger, 2004a; Stark et al., 2002b), but some investigations have provided contrary evidence (Bobier et al., 1992; Charman & Tucker, 1978; Stark & Takahashi, 1965; Troelstra et al., 1964; van der Wildt, Bouman, & van de Kraats, 1974). The reasons for the disagreement have been summarized by Kruger et al. (1997a), Lee et al. (1999) and Stark et al. (2002b).

Chromatic dispersion of light by the ocular media produces a chromatic-difference-of-focus across the visible spectrum that approaches 2.5 diopters between 380 nm and 760 nm. This results in a difference in contrast between the long- middle- and short-wavelength components of the broadband retinal image (Marimont & Wandell, 1994) that provides a signed chromatic signal for accommodation (Flitcroft, 1990; Kruger et al., 1995a). Although recent calculations show that monochromatic aberrations reduce the difference in contrast between the wavelength components of the retinal image especially when the pupil is large (McLellan, Marcos, Prieto, & Burns, 2002), experiments show that when the pupil size is moderate (3 mm) LCA provides an effective directional stimulus (e.g. Kruger et al., 1993, 1997a, 1997b; Kruger & Pola, 1986; Stone, Mathews, & Kruger, 1993). Since the rate of change in focus as a function of wavelength (LCA) is much larger for short-wavelength light than for long-wavelength light (Bedford & Wyszecki, 1957; Thibos, Ye, Zhang, & Bradley, 1992) the “chromatic-difference-of-contrast” per nanometer change in wavelength is larger for short-wavelength light than for longer wavelengths (Marimont & Wandell, 1994).

As a consequence of LCA the three cone types (long-, middle- and short-wavelength-sensitive cones) effectively sample the retinal image in three different focal planes (Crane, 1966). Thus a comparison of the cone-contrasts

of the image, at a single plane of focus, could provide the sign of defocus (Flitcroft, 1990). In support of this view, dynamic accommodative gain (ratio of response amplitude to stimulus amplitude) increases monotonically when the spectral bandwidth of illumination is increased from narrowband monochromatic light to broadband white light (Aggarwala et al., 1995a; Kotulak et al., 1995). In addition, simulations of the effects of defocus and LCA drive accommodation in the predicted direction (Kruger et al., 1995a, Lee et al., 1999; Rucker & Kruger, 2004a; Stark et al., 2002b). These experiments support the notion that L- and M-cones extract a chromatic signal from the retinal image that provides the sign of defocus. Recently, Rucker and Kruger (2004a) altered L- and M-cone contrasts independently and found that the ratio of L-cone contrast to M-cone contrast significantly alters the mean level of accommodation. At both luminance and chromatic borders, high L-cone contrast combined with low M-cone contrast reduces accommodation for near, while high M-cone contrast with low L-cone contrast increases accommodation for near.

Since the rate of change of defocus is greater for short-wavelength light than for long-wavelength light, the participation of S-cones in the process might provide a stronger chromatic signal for accommodation than the response from a comparison of L- and M-cone contrasts. Rucker and Kruger (2001) isolated S-cones and showed that some subjects can accommodate using only S-cones; however the dynamic response (gain) from S-cones alone was smaller than the dynamic response from L- and M-cones together. In addition latencies and time-constants of accommodation to step changes in target vergence were significantly longer for S-cones alone than for LM-cones (Rucker & Kruger, 2004b). Thus the dynamic accommodation response from S-cones might be too slow to improve the directional signal from LCA. In the present experiment we examine dynamic accommodation at 0.2 Hz mediated by LM-cones with and without S-cones, both with and without LCA.

2. Methods

2.1. Subjects

Twenty seven subjects volunteered to participate in the experiment. Two subjects dropped out before data collection had been completed, and two subjects were eliminated during preliminary trials because they could not accommodate to the target in the Badal stimulus system. The remaining 23 subjects participated in the study and were paid for participation. All subjects had 6/6 visual acuity or better, normal color vision (Nagel anomaloscope and D-15 test) and no history of strabismus, amblyopia, ocular disease, injury, or surgery. Sub-

jects' ages ranged from 22 to 28 years. Spherical refractions ranged from plano to -7.5 D, with cylinders up to -0.83 D. Refractive errors were corrected by the subjects' habitual contact lenses or by trial lenses. Subjects gave informed consent to participation, the experiment was approved by the Institutional Review Board of the College, and followed the tenets of the Declaration of Helsinki.

2.2. Apparatus

Accommodation was monitored by a high-speed infrared optometer while the subject viewed a vertical square-wave grating (2.2 cpd; 0.53 contrast) in a Badal stimulus system. The infrared optometer monitors the refractive state of the eye continuously along the vertical meridian of the eye at 100 Hz. The optometer is insensitive to changes in pupil size for pupils larger than 3 mm in diameter, and to eye movements within 2° of the target center. The design and operating principles of the infrared optometer have been described previously (Kruger, 1979).

The Badal optical system is similar to the stimulus system used by Rucker and Kruger (2004b) to examine the step response of accommodation mediated by S-cones alone and with LM-cones. Fig. 1 is a schematic representation of the optical system used for presenting sinusoidally moving targets to the eye. The lenses are all

computer-optimized achromats. The optical system includes an illumination system illustrated by dashed rays, and a superimposed target system illustrated by solid rays. Light from a tungsten-halogen source S is collimated by lens L1 and split into two channels by pellicle beamsplitter 1. Light transmitted by beamsplitter 1 is filtered by a 420 nm interference filter (10 nm bandwidth) to provide blue light for illuminating the grating target from behind. Light reflected by beamsplitter 1 is filtered by a 550 nm interference filter (10 nm bandwidth) to provide green light that is reflected by mirrors 1 and 2 and then recombined with the blue light by pellicle beamsplitter 2. Lens L2 focuses the light source at the front-surface mirror 3, lenses L3 and L4 refocus the light source in the plane of an artificial pupil, and lenses L5 and L6 focus the light source in the pupil of the subject's eye, after reflection at the mirrored surfaces of right-angled prisms 1 and 2. The light source is larger than the artificial pupil which is imaged in the subject's pupil plane as a 3 mm artificial pupil.

The grating target is a 35 mm photographic slide (2.2 c/d vertical square-wave grating with 0.57 contrast) illuminated from behind by collimated light. Light from the grating target (solid rays) is collimated by lens L4, and focused by lens L5 in the focal plane of Badal lens L6, after reflection by prisms 1 and 2. Motion of prism 1 (as shown by the arrow) moves the grating image toward and away from lens L6, thus altering the dioptric

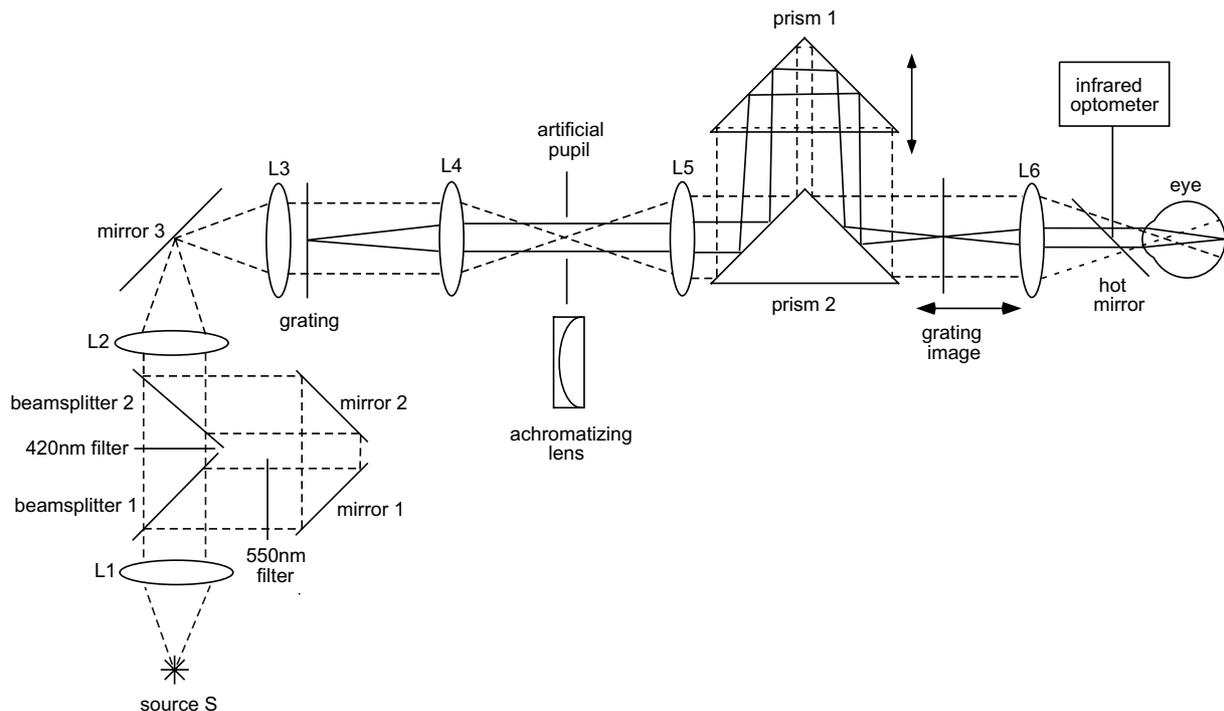


Fig. 1. Schematic representation of the apparatus for monitoring accommodation and presenting moving targets to the eye. Dashed rays illustrate the illumination system, and solid rays illustrate the target system. An achromatizing lens can be inserted to neutralize the longitudinal chromatic aberration of the eye.

stimulus to accommodation. The subject views the grating image in Maxwellian view in Badal lens L6. A shutter (not shown) can eliminate the 420 nm blue light to allow presentation of a green grating or a green + blue grating, and neutral density filters (not shown) are used to equate the luminance of the grating in the various illumination conditions. A blurred field stop (not shown), positioned -5.2 D beyond the far point of the corrected eye limits the field of view to 9.2° .

An achromatizing lens can be placed in the artificial pupil plane to neutralize the longitudinal chromatic aberration of the eye. The lens is a cemented doublet that has zero power at 588 nm, positive power at longer wavelengths and negative power at shorter wavelengths (Kruger et al., 1993). Without the achromatizing lens in the stimulus system mean target vergence at the eye was -2.00 D for both 550 nm and 420 nm light. The achromatizing lens corrects for 1.04 D of LCA between 420 nm and 550 nm and since the average amount of LCA between 550 nm and 420 nm is actually 1.19 D (Thibos et al., 1992) the achromatizing lens under-corrects LCA by 0.15 D between 420 nm and 550 nm. The effect of the achromatizing lens is illustrated in Fig. 2.

2.3. Calibrations

Target vergence was measured through the Badal optical system by using a telescope to view the square-wave grating target along the optical axis of the stimulus system. The telescope was positioned close to the position of the subject's eye (in the focal plane of the Badal lens L6) and the telescope was focused for optical infinity. Trial lenses were placed in front of the telescope in 0.12 D increments until optimal focus of the grating target was achieved. Measurements were made with the target illuminated by 420 nm light and 550 nm light with and without the achromatizing lens in place. Since all the lenses in Fig. 1 are achromatic doublets, target vergence was the same for 420 nm and 550 nm light without the achromatizing lens in place. When the achromatizing lens was added to the system the mean vergence of the target at the eye increased to -2.58 D for 550 nm light and to -3.62 D for 420 nm light, providing a correction of 1.04 D for LCA between these wavelengths (Fig. 2). Since the achromatizing lens under-corrects LCA by 0.15 D between 550 nm and 420 nm, the mean stimulus to accommodation was -2.58 D for 550 nm light, and -2.43 D for 420 nm light (instead of

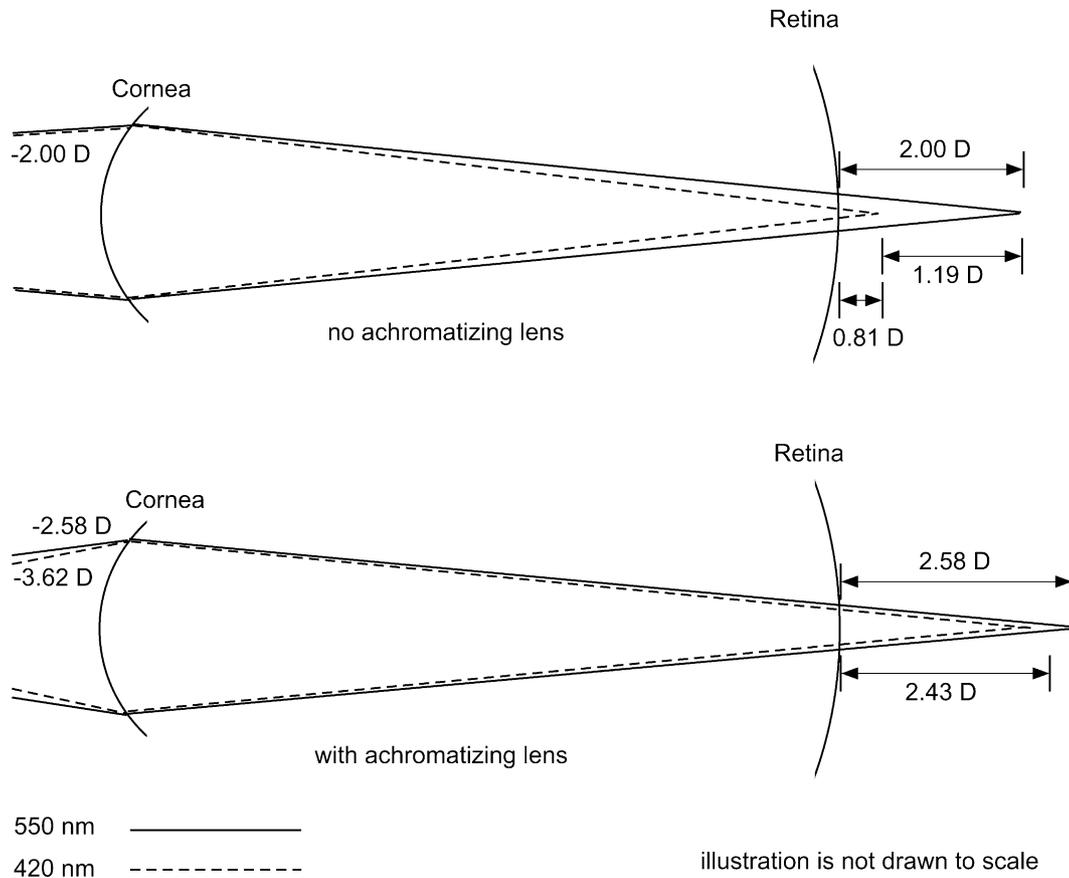


Fig. 2. Ray diagrams (not drawn to scale) illustrate the effect of the achromatizing lens on the vergence of light arriving at the cornea, and the effect on the stimulus for accommodation. The eye is accommodating for far (optical infinity). Solid rays are for 550 nm light, and dashed rays are for 420 nm light. The achromatizing lens under-corrects LCA by 0.15 D.

–2.58 D for both wavelengths). Mean target vergences and mean stimulus to accommodation are summarized for the three illumination conditions in Table 1.

Target luminance and spectral composition were measured through the Badal optical system using the method of Westheimer (1966) for Maxwellian view optics.

The infrared optometer was calibrated for each subject’s eye using a high contrast white Maltese cross as the target (Kruger & Pola, 1986). The Maltese cross includes multiple spatial frequencies and orientations and a central fixation point, and provides an optimal stimulus for accommodation. The method used to calibrate the optometer for each subject’s eye has been described previously (Lee et al., 1999). The method involved simultaneous measurement of optometer voltage output and subjective focus (using a specially designed bichromatic stigmascopes), while the target was positioned at several different accommodation stimulus levels (e.g. 0, –1, –2, –3, –4 and –5 D). Dioptric measures of accommodative response were calculated from the stigmascopes target position, and a linear equation was obtained relating accommodation response in diopters and infrared optometer output (voltage). The method calibrated target vergence with reference to 557 nm light. Computer software compensated for the power and vertex distance of the trial lenses that were placed in front of the subject’s eye, and for the thickness of the hot mirror, to ensure that the mean accommodation stimulus was always –2.00 D.

2.4. Procedures

Subjects were positioned on a chin and forehead rest and the left eye was aligned with the Badal optometer while the examiner monitored eye position using an infrared camera and video display. The right eye was occluded by an eye patch. The subject altered the horizontal position of the left eye using a screw-driven slide to align the visual achromatic axis of the eye (Thibos, Bradley, Still, Zhang, & Howarth, 1990) with the optical axis of the stimulus system (Lee et al., 1999). The examiner noted the position of Purkinje image 1 on the video display, and the eye was positioned in this manner

throughout the experiment. This method of positioning the eye ensured that transverse chromatic aberration was minimized for foveal viewing of the vertical grating during the experimental trials. The room was darkened during the trials and the target was the only visible stimulus. The subject was asked to attend to the center of the target and instructed to “Keep the target clear using the same type of effort as when reading a book.”

There were three illumination conditions: 1. A “Green” condition in which the target was illuminated by monochromatic 550 nm light (10 nm bandwidth; 30 cd/m²) to stimulate both L- and M-cones without LCA; 2. A “Green + Blue + LCA” condition in which the target was illuminated by monochromatic 550 nm light (15 cd/m²) and 420 nm light (10 nm bandwidth; 15 cd/m²) to stimulate L-, M- and S-cones with normal LCA between 550 nm and 420 nm. 3. A “Green + Blue – LCA” condition in which the target was illuminated by monochromatic 550 nm light (15 cd/m²) and 420 nm light (10 nm bandwidth; 15 cd/m²) to stimulate L- M- and S-cones, viewed through an achromatizing lens to eliminate LCA.

Each trial was 40.96 s in duration with a break of approximately 1 min between trials. During the trial the target moved sinusoidally toward and away from the eye at 0.2 Hz. The moderate temporal frequency was chosen because dynamic accommodative gain is still relatively high at 0.2 Hz (Mathews & Kruger, 1994). The spatial frequency of the grating (2.2 cpd) is a compromise, because S-cones respond best below 2 cycles per degree (Daw & Enoch, 1973; Hess, Mullen, & Zrenner, 1989; Humanski & Wilson, 1992; Mollon, 1982; Swanson, 1989) while dynamic accommodation responds best between 3 and 5 cycles per degree (Mathews & Kruger, 1994; Stone et al., 1993). The three illumination conditions were presented 10 times each in random order (30 trials).

2.5. Analysis

Voltage output from the infrared optometer was sampled at 100 Hz and the data from each trial were stored for analysis. Software written in the Asyst programming language (Keithley) was used to analyze the data. Blinks

Table 1

Mean target vergence at the eye, mean stimulus to accommodation, mean accommodation response, and mean accommodation error for the three illumination conditions

	Green	Green + Blue + LCA		Green + Blue – LCA	
	550 nm	550 nm	420 nm	550 nm	420 nm
Mean target vergence (D)	–2.00	–2.00	–2.00	–2.58	–3.62
Mean acc stimulus (D)	–2.00	–2.00	–0.81	–2.58	–2.43
Mean acc response (D)	1.81	1.50	1.50	2.40	2.40
Mean acc error (D)	0.19	0.50	– 0.69	0.18	0.03
	Under-acc	Under-acc	Over-acc	Under-acc	Under-acc

were removed manually and the data were scaled according to the subject's calibration. The mean and linear trend were subtracted from the data before analysis and a Hamming window was applied. Dynamic gain and phase-lag of accommodation were determined at the temporal frequency of the stimulus motion (0.2 Hz) using a fast Fourier transform (FFT) of the data. Dynamic gain is the magnitude of the response FFT at 0.2 Hz divided by the magnitude of the stimulus FFT at 0.2 Hz. Temporal phase-lag is the distance in degrees from the peak of the response to the peak of the stimulus motion. Gains and temporal phase-lags for each trial were vector averaged to obtain mean gain and phase-lag for each condition. Mean gains and phase-lags for each subject were each compared separately among conditions using one-way ANOVA with correlated subjects and paired *t*-tests.

3. Results

Mean dynamic gains and phase-lags for the three conditions are summarized in Table 2, and gains are illustrated in Fig. 3. Mean gains varied widely among the 23 subjects. In the "Green" condition gain varied from a minimum of 0.03 to a maximum of 0.62 with an average gain of 0.33. Mean gains also varied widely among the subjects in the "Green + Blue + LCA" con-

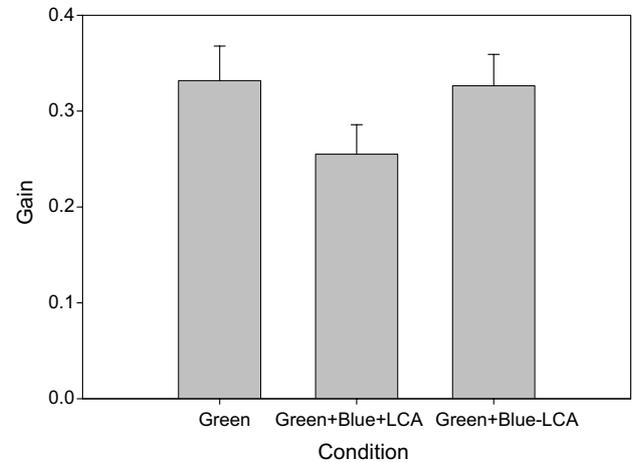


Fig. 3. Gains for the three experimental conditions. Error bars are standard errors of the mean.

dition (0.03–0.58) and in the "Green + Blue – LCA" condition (0.07–0.53). Mean gains for the three conditions were statistically different from each other ($F = 14.01$; $p < 0.0001$, ANOVA). Average gain was the same in the "Green" and "Green + Blue – LCA" conditions ($p = 0.6984$), average gain was reduced by a small but significant amount in the "Green + Blue + LCA" condition ($p = 0.0003$), and the gains for the "Green + Blue + LCA" and the "Green + Blue –

Table 2
Mean dynamic gains and mean phase-lags for the three illumination conditions

Subject	Mean gains			Mean phase-lags		
	Green	Green + Blue + LCA	Green + Blue – LCA	Green	Green + Blue + LCA	Green + Blue – LCA
1	0.52	0.46	0.52	–53	–56	–57
2	0.26	0.28	0.23	–75	–66	–76
3	0.53	0.36	0.41	–75	–70	–69
4	0.50	0.46	0.40	–58	–56	–57
5	0.53	0.58	0.53	–58	–59	–57
6	0.62	0.30	0.49	–61	–58	–49
7	0.16	0.07	0.17	–72	–23	–85
8	0.03	0.03	0.07	–74	–154	–67
9	0.23	0.19	0.28	–75	–68	–67
10	0.13	0.14	0.16	–76	–104	–92
11	0.31	0.22	0.37	–71	–76	–56
12	0.13	0.06	0.17	–96	–78	–80
13	0.09	0.08	0.09	–90	–87	–75
14	0.31	0.23	0.36	–67	–89	–68
15	0.33	0.19	0.36	–37	–59	–42
16	0.52	0.40	0.47	–72	–74	–69
17	0.41	0.19	0.38	–61	–57	–49
18	0.15	0.15	0.16	–66	–86	–78
19	0.20	0.20	0.17	–88	–93	–88
20	0.42	0.34	0.40	–55	–67	–48
21	0.29	0.16	0.26	–65	–69	–85
22	0.52	0.46	0.68	–49	–59	–59
23	0.42	0.29	0.35	–65	–67	–63
Ave	0.33	0.25	0.33	–68	–73	–67
SD	0.17	0.15	0.16	13	24	14

LCA” conditions also were significantly different ($p = 0.0003$).

Mean temporal phase-lags also varied widely among the subjects, but the average phase-lags for the 23 subjects were similar for the three conditions: -68° in the “Green” condition, -73° in the “Green + Blue + LCA” condition, and -67° in the “Green + Blue – LCA” condition. Mean phase-lags for the three conditions were not significantly different from each other ($F = 1.1733$; $p = 0.3188$, ANOVA).

Mean accommodation levels for the three conditions are summarized in Table 3 and Fig. 4. Mean accommodation level also varied widely among the subjects, but changed significantly between conditions ($F = 7.39$; $p = 0.001$). When LCA was neutralized by the achromatizing lens the stimulus increased to -2.58 D for 550 nm light, and the mean response increased to 2.4 D. This resulted in a lag of accommodation of 0.18 D, which was the same as the lag of accommodation in the “Green” condition (0.19 D). The increase in mean response with the achromatizing lens in place is attributed to the increase in the stimulus to accommodation from the achromatizing lens. On the other hand, the averaged mean level decreased significantly from 1.81 D to 1.50 D when short-wavelength light was added to the stimulus with normal LCA ($p < 0.001$), increasing the lag of accommodation to 0.5 D (for a -2.00 D stimulus to accommodation at 550 nm). Thus the addition of

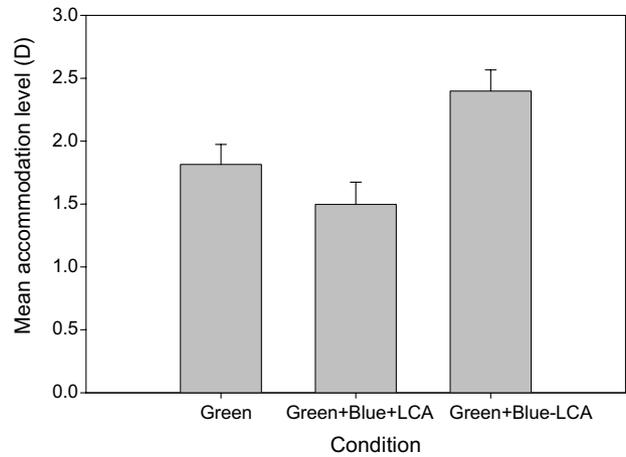


Fig. 4. Mean accommodation level for the three experimental conditions. Error bars are standard errors of the mean.

short-wavelength light with LCA increased the lag of accommodation.

4. Discussion

4.1. Wide variation in accommodation response among subjects

A striking result in the present experiment is the very wide variation in dynamic gain from one subject to another. Some subjects responded poorly to the sinusoidal changes in target vergence with very low gains (e.g. 0.03) while others responded well with gains as high as 0.62. Wide variation in dynamic gain between subjects is typical for experiments of this type, and wide variation in accommodation to blur-driven accommodation has been reported by several investigators (Aggarwala et al., 1995a, 1995b; Campbell & Westheimer, 1959; Charman & Tucker, 1978; Fincham, 1951; Kruger et al., 1993, 1997a, 1997b; Schaeffel, Wilhelm, & Zrenner, 1993). Broad differences in gain are common for targets illuminated by narrowband monochromatic light, as well as for targets illuminated by broadband “white” light (e.g. Aggarwala et al., 1995a, 1995b; Kruger et al., 1993, 1997a, 1997b). Subjects also show large differences in accommodation to the effects of LCA (Fincham, 1951; Kruger et al., 1993, 1995a, 1995b, 1997a, 1997b; Lee et al., 1999; Rucker & Kruger, 2004a; Stark et al., 2002b; Troelstra et al., 1964). In addition to large differences in reflex (blur-driven) accommodation among subjects, there are also wide differences in other types of accommodation, including voluntary accommodation (Cornsweet & Crane, 1973; Marg, 1951; McLin & Schor, 1988; Provine & Enoch, 1975; Stark & Kruger, 2002), tonic accommodation (Leibowitz & Owens, 1975, 1978; Rosenfield, Ciuffreda, Hung, & Gilmartin, 1994) and proximal

Table 3
Mean accommodation levels for the three illumination conditions

Mean accommodation response levels (D)			
Subject	Green	Green + Blue + LCA	Green + Blue – LCA
1	3.67	3.53	3.84
2	-0.23	-0.61	0.81
3	1.33	0.09	1.88
4	2.33	1.58	2.98
5	1.85	0.85	2.08
6	3.00	2.02	3.67
7	1.88	1.40	2.40
8	1.06	1.39	1.15
9	1.40	0.87	1.79
10	1.22	1.34	1.92
11	1.16	0.49	1.45
12	1.85	1.68	2.17
13	1.75	1.64	1.85
14	1.43	0.99	2.03
15	1.21	1.20	1.84
16	2.17	1.95	3.12
17	2.28	2.15	2.92
18	2.20	1.93	2.57
19	1.97	1.85	2.52
20	2.15	2.27	3.27
21	1.55	1.44	2.11
22	2.36	1.92	3.43
23	2.14	2.45	3.32
Ave	1.81	1.50	2.40
SD	0.76	0.84	0.81

accommodation (Ittelson & Ames, 1950; Kruger & Pola, 1985, 1986; McLin, Schor, & Kruger, 1988; Stark & Kruger, 2002; Takeda, Iida, & Fukui, 1990). In fact the wide variation in accommodative response is typical of all types of accommodation, and is a hallmark of the accommodation response.

4.2. Cone contributions to blur-driven accommodation

Several previous experiments suggest that L- and M-cones extract a chromatic signal [L–M] from the retinal image that provides the sign of defocus (Aggarwala et al., 1995a; Kotulak et al., 1995; Kruger et al., 1997b, Lee et al., 1999; Rucker & Kruger, 2004a; Stark et al., 2002b). Recently Rucker and Kruger (2004a) altered the ratio of L- and M-cone contrasts directly and found that changes in the L/M-cone contrast ratio produce significant changes in the mean level of accommodation. When high L-cone contrast was combined with low M-cone contrast the mean level of accommodation was reduced for near. Conversely, when high M-cone contrast was combined with low L-cone contrast accommodation increased for near. These ratios of L/M-cone contrasts simulate myopic and hyperopic defocus respectively. The result confirmed the hypothesis that LCA alters the L/M-cone contrast ratio, and provides a directional signal for accommodation (Rucker & Kruger, 2004a). Thus L- and M-cones contribute to a chromatic (L–M) mechanism that controls both static and dynamic accommodation.

Since the rate of change in focus as a function of wavelength (LCA) is much larger for short-wavelength light than for long-wavelength light (Bedford & Wyszecki, 1957) the participation of S-cones in the process may provide a stronger chromatic signal ($S - [L + M]$) for accommodation than from a comparison of L- and M-cone contrasts (Flitcroft, 1990). A contribution from S-cones has been demonstrated by Rucker and Kruger (2001, 2004a) who found that the eye over-accommodated for near targets when the response was driven by isolated S-cones. In the absence of signals from LM-cones, the eye focused the blue component of the retinal image substantially in front of the retina, despite the resulting blur from defocus. A similar result was obtained by Seidemann and Schaeffel (2002). One explanation for the over-accommodation by isolated S-cones may be that S-cones “prefer” myopically defocused images, since this is the habitual focus condition for the blue component of the image when viewing in broadband white light. The relatively coarse S-cone retinal mosaic may be protected from aliasing by the presence of LCA, which ensures that the high spatial frequencies of the blue component of the image do not reach the retina (Williams, Collier, & Thompson, 1983).

Despite the evidence that S-cones can control accommodation on their own, the present results show no

improvement in dynamic gain or phase-lag when short-wavelength light was added to the stimulus with or without LCA. This suggests that a directional signal from a chromatic mechanism that compares S- and LM-cone contrasts ($S - [L + M]$) does not assist accommodation at 0.2 Hz. One explanation is that the accommodation response mediated by S-cones is too slow to improve the gain and phase-lag of the response at the temporal frequency used in the present experiment (0.2 Hz). In support of this explanation, Rucker and Kruger (2004b) found that the latencies and time-constants for the accommodation response mediated by S-cones alone to step changes in vergence were two to three times longer than the latencies and time-constants for accommodation mediated by LM-cones. Thus the slow accommodation response from S-cones may actually reduce dynamic gain at 0.2 Hz. In the present experiment gain was reduced by a small amount (0.33–0.25) in the Green + Blue + LCA condition ($p = 0.0003$). This is in contrast to the increase in dynamic gain in all the previous experiments where LCA was added between L- and M-cones (Aggarwala et al., 1995a, 1995b; Kotulak et al., 1995; Kruger et al., 1993, 1995a, 1995b, 1997a, 1997b; Kruger & Pola, 1986). Kruger et al. (1995b) used a combination of monochromatic red (600 nm) and green (520 nm) light to show that normal amounts of LCA increase dynamic gain significantly. The explanation for the decrease in gain in the present experiment may be that LCA was absent between L- and M-cones, but there was a normal amount of LCA between S-cones and LM-cones. Thus gain was impaired by a difference in S- and LM-cone contrasts in the absence of a difference between L- and M-cone contrasts. It seems that LCA between L- and M-cones provides a powerful chromatic signal that can overcome the effect of a larger depth-of-focus from LCA in “white” light.

Another explanation for the reduced gain in the presence of LCA in this experiment is that the combination of green (550 nm) and blue (420 nm) light increased the depth-of-focus of the eye. For an accommodation mechanism that changes focus to maximize luminance contrast ($L + M$) using signals from L- and M-cones, illuminating the target with a combination of green and blue light might provide a larger range over which focus can change without significantly altering luminance contrast. Thus in the present experiment, the reduction in gain in the presence of LCA could come from an increased depth-of-focus for LM-cones as well as a slow accommodation response from S-cones.

A larger depth-of-focus also could explain the larger lag of accommodation in the presence of LCA in this experiment. Rucker and Kruger (2004b) found that the mean static accommodation level to a near target (2.00 D) was more accurate when all three cone types participated than when only L- and M-cones were involved. When S-cones were included without LCA the

lag of accommodation was 0.13 D. But the eye under-accommodated substantially for the “yellow” component of the near target when LCA was added (Rucker & Kruger, 2004b). A similar result was found in the present experiment when LCA was included in the stimulus (Table 1). The mean lag of accommodation for 550 nm light increased from 0.18 D without LCA to 0.50 D with LCA. In the presence of LCA blue light (420 nm) was focused in front of the retina (−0.69 D) while green light (550 nm) was focused behind the retina (0.50 D). Thus the habitual lag of accommodation might represent a balance between S-cone contrast and LM-cone contrast. The reduction in mean accommodation level when blue light was added to the stimulus together with LCA could come from a chromatic signal $[S - (L + M)]$ that represents the difference between S- and LM-cone contrasts (Rucker & Kruger, 2004a).

The increase in mean accommodation level without LCA can be attributed to the effect of the achromatizing lens. With the achromatizing lens in place (Green + Blue – LCA condition) the mean stimulus to accommodation increased by −0.58 D, the mean response increased by 0.59 D, and the lag of accommodation remained essentially the same (0.18 D) as in the “Green” condition (0.19 D).

Finally, it is important to recognize that the present method of using monochromatic lights (420 nm + 550 nm) to include S-cones does not provide definitive evidence for an S-cone contribution to the mean accommodative response, because L- and M-cones respond to both short- and long-wavelength light (Smith & Pokorny, 1975). Thus the increased lag of accommodation in the presence of LCA could come from LM-cones alone, and might not involve S-cones at all. In summary, both the reduction in dynamic gain and the increased lag of the mean accommodation level could result either from a blue-yellow chromatic signal or from a larger depth-of-focus for LM cones in the presence of LCA.

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