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The role of short-wavelength sensitive cones and chromatic aberration in the response to stationary and step accommodation stimuli

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Abstract

The aim of the experiment was to test for a contribution from short-wavelength sensitive cones to the static and step accommodation response, to compare responses from short and long- plus middle-wavelength sensitive cone types, and to examine the contribution of a signal from longitudinal chromatic aberration to the accommodation response. Accommodation was monitored continuously (eight subjects) to a square-wave grating (2.2 c/d; 0.57 contrast) in a Badal optometer. The grating stepped (1.00 D) randomly towards or away from the eye from a starting position of 2.00 D. Five illumination conditions were used to isolate cone responses, and combine them with or without longitudinal chromatic aberration. Accuracy of the response before the step, step amplitude, latencies and time-constants, were compared between conditions using single factor ANOVA and *t*-test comparisons. Both S-cones and LM-cones mediated static and step accommodation responses. S-cone contrast drives "static" accommodation for near, but the S-cone response is too slow to influence step dynamics when LM-cones participate.

Keywords: Accommodation; Longitudinal chromatic aberration; Short-wavelength sensitive cones; Neural pathways

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1. Introduction

Many investigators have suggested that longitudinal chromatic aberration (LCA) plays a role in providing a directional signal for defocus (Aggarwala, Kruger, Mathews, & Kruger, 1995; Aggarwala, Nowbotsing, & Kruger, 1995; Campbell & Westheimer, 1959; Crane, 1966; Fincham, 1951; Flitcroft, 1990; Flitcroft & Judge, 1988; Kotulak, Morse, & Billock, 1995; Kruger, Aggarwala, Bean, & Mathews, 1997a; Kruger, Mathews, Aggarwala, & Sanchez, 1993; Kruger, Mathews, Aggarwala, Yager, & Kruger, 1995; Kruger, Mathews, Katz, Aggarwala, & Nowbotsing, 2000; Kruger & Pola, 1986; Lee, Stark, Cohen, & Kruger, 1999; Smithline, 1974; Stark, Lee, Kruger, Rucker, & Ying, 2002; Toates, 1972). As a result of LCA short-wavelength light (e.g. 420 nm) is refracted more strongly than long-wavelength light (e.g. 580 nm), and this results in myopic focus for short wavelength light (420 nm) of approximately 1.33 D (Bedford & Wyszeki, 1957). This extended range of focus affects the contrast of long, middle and short wavelength components of the retinal image for spatial frequencies above approximately 1 cycle per degree (c/d) (Marrimont & Wandell, 1994) and produces a chromatic signal at luminance borders that indicates the sign of defocus.

The effects of LCA on image contrast are moderated to some extent by monochromatic aberrations. Recent calculations show that monochromatic aberrations reduce the effects of LCA when pupils are large (McLellan, Marcos, Prieto, & Burns, 2002). Despite the effects of monochromatic aberrations, there is strong evidence that LCA provides a powerful direction signal for accommodation when the pupil is small (3 mm) (Kruger, Mathews, et al., 1995; Kruger et al., 1993; Kruger, Nowbotsing, Aggarwala, & Mathews, 1995; Stone, Mathews, & Kruger, 1993). Indeed simulations of retinal images affected by defocus and LCA drive accommodation in predicted directions (Lee et al., 1999; Stark et al., 2002). Recently, Lee et al. (1999), and Stark et al. (2002) showed that a difference in contrast between

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long- and middle-wavelength sensitive cones, across luminance borders, provides a signed accommodation signal. Myopic defocus is specified when long-wavelength sensitive cone contrast is higher than middle-wavelength sensitive cone contrast, and hyperopic defocus is specified when long-wavelength sensitive cone contrast is lower than middle-wavelength sensitive cone contrast. A comparison of long and middle-wavelength cone contrast specifies the sign of ocular defocus for stationary and moving stimuli (Aggarwala, Kruger, et al., 1995; Kruger, Mathews, Katz, Aggarwala, & Nowbotsing, 1997b; Lee et al., 1999).

It is less clear that a signal from a difference in contrast between S- and LM-cones provides a signed accommodation response. It has been considered unlikely that S-cones contribute to accommodation, or to a signal from LCA, since S-cones are absent from the central fovea (Wald, 1967; Williams, MacLeod, & Hayhoe, 1981). However, there is evidence for S-cone contributions to dynamic accommodation responses. Aggarwala, Stark, and Kruger (1999) found that chromatic aberration stimulates accommodation in both red–green and blue–yellow color directions. In addition, Rucker and Kruger (2001) isolated S-cone accommodation responses and found that S-cones can mediate dynamic reflex accommodation responses to a grating moving with sum-of-sines motion.

The aim of the present experiment is to determine whether S-cones and LM-cones mediate an independent reflex accommodation response to static and dynamic components of a step change in vergence; to determine whether S-cones continue to contribute when LM-cones are present; and to determine whether a signal from LCA contributes to the response.

2. Methods

The subject fixated a back illuminated square-wave grating (2.2 c/d 0.57 modulation) in a Badal stimulus system. The grating stepped 1.00 D towards or away from the eye from an initial position of 2.00 D.

2.1. Apparatus for measuring accommodation responses

An infrared (IR) recording optometer and Badal optical system (Kruger, 1979) were used to measure accommodation responses and to present stimuli. The apparatus has been described in detail by Lee et al. (1999).

The IR recording optometer measures dynamic changes in the power of the vertical meridian of the eye with a sampling rate of 100 Hz. The optometer output is a voltage signal that varies linearly with the accommodation response up to 6.00 D with a resolution of 0.10 D, and cut-off frequency of 10 Hz. The optometer operates with a minimum pupil size of 3 mm and tolerates eye movements ±3° from central fixation. Position of the subject is maintained with a chin and headrest and alignment of the subject is monitored continuously by viewing an image of the pupil and Purkinje image 1, with an infrared camera and video monitor.

2.2. Badal stimulus system

The Badal stimulus system has been described in part in previous papers (Cornsweet & Crane, 1970; Kruger et al., 1993). The advantage of the Badal system is that a dioptric change in target distance occurs without a change in visual angle subtended by the target.

Fig. 1(A) is a schematic of the optical system for presenting grating targets to the eye. Dashed lines illustrate the illumination system, while solid lines illustrate the target system. Light from source S1 (100 W tungsten–halogen lamp) 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), and illuminates grating 1 from behind. Light reflected by beamsplitter 1 is filtered by 580 nm interference filter (10 nm bandwidth), reflected at mirrors 1 and 2 and illuminates grating 2 from behind. Light from source S1 is focussed by lens L2 at mirror 3. Lenses L3 and L4 refocus the source in the plane of an artificial pupil, and lenses L5 and L6 focus the source in the pupil of the subject's eye. The lenses that image the target gratings are all computer-optimized achromats.

Gratings 1 and 2 are a pair of matched photographic slides (2.2 c/d vertical square-wave gratings with 0.57 contrast). Light from the two gratings is combined by pellicle beamsplitter 2, the light is collimated by lens L2, and the grating images are brought to focus in the same plane by lens L3. The two grating images are aligned laterally to have the same spatial phase. Light from the combined grating images is collimated by lens L4, and focussed by lens L5 in the focal plane of lens L6, after reflection by prisms 1 and 2. Motion of prism 2 (as shown by the arrow) moves the grating images toward and away from lens L6, thus altering the dioptric stimulus to accommodation. The subject views the target (in Maxwellian view) in Badal lens L6. A shutter in front of the blue and yellow gratings allows presentation of a blue grating, a yellow grating or a blue and yellow grating. The position of the yellow grating can be altered along the optical axis to neutralize the longitudinal chromatic aberration of the subject's eye. Neutral density filters equate the luminances of the blue, yellow and blue and yellow gratings. Source S2 provides an intense yellow "wash" (adapting field) that can be superimposed over the blue grating to isolate S-cones.

The accommodation stimulus was controlled by computer software that moved a motorized prism along

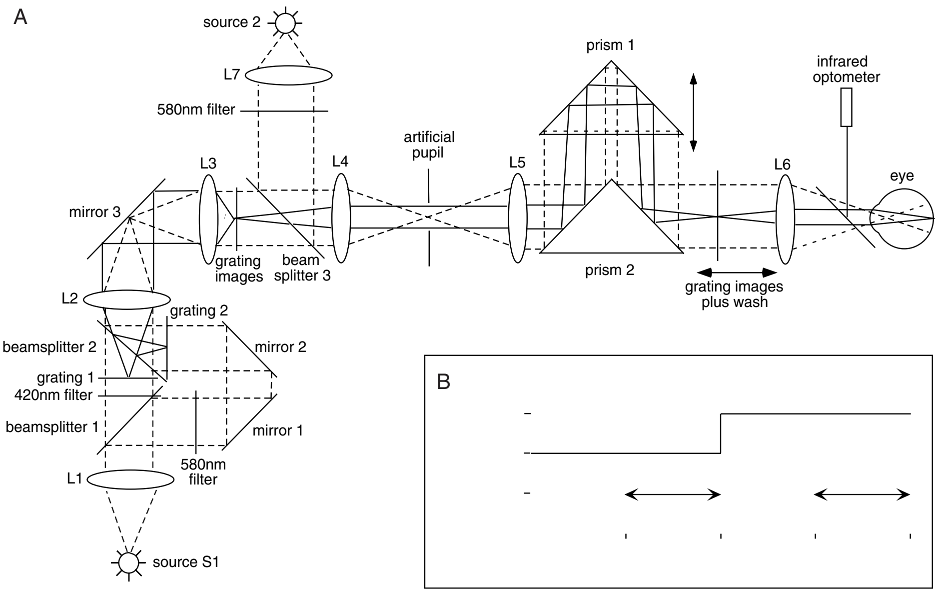

Fig. 1. (A) Badal stimulus system for presenting moving grating targets to the eye. Dashed rays illustrate the illumination system, and solid rays describe the target system. (B) Time course for a 20 s trial. The target steps from 2.00 to 3.00 D after the first 10 s of the trial. Horizontal arrows illustrate the two 5 s periods that were used to calculate the static accommodation levels before and after the step.

the optical axis of the Badal system (Kruger et al., 1993). The software corrected for the subject's Rx, the trial lenses in place at spectacle plane and vertex distance, and produced the correct accommodation stimulus with an accuracy of ±0.12 D. The reference wavelength of 557 nm was used to calibrate target vergence. The vergence required to provide a 2.00 D stimulus in 420 nm light (blue grating) was calculated for each subject (Thibos, Ye, Zhang, & Bradley, 1992) and the prism was positioned appropriately. A field stop with blurred edges (5.20 D beyond an emmetrope's far point) limited the field of view to 9.2 deg. Monochromatic aberrations were minimized by imaging a 3 mm artificial pupil in the subject's real pupil plane (Liang & Williams, 1997; Walsh & Charman, 1985).

It was important to align the achromatic axis of the subject's eye with the optical axis of the Badal stimulus system (Lee et al., 1999; Thibos, Bradley, Still, Zhang, & Howarth, 1990) to minimize transverse chromatic aberration. The method of alignment has been described in detail by Lee et al. (1999).

2.3. Calibrations

Photometry was performed through the Badal stimulus system using the method of Westheimer (1996). Measurements were made using a Pritchard Spectralradiometer (Spectra-Scan ^{PR}704, Photo Research). Calibration of the accommodative response involved a method to relate subjective focus for a target at different accommodation levels with optometer output (Lee et al., 1999). Measurement of the gradient of the stimulus/response function for each subject was necessary to compensate for individual variations in this relationship. In this method red (642 nm) and blue green (500 nm) vernier lines were superimposed on a back-illuminated white Maltese cross. The difference in refractive error between these two wavelengths is 0.73 D (Thibos et al., 1992) with 557 nm as the mid-point. When the red and green lines are equally blurred the vernier target straddles the plane of the subject's retina. Subjects viewed the Maltese cross and vernier target at several different accommodative stimulus levels (e.g. 1.00, 2.00, 3.00, 4.00, 5.00 D). At each stimulus level the subject adjusted the superimposed red and green vernier lines until they were equally blurred. This provided a subjective measurement of focus while a simultaneous objective measurement of optometer voltage output was recorded. Principle axis regression (Sokal & Rohlf, 1981) was then used to obtain a linear equation relating accommodation response to infrared optometer output over the range measured.

2.4. Subjects

Subjects were required to have visual acuity of 6/6 or better with a left eye/right eye difference of less than one line. Subjects were excluded from the study for ocular injury or disease, amblyopia, defective color vision, or excessive blinking. Subjects were not excluded for sustained over-accommodation since previous experiments demonstrated that this may occur in response to some stimulus conditions (Rucker & Kruger, 2001). In the present experiment monochromatic light was used to isolate S-cones and LM-cones. However some subjects accommodate very poorly in monochromatic light, and some cannot accommodate at all (Fincham, 1951; Kruger et al., 1993). Therefore a gain of 0.2 was used as the cut-off point for including subjects in the study. Twelve subjects presented, one was excluded for spasm of accommodation, one for excess blinking, and two for having low gain in monochromatic light. The remaining eight subjects were selected to participate. They ranged in age from 23 to 28 years and all were optometry students. Spherical refractions ranged from plano to −8.75 D with cylinders from −0.25 to −1.25 D. Refractive errors were corrected by contact lenses or trial lenses.

Subjects gave informed consent, the experiment was approved by the Institutional Review Board of the college, and followed the tenets of the Declaration of Helsinki. Subjects were paid for participation.

2.5. Procedures

During preliminary examinations case histories were recorded, color vision, subjective refraction, visual acuity and amplitude of accommodation were measured. Lenses were placed in front of the left eye to correct for ametropia and the right eye was patched. The subject was positioned on a chin and headrest mounted on a three-way stage. Eye position was monitored by video and the Purkinje image 1 was used to align the achromatic axis of the eye with the optical axis of the stimulus system. The subject was instructed to "keep the grating clear with about as much effort as if you were reading a book". The room was darkened and the subject was unable to see the surrounding apparatus while viewing the grating. There were no external cues to guide the direction of the subject's accommodation.

Each experimental trial lasted 20.48 s (see Fig. 1B). The target grating remained stationary at 2.00 D for the first 10.24 s of the trial, and then stepped randomly toward or away from the eye (1.00 D) and then remained stationary for the final 10.24 s of the trial. There were eight trials of each condition performed in eight separate blocks with the exception of one subject (seven trials). Conditions were randomized without replacement within a block. Subjects adapted to each condition for a minimum of one minute, and there were two minutes of dark adaptation between conditions. Adaptation times were sometimes longer because of difficulty in aligning the subject.

2.6. Measurement of LCA

LCA has been measured by several investigators with consistent results, but there is some variation at short wavelengths (Bedford & Wyszeki, 1957; Howarth & Bradley, 1986; Lewis, Katz, & Oehrlein, 1982; Mandelman & Sivak, 1983; Powell, 1981; Thibos et al., 1990). LCA was found for each subject by measuring the far point of the eye at six wavelengths between 420 and 624 nm, through a Badal stimulus system (4.00 D achromat lens; 1.00 D = 6.25 cm). Head position was fixed using a head support and chin rest. The room was darkened to take advantage of the reduction in the depth of focus with a large pupil. The subject fixated the center of a 2.2 c/d square-wave grating with 0.57 contrast modulation (35 mm photographic transparency), back illuminated by a tungsten–halogen lamp. Interference filters (420, 430, 506, 556, 580, 624 nm) were inserted in the light path and the measurement of the subject's far point recorded. The luminance of all targets was maintained at 20 cd/m^2 by neutral density filters. The target was moved slowly towards the eye and the "first clear" point was recorded. Conditions were randomized and repeated six times. Linear regression was used to fit a curve to the data for each subject, and LCA was calculated between 420 and 580 nm. This allowed accurate neutralization of LCA for each subject.

2.7. Illumination conditions

Five illumination conditions were used to test for S-cone and LM-cone accommodation responses, with and without longitudinal chromatic aberration. In addition two defocus conditions were used to test for an accommodation response to a random near or far step in each illumination condition. The illumination conditions are summarized in Table 1 and illustrated by Fig. 2.

In the "Blue" condition S-cone accommodation responses were isolated with a blue grating (420 nm; 10 nm bandwidth; 154 trolands) with a superimposed yellow adapting field (578 nm; 10 nm bandwidth; 8920 trolands). S-cone contrast was high (0.565 modulation) while L- and M-cone contrasts were low (0.0078; 0.0138 modulation). The grating was positioned to present a stimulus of 2.00 D when illuminated with 420 nm light.

In the "Yellow" condition LM-cone accommodation responses were isolated with a yellow grating (580 nm; 10 nm bandwidth; 164 troland). The grating was positioned to present a 2.00 D accommodation stimulus when illuminated with 580 nm light. The yellow grating was displaced along the *z*-axis, relative to the blue grating, by an amount equal to the LCA of the eye.

In the "Blue + Yellow" and "Blue + Yellow + LCA" conditions the blue and yellow gratings were superimposed in the same spatial phase. Retinal illumination was maintained at 164 trolands with neutral density filters. The yellow grating was adjusted along the *z*-axis, relative to the blue grating, to neutralize or introduce LCA, according to the subject's individual measured LCA.

LCA was introduced in "Blue + Yellow + LCA" by positioning the blue and yellow gratings at the *same* target distance along the *z*-axis. As a result the 420 nm

Table 1
Summary of conditions

Condition	Cone response	Method	Stimulus (D)
Blue	S	420 nm grating+ 578 nm adapting field	2.00
Yellow	LM	580 nm grating	2.00
Yellow + Blue	S + LM	420 nm grating+ 580 nm grating	2.00 2.00
Yellow + Blue + LCA	S + LM	420 nm grating 580 nm grating	2.00 3.33
Low Blue	S	420 nm grating+ 578 nm adapting field	2.00

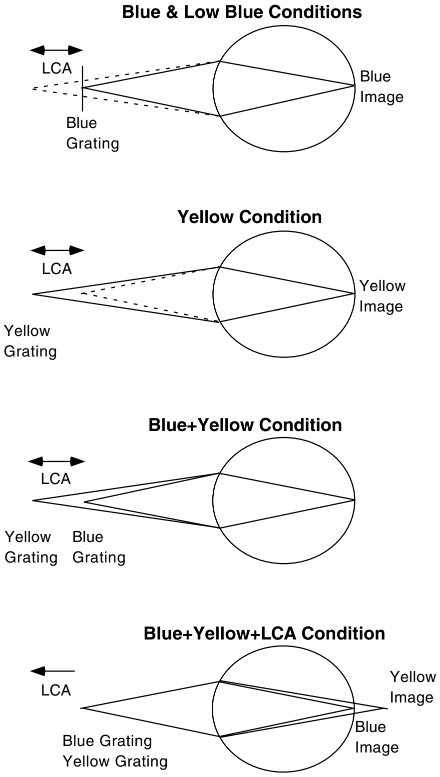

Fig. 2. The diagrams illustrate the relative positions of the blue and yellow grating targets in the stimulus system for the five illumination conditions. The eye is illustrated accommodating accurately for the stimulus distance (2.00 D) at the beginning of the trial. In the presence of LCA (“Blue + Yellow + LCA” condition) blue light is in focus on the retina, and yellow light is focused behind the retina.

blue target presented a stimulus of 2.00 D, while the 580 nm yellow target presented a stimulus of 2.00 D + LCA. Since the LCA between 420 and 580 nm is approximately 1.33 D the yellow grating presented an accommodation stimulus of approximately 3.30 D.

In “Blue + Yellow” both gratings presented a 2.00 D stimulus to accommodation. To achieve this the 580 nm yellow target was re-positioned along the *z*-axis, relative to the blue grating, by an amount equal to the LCA of the subject’s eye (approximately 1.33 D). This resulted in the blue and yellow images forming in the same optical plane in the eye.

The fifth condition, the “Low Blue” condition, controlled for the possibility that L- and M-cones contributed in the “Blue” condition. The “Low Blue” condition also controlled for effects of macular pigmentation, and for the possibility that the sensitivity of the S-cones was reduced as a result of second-site adaptation (Swanson, 1996). The “Low Blue” condition was the same as the “Blue” condition except that the cone contrast for L- and M-cones was roughly halved (0.0046 and 0.0085), while S-cone contrast remained at 0.57. The responses for this condition should be the same as in the “Blue” condition if macular pigment and L- and M-cones do not contribute to the response.

To determine the cone contrasts for each illumination condition, relative cone-excitations for the peaks and troughs of the grating were calculated using Smith and Pokorny (1975) cone fundamentals for 420 and 580 nm light. Michelson cone-contrasts were then calculated for each cone class (L-, M- and S-cones) using the formula: $\text{Contrast} = (E_{\max} - E_{\min})/(E_{\max} + E_{\min})$, where $E_{\max}$ is the maximum cone excitation for the grating plus the adapting field, and $E_{\min}$ is the minimum cone excitation for the grating plus the adapting field.

2.8. Analysis

Artifacts as a result of blinking were removed from each 20.48 seconds trial using standard signal processing procedures (Lee et al., 1999). Then, data from all the subjects were pooled for each condition to produce a grand mean, and exponential functions were fitted. Time constants and latencies were calculated for each condition using the pooled data. After this analysis, exponential functions were fitted to the data from individual subjects for the “Yellow” and “Blue + Yellow + LCA” conditions. Time constants and latencies for these two conditions were then calculated and compared using a two-way ANOVA.

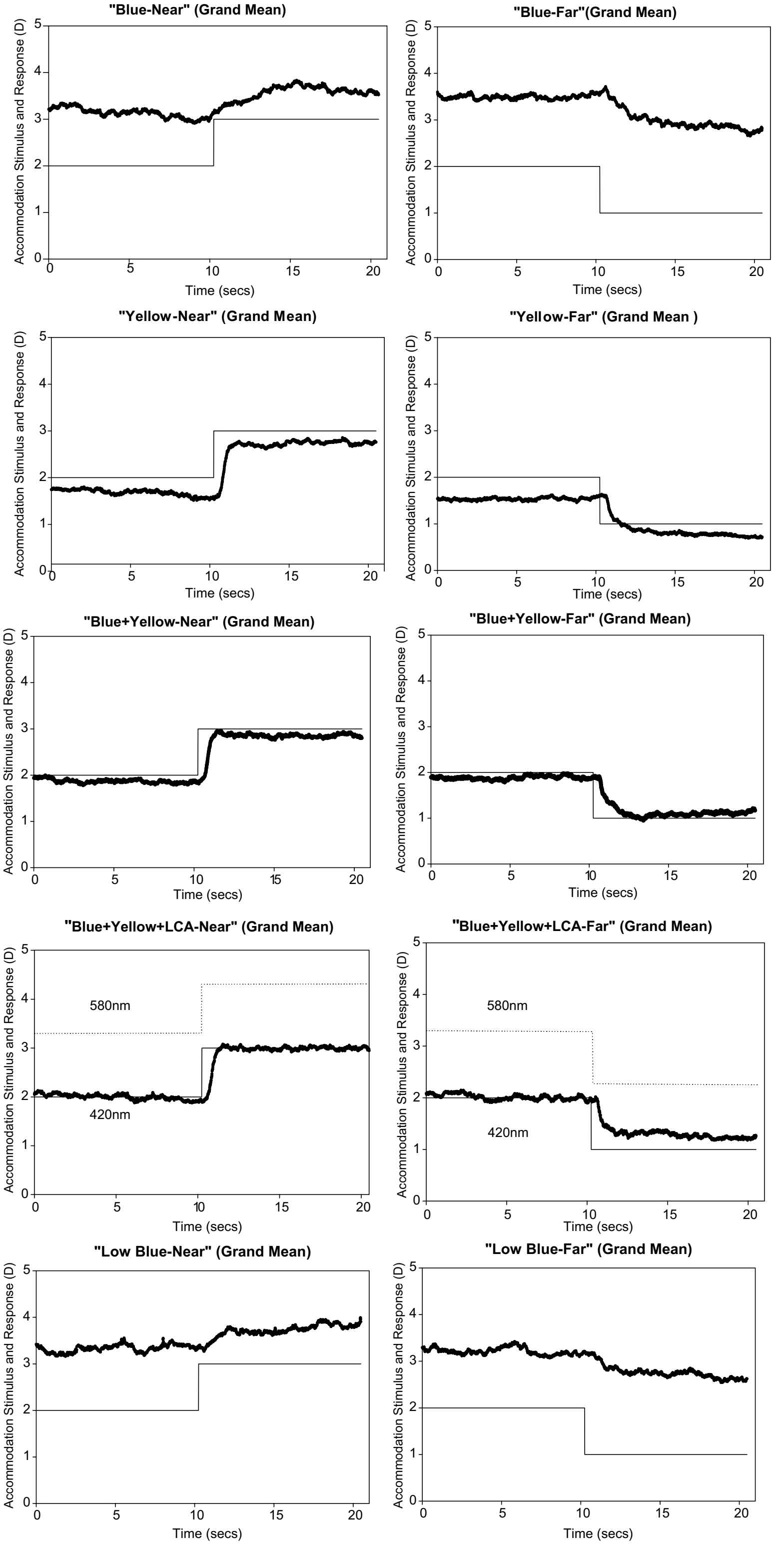

Fig. 3. Graphs show time course of grand mean accommodation responses under each illumination condition. The stimulus is represented by (–), the responses by (·). The stimulus started at 2.00 D and stepped near or far by 1.00 D after 10.24 s. In the "Blue + Yellow + LCA" condition the stimulus shown is for 420 nm light: the stimulus for 580 nm light was 1.33 D more than for 420 nm light.

"Static" responses were determined for each trial by averaging the data for the 5 s just before the step. These "static" responses were compared across illumination conditions. In addition, data for the final 5 s of the trial were averaged to provide static "near" and "far" responses. In Fig. 1(B) horizontal arrows illustrate the two

5 second periods that were used to calculate the “static” responses before the step, and the “near” and “ far” accommodation levels. The difference between the “near” and “far” responses gave a measure of “step amplitude” for each illumination condition, which was compared using a single factor ANOVA and *t*-tests for paired samples. *T*-tests were performed only if the *F* value was significant at the $\alpha = 0.05$ level. The 5 second time periods that were selected for analysis provided sufficient time for the response to stabilize after the start of the trial, and time for accommodation to stabilize after the step change in target distance.

3. Results

Pooled data for all the subjects in each illumination condition are shown in Fig. 3. It is clear from the data that the presence of S-cone contrast affected the mean dioptric level of the “static” response. For the period before the step “static” responses showed a significant difference between conditions when tested with ANOVA ($F = 2.16$; $p = 0.035$). In the “Blue” condition most subjects (6 of 8) over-accommodated (mean 3.31 D; S.D. 1.77), whereas in the “Yellow” condition most subjects (5 of 8) under-accommodated (mean 1.61 D; S.D 1.14 D). The “static” response increased for near when S-cone contrast was added to LM-cone contrast (6 of 8). The average response was more accurate when all three cone types were present (“Blue + Yellow”; mean 1.87 D; S.D. 1.42 D) than in the “Blue” ($p = 0.00032$) or “Yellow” ($p = 0.05$) conditions. The introduction of LCA did not change the “static” response. Static responses for “Blue + Yellow + LCA” (mean 2.00 D; S.D 1.48 D) and “Blue + Yellow” conditions were not significantly different ($p = 0.219$).

Fig. 4 shows that the “static” accommodation level varied widely among subjects. Three subjects (#3, #6, #7) under-accommodated substantially for the mean stimulus level (2.00 D) in the “Yellow” condition, and two subjects (#5, #8) over-accommodated. However, all the subjects accommodated substantially more for near in the “Blue” condition than in the “Yellow” condition.

For the period after the step, responses to “BlueNear” were significantly different to those of “BlueFar” ($p = 0.008$) and responses to “YellowNear” were significantly different to “YellowFar” ($p = 0.003$). This suggests that the S- and LM-cone responses followed the direction of the step correctly.

Grand mean response latencies also varied with illumination condition (Table 2). Latencies were shorter for far in the “Yellow” condition, and shorter for near in the “Blue” condition. Latency ranged from 311 ms in “BlueNear” to 575 ms in “BlueFar”, while in the “Yellow” condition latency ranged from 340 ms (far) to 487 ms (near). The addition of S-cone contrast to LM-cone contrast (“Blue + Yellow”) produced latencies that were similar to the “Yellow” condition. Noisy data may have contributed to the very short latency of 165 ms in the “LowBlue” condition. In summary, addition of

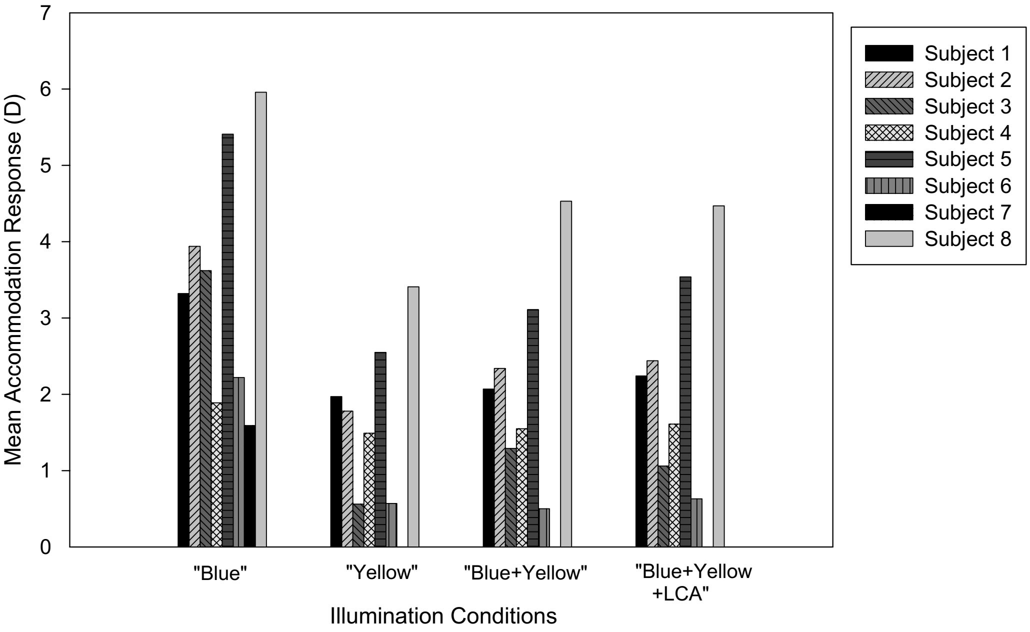

Fig. 4. “Static” accommodation responses for each subject, in each illumination condition. Although there is considerable inter-subject variation in the “static” response all subjects demonstrated an increased accommodation response in the “Blue” condition and increased accuracy when all three cone types contributed.

Table 2
Summary of results

	Blue		Yellow		Yellow + Blue		Yellow + Blue + LCA		Low Blue	
Pre-step										
Pre-step response x_i (D)	3.31		1.61		1.87		2.00		3.27	
Post-step	Far	Near	Far	Near	Far	Near	Far	Near	Far	Near
Post-step response x_f (D)	2.81	3.65	0.77	2.74	1.09	2.85	1.27	3.00	2.69	3.79
Time constant τ (ms)	2022	1523	882	241	525	176	457	208	1449	1771
Mean τ (ms)	1772		561		350		332		1610	
Latency (ms)	575	311	340	487	388	465	301	466	219	119.7
Mean latency (ms)	443		413		426		384		169	
Step amplitude (near–far)	0.84		1.97		1.76		1.73		1.10	

S-cone contrast to LM-cone contrast produced no significant difference in latency for focus direction or illumination condition at the $\alpha = 0.05$ level, even with the introduction of LCA.

There was a notable difference in the time course of the grand mean step response in the "Blue" condition compared to the other conditions (Fig. 3 and Table 2). The time constant for the "BlueNear" condition was 1523 ms compared to 241 ms for the "YellowNear" condition. The step response mediated by S-cones was thus considerably slower than the step response mediated by LM-cones. There was also a noticeable difference in the grand mean time constants between the near and far responses. Time constants were faster for near steps than for far steps in the "Blue", "Yellow", "Blue + Yellow" and "Blue + Yellow + LCA" conditions (Table 2). For example, the near step time constant for "Yellow" was 241 ms compared to 882 ms for the far step. To summarize, S-cone step responses were slower than LM-cone step responses, and the response to the near step was faster than the response to the far step for both cone types.

Time constants also were calculated for individual subjects to test for a significant statistical difference in step dynamics when S-cone contrast is added to LM-cone contrast. Time constants for the "Yellow" and "Blue + Yellow + LCA" conditions were compared using a two-way ANOVA for focus direction (near or far) and illumination condition. There was a significant difference in time constants for direction of focus at the $\alpha = 0.05$ level, but not for illumination condition. For the "Yellow" and "Blue + Yellow + LCA" conditions the "near" response was faster than the "far" response, but the addition of S-cone contrast, with or without LCA, did not significantly alter the time course of the step response.

Table 2 shows that there were large differences in step amplitude ("near"–"far") across conditions ($F = 4.65$; $p = 0.0048$). Mean step amplitude was greater and more accurate ($p = 0.008$) for the "Yellow" (1.97 D; S.D 0.42 D) condition than the "Blue" (0.84 D; S.D. 0.61 D) condition, but step amplitude in "Blue + Yellow" condition (1.76 D; S.D. 0.49 D) was not significantly different to the "Yellow" condition (1.97 D; S.D. 0.42 D). In fact, step amplitude for the "Blue + Yellow + LCA" condition (1.73 D; S.D. 0.47 D) was not significantly different to step amplitude in the "Blue + Yellow" (1.76 D; S.D. 0.49; $p = 0.967$) or "Yellow" ($p = 0.139$) conditions. Thus, the addition of S-cone contrast to LM-cone contrast did not affect step amplitude even with the introduction of LCA.

The responses in "Blue" and "Low Blue" illumination conditions were not significantly different. The "Low Blue" condition produced mean "static" responses of 3.27 D (S.D. 0.08 D), which were not significantly different to the "static" responses in the "Blue" condition (mean 3.31 D; S.D. 0.06). Step amplitude also was not significantly different in the "Blue" (mean 0.80 D; S.D. 0.61 D) or "Low Blue" (mean 1.10 D; S.D. 0.70 D) conditions ($p = 0.403$). The "Low Blue" condition clearly mediated a reflex accommodation response since "low BlueNear" was significantly different to "low BlueFar" ($p = 0.001$). These results suggest that L- and M-cone contrast did not contribute to the responses in the "Blue" condition.

4. Discussion

Our goals were to determine whether S-cones and LM-cones mediate independent reflex (blur-driven) accommodation responses to static and dynamic components of a step change in target distance; to determine whether S-cones continue to contribute when LM-cones are present; and to determine whether a signal from LCA contributes to the response. Our results suggest that S-cones and LM-cones can mediate independent accommodation responses. In the absence of LM-cone contrast, S-cone contrast drives the "static" accommodation level for near. Both S- and LM-cones mediate a signed step response, but the S-cone responses are significantly slower than LM-cone responses: LM-cones mediate a fast step response, while S-cones mediate a slower more gradual response. Lastly, an S-cone contribution to a signal from LCA did not change the static or dynamic response.

The present results support and extend previous findings that S-cones contribute to the accommodative process (Aggarwala et al., 1995; Aggarwala et al., 1999), and that subjects can accommodate using only S-cones (Rucker & Kruger, 2001). Aggarwala, Kruger, et al. (1995) found that the dynamic response (gain) improved when the spectral bandwidth of the illumination was broadened to include short wavelength light. Using a simulation paradigm to drive accommodation, Aggarwala et al. (1999) found evidence that both red–green and yellow–blue opponent mechanisms contribute to dynamic accommodation. Recently, Rucker and Kruger (2001) isolated S-cone accommodation responses and found that S-cones can mediate a reflex accommodation response to a 3 c/d grating moving with a sum-of-sines motion. While both LM- and S-cones respond to the step stimulus (Fig. 3) the present results indicate significant differences between the LM- and S-cone contributions to the static and dynamic components of the response.

Pooling the data from all the subjects obscures large differences in the "static" responses of the subjects, but the pooled data are instructive because they summarize the "static" results (see Table 2, pre-step responses). On average, subjects over-accommodated substantially for the target distance (2.00 D) in the "Blue" condition (3.31 D); they under-accommodated by a small amount in the "Yellow" condition (1.61 D); and the responses were most accurate when all three cone types were present (1.87 D). Adding LCA to the stimulus did not alter the "static" response.

Fig. 4 shows that the "static" accommodation response varied widely among the eight subjects. Some over-accommodated substantially for the target vergence (2.00 D) while others under-accommodated substantially. The relatively low spatial frequency of the grating target (2.2 c/d) and relatively small artificial pupil (3 mm) used in the experiment allow the eye to over- or under-accommodate by more than 2.00 diopters without a complete loss of image contrast (Smith, 1982). In fact image modulation with a 3 mm pupil, for a 2.2 c/d grating with 0.57 modulation, is only reduced from 0.57 to 0.33 with 2.00 D defocus (Smith, 1982). Thus the grating target was above the threshold for initiating accommodation, despite substantial defocus. Subjects accommodated in the correct direction to the step changes in target vergence, despite substantial under- or over-accommodation by some subjects. This suggests that the eye was not accommodating to maximize luminance contrast of the retinal image. Instead, accommodation seems to be responding to changes in target vergence per se (Kruger et al., 1997a).

In the present experiment monochromatic illumination was used to isolate S-cones and LM-cones, and this may have contributed to the inaccurate "static" responses of the subjects. Previous investigations have examined "static" accommodation in monochromatic light, and have described wide variation in the responses (e.g. Campbell & Westheimer, 1959; Charman & Tucker, 1978; Fincham, 1951). This may be attributable to variable sensitivity to the effects of LCA (Aggarwala, Nowbotsing, et al., 1995; Fincham, 1951; Kruger et al., 1993; Troelstra, Zuber, Miller, & Stark, 1964).

Despite the large differences in the "static" accommodation level of each subject, the responses of the subjects changed in the same way to the various illumination conditions. All of the subjects accommodated most strongly for near in the "Blue" condition, which provided S-cone contrast in the absence of LM-cone contrast. This result agrees with the view that a chromatic mechanism ($S-[L+M]$) provides a signed signal that drives accommodation for near when S-cone contrast is higher than LM-cone contrast (Aggarwala, Kruger, et al., 1995; Flitcroft, 1990). The strong response for near may have been enhanced because luminance contrast (LM-cone contrast) was absent from the stimulus in the "Blue" condition and this should provide an open-loop stimulus with regard to luminance contrast (Schrödinger, 1925; Eisner & MacLeod, 1980; Cavanagh, MacLeod, & Anstis, 1987; Stockman, MacLeod, & DePriest, 1991). Also, S-cones have lower spatial acuity than LM-cones (Daw & Enoch, 1973; Hess, Mullen, & Zrenner, 1989; Humanski & Wilson, 1992; Swanson, 1989) so depth-of-focus should be larger for S-cones than for LM-cones. Thus in the "Blue" condition the open-loop stimulus and large depth-of-focus could have facilitated the strong near response to high S-cone contrast in the absence of LM-cone contrast.

All of the subjects showed less accommodation for near in the "Yellow" condition (L- and M-cones) compared to the "Blue" condition (Fig. 4), although subjects still showed considerable over- or under-accommodation for the target distance (2.00 D). In the "Yellow" condition L- and M-cone contrasts were the same, so that the chromatic signal from L- and M-cones (L-M) was an open-loop stimulus, while the luminance signal ($L+M$) was closed-loop. Thus in the "Yellow" condition accommodation was controlled by a closed-loop luminance signal from LM-cones, and the chromatic signal was absent.

S-cone contrast was added to LM-cone contrast in the "Blue + Yellow" condition", and the "static" response increased by a small amount for some subjects. In this illumination condition the chromatic signal ($S–[L+M]$) is open-loop, because S-cone contrast and LM-cone contrasts were all the same. The presence of LM-cone contrast seems to counteract the directional signal from S-cones that drives accommodation for near.

Finally, when LCA was added to the stimulus there was little or no change in the "static" level of accommodation. One might conclude that LCA plays no role. However, the stimulus to accommodation was 2.00 D in the "Blue + Yellow" condition, but when LCA was added to the stimulus the vergence of the yellow component of the stimulus (580 nm) increased from 2.00 to 3.33 D, while the vergence of the blue component of the stimulus (420 nm) remained at 2.00 D (Fig. 2). Although the vergence of the yellow component of the stimulus (580 nm) increased from 2.00 to 3.33 D, the "static" accommodation response remained essentially the same. Since L- and M-cones respond to both short- and long-wavelength light, L- and M-cones could have responded to the vergence of the blue component of the stimulus when LCA was added, and not to the vergence of the yellow component. This type of under-accommodation for long-wavelength light in the presence of LCA is in line with the notion that LCA "spares" accommodation for near targets, by allowing the eye to focus short-wavelength light on the retina and long-wavelength light behind the retina (Bobier & Sivak, 1978; Le Grand, 1967; Millodot & Sivak, 1973). In this view, the eye accommodates the least amount necessary to provide a relatively "clear" retinal image. There are also investigators who disagree with the notion that LCA spares accommodation (Bobier, Campbell, & Hinch, 1992; Charman & Tucker, 1978) but the present findings seem to support the idea.

Latencies in the present experiment are similar to the latencies measured by previous investigators (Campbell & Westheimer, 1960; Kasai, Unno, Fujii, Sekiguchi, & Shinohara, 1971; O'Neill & Stark, 1968; Phillips, Shirachi, & Stark, 1972; Shirachi et al., 1978; Stark, Takahashi, & Zames, 1965; Tucker & Charman, 1979). Latencies were faster for far steps than for near steps in the Yellow, Blue + Yellow, and Blue + Yellow + LCA conditions. Some of the previous investigations found that latencies were faster for near steps than for far steps (Campbell & Westheimer, 1960; Phillips et al., 1972; Shirachi et al., 1978; Stark et al., 1965; Tucker & Charman, 1979), while others have found the reverse (Kasai et al., 1971; O'Neill & Stark, 1968). Monochromatic lights were used in the present experiment to isolate S- and LM-cones, while previous experiments used broadband "white" light to illuminate the target.

The latencies in the different illumination conditions suggest differences for different types of cones. In the "Blue" condition, latencies were much faster for near steps (311 ms) than for far steps (575 ms) while the reverse was true for the "Yellow" condition (Table 2). Since 6 of 8 subjects were over-accommodating for the target distance in the "Blue" condition, this suggests that S-cones mediate a faster reaction to a reduction in myopic defocus (near step) that brings the image closer to the retina, than to an increase in myopic defocus (far step). On the other hand, 6 of 8 subjects under-accommodated in the "Yellow" condition, and the faster response to far steps suggests that LM-cones mediate a faster response to a reduction in hyperopic defocus (far step) than to an increase in hyperopic defocus.

The time constants for the step response in the Yellow, Blue + Yellow, Blue + Yellow + LCA conditions are similar to the time constants reported by previous investigators, although the present time constants were shorter for near steps than for far steps. This concurs with the findings of Tucker and Charman (1979) and Shirachi et al. (1978) who reported shorter time constants for near steps than for far steps. On the other hand Campbell and Westheimer (1960) found shorter time constants for far step responses. Again, different stimulus conditions might contribute to the differences among investigations. Most striking however, is that time constants were much larger in the Blue and Low-Blue conditions than in the other conditions. Clearly the S-cone mediated accommodation response is much slower than the response mediated by LM-cones.

Neither the addition of S-cone contrast nor the introduction of LCA improved the time course of the dynamic response. With post-hoc knowledge of the slow time course of the S-cone step response ($\tau = 1772$ ms) it is not surprising that the time course of the response is independent of both S-cones and an S-cone signal from chromatic aberration. The LM-cone step response ($\tau = 561$ ms) is completed well before the S-cone step response, suggesting an important role for a mechanism sensitive to luminance contrast for controlling step dynamics. This does not detract from evidence that a signed chromatic signal from a comparison of L- and M-cone contrasts also contributes to the accommodation response (Aggarwala, Nowbotsing, et al., 1995; Kotulak et al., 1995; Lee et al., 1999; Stark et al., 2002).

Amplitude of step responses also varied between cone types. Step amplitude was greater for LM-cones (mean 1.97 D) than for S-cones (mean 0.84 D). The difference in step amplitude could be a result of the difference in spatial acuity between S- and LM- cone types, resulting in a difference in depth of focus for the two conditions. In a closed-loop negative feedback system that monitors luminance contrast, depth of focus alters response magnitude (Campbell & Westheimer, 1957; Hennessy, Iida, Shiina, & Leibowitz, 1976), and negative feedback improves the accuracy of the response (Bobier et al., 1992; Charman & Tucker, 1978; Heath, 1956; Phillips & Stark, 1977; Stark & Takahashi, 1965; Troelstra, 1964; Wolfe & Owens, 1981). Since S-cones have lower visual acuity than LM-cones (Daw & Enoch, 1973; Hess et al., 1989; Humanski & Wilson, 1992; Swanson, 1989) depth of focus should be greater for S-cones than for LM-cones, resulting in smaller step amplitude and increased noise for S-cone responses.

5. Conclusion

S-cones on their own can mediate static accommodation as well as signed responses to step changes in dioptric vergence. The eye over-accommodates for the target distance when the response is mediated by S-cones alone, and the step response is much slower and the amplitude is much smaller than the response mediated by LM-cones. The accommodation response mediated by S-cones is too slow to assist the dynamic response to step changes in dioptric vergence. The "static" response (mean for eight subjects) was more accurate when all three cone types participated. Finally, LCA did not alter the mean response.

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