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Isolated short-wavelength sensitive cones can mediate a reflex accommodation response

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Abstract

Both long- and middle-wavelength sensitive cones mediate the reflex accommodation signal but the contribution from the short-wavelength sensitive cones is unknown. A short-wavelength sensitive cone contribution could extend the range of the signed defocus signal from chromatic aberration. The aim was to determine whether isolated short-wavelength sensitive cones mediate reflex accommodation independently of long- and middle-wavelength sensitive cones. Accommodation was monitored continuously (eight subjects) to a sine-wave grating (3 cpd; 0.53 contrast) moving with a sum of sines motion in a Badal optometer. Two illumination conditions were used: a 'blue' condition that isolated short-wavelength sensitive cones, and a 'white' control condition that stimulated all three cone types. Of the eight subjects, two responded equally in the 'white' and 'blue' condition, four gave reduced responses in the 'blue' condition and two failed to respond in both conditions. The mean response in the 'blue' condition was reduced by 50% compared to the 'white' condition. Further analysis indicated that four of the eight subjects gave responses that were considerably greater than noise (S.D. > 1.82) when short-wavelength sensitive cones were isolated. Some subjects can accommodate using only S-cones. © 2001 Elsevier Science Ltd. All rights reserved.

Keywords: Accommodation; Short-wavelength sensitive cones; Blur; Defocus

1. Introduction

The stimuli for accommodation, and the mechanisms that mediate the optical signals that specify the sign of defocus, have been debated for more than 50 years. Discovery of these signals may have important ramifications not only for accommodation but also for the process of emmetropization. Experiments have demonstrated growth responses that are sensitive to the sign of lens induced retinal defocus (myopic or hyperopic), in chicks (Schaeffel, Glasser, & Howland, 1988; Irving, Sivak, & Callender, 1992; Wildsoet & Wallman, 1995; Nevin, Schmid, & Wildsoet, 1998) and in rhesus monkeys (Hung, Crawford, & Smith III, 1995; Smith III, Hung, & Li-Fang, 1999). Two opposing views have developed for the stimulus of reflex accommodation.

The standard view is that the change in *luminance contrast* of the retinal image is the stimulus to accommodation. Accurate focus using the even-error stimulus from luminance contrast relies on negative feedback, as the optical system searches for the point of maximal luminance contrast and smallest blur-circle diameter (Heath, 1956; Troelstra, Zuber, Miller, & Stark, 1964; Stark & Takahashi, 1965; Phillips & Stark, 1977; Charman & Tucker, 1978; Wolfe & Owens, 1981; Bobier, Campbell, & Hinch, 1992). An alternative view (Fincham, 1951) is that the stimulus has odd-error qualities that change with the state of defocus, in front or behind the retina.

Fincham (1951) proposed that odd-error stimuli are derived from longitudinal chromatic aberration (LCA) and from the vergence of the incident light. These odd-error stimuli have been investigated to different degrees.

Fincham (1951) suggested that in monochromatic light accommodation responds to light vergence using directionally sensitive cones (Stiles & Crawford, 1933) to determine the angle of incidence of rays from the edges of the pupil. In fact, subjects can accommodate without feedback in monochromatic light, suggesting

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that the vergence stimulus is an odd-error signal with directional quality (Kruger, Mathews, Katz, Aggarwala, & Nowbotsing, 1997). However, the idea that the eye responds to light vergence remains largely unexplored. Since 1951, several studies have supported the idea that chromatic aberration provides a direction signal to reflex accommodation in humans (Campbell & Westheimer, 1959; Crane, 1966; Toates, 1972; Smithline, 1974; Kruger & Pola, 1986; Flitcroft, 1990; Kruger, Mathews, Aggarwala, & Sanchez, 1993; Aggarwala, Nowbotsing, & Kruger, 1995b; Kruger, Mathews, Aggarwala, Yager, & Kruger, 1995; Kotulak, Morse, & Billock, 1995; Kruger et al., 1997) and in rhesus monkeys (Flitcroft & Judge, 1988). Several experiments compared the response in monochromatic and white light, thereby comparing the response with and without a signal from LCA. Some investigators found an increased response in white light compared to monochromatic light, indicating a contribution from the additional LCA component of the signal (Kruger & Pola, 1986; Kruger et al., 1993, 1995; Aggarwala, Nowbotsing, & Kruger, 1995b). However, other experiments have demonstrated equal responses under monochromatic and white light conditions (Van der Wildt, Bouman, & van de Kraats, 1974; Charman & Tucker, 1978).

The disagreement over the nature of the stimulus arises from several factors, including the introduction of voluntary accommodation, subjective methods of measuring accommodation, instruction, training, and small subject numbers. The influence of each of these factors has been summarized by Kruger et al. (1993, 1995), Lee, Stark, Cohen, and Kruger, 1999 and Kruger, Mathews, Aggarwala, Stark, Bean, Lee, and Cohen (2000). Van der Wildt et al. (1974) used a single subject and in the experiment of Charman and Tucker (1978) voluntary accommodation was encouraged. When small numbers of subjects are used a possibility exists that the subject will be one of those who respond equally well in white and monochromatic light, since subjects vary in their ability to respond without LCA (Fincham, 1951; Kruger & Pola, 1986; Kruger et al., 1993). Also, voluntary accommodation can mask the effect of LCA, especially when the target is stationary (Kruger et al., 1997). It is important to recognize that LCA is a powerful aspect of the dioptric stimulus. Dynamic gain can double in the presence of LCA, and large fluctuations of focus that sometimes occur in monochromatic light are eliminated in the presence of LCA (Kruger et al., 1995). But it is also important to recognize that LCA is not the exclusive stimulus for accommodation, because subjects continue to accommodate to some extent in monochromatic light. The ability of subjects to accommodate in monochromatic light without feedback (Carter, 1962; Kruger et al., 1997) indicates that the even-error signal from changes in luminance contrast, (the standard view of the stimulus), is also not the sole signal for reflex accommodation.

It has been suggested that the signal from LCA is derived from a comparison of cone contrasts (Flitcroft, 1990; Kruger et al., 1995), and there is agreement that long-wavelength sensitive cones (L-cones) and middle-wavelength sensitive cones (M-cones) mediate this signal (Crane, 1966; Aggarwala, Kruger, Mathews, & Kruger, 1995a; Kotulak et al., 1995). Simulations based on a comparison of normalized L- and M-cone contrasts drive accommodation in the predicted direction (Kruger et al., 1995; Lee et al., 1999). However, the situation regarding S-cones is less clear.

It seems unlikely that S-cones contribute to reflex accommodation because they are absent from the central fovea (Wald, 1967; Williams, MacLeod, & Hayhoe, 1981). In addition, the spectral sensitivity of the eye (Smith & Pokorny, 1975) reduces the effectiveness of short wavelength light (Boynton, 1979) and S-cones do not appear to contribute to tasks which require intensity discriminations (Schrödinger, 1925; Whittle, 1974; Tansley & Boynton, 1978; Eisner & MacLeod, 1980; Cavanagh, MacLeod, & Anstis, 1987). On the other hand the accommodation response is slow (350 ms latency) and accommodation responds best to spatial frequencies between 3 and 5 cpd (Owens, 1980), parameters that are within the operating range for S-cones. Also, since LCA is most severe at short wavelengths, S-cone participation would provide an enhanced signal to accommodation from LCA.

In support of S-cone involvement, several experiments have demonstrated an accommodation response to targets illuminated by short wavelength light (Van der Wildt et al., 1974; Charman & Tucker, 1978; Kergoat & Lovasik, 1990). In addition, an increased response was observed when the spectral bandwidth of the illumination was broadened to include short wavelength light (Aggarwala et al., 1995a). However, these experiments did not attempt to isolate the S-cone response, and the accommodation response may have been the result of the L- or M-cone contribution at short-wavelengths.

The present experiment is the first in a series of experiments that will investigate the S-cone contribution to reflex accommodation. The aim of this experiment is to determine whether isolated S-cones can mediate reflex accommodation independently of L- and M-cones.

2. Experimental methods

Two experiments were performed. The first experiment was designed to measure S-cone mediated reflex accommodation responses. The second experiment was a control experiment to determine whether L- and

M-cones contributed to responses measured in Section 2.1, and to control for reductions in S-cone sensitivity that may have resulted from the experimental conditions.

2.1. Experiment 1. Measurement of S-cone mediated reflex accommodation responses

2.1.1. Apparatus

Accommodation was monitored continuously by a high-speed infrared recording optometer while the subject viewed a target moving under computer control in a Badal stimulus system. The infrared optometer and stimulus system have been described in detail in previous papers (Kruger, 1979; Kruger et al., 1993, 1997). A schematic diagram of the present stimulus system is shown in Fig. 1. An artificial 3 mm pupil was imaged in the subjects' real pupil plane to minimize monochromatic aberrations. Accommodation was monitored continuously by an infra-red optometer and the voltage output was recorded by polygraph and sampled at 100 s^{-1} by computer. The recording optometer allows small eye movements (up to 3°). Natural pupil diameters of 3 mm in diameter or greater were maintained without the use of a mydriatic.

2.1.2. Target

The target was a photographic transparency of a 3 cpd sinewave grating with 0.53 Michelson contrast. Reflex accommodation responds particularly well to standard grating targets at this spatial frequency (Owens, 1980; Mathews & Kruger, 1994) and the influence of LCA is prominent at 3 cpd. (Stone, Mathews, & Kruger, 1993). Also, at 3 cpd the grating is within the range of S-cone spatial contrast sensitivity, which peaks around 1.4 cpd with a maximum S-cone grating acuity of 5–10 cpd (Daw & Enoch, 1973; Mollon, 1982; Hess, Mullen, & Zrenner, 1989; Swanson, 1989; Humanski & Wilson, 1992). The grating target subtended 6° at the eye and was limited by a blurred field stop (− 6 D).

2.1.3. Calibrations

Photometry was performed through the Badal stimulus system using the method of Westheimer (1966) for Maxwellian view optics. Measurements were made using a Pritchard spectral-radiometer (Spectra-Scan PR704, Photo Research). Mean retinal illuminance was 82 trolands for the blue/black grating, and 4267 trolands for the yellow adapting field. In the 'white' condition the CIE co-ordinates were (0.490, 0.433) and retinal illuminance was 82 trolands. For a 3 mm pupil the mean luminance of the blue/black grating and the black/white grating was calculated to be 11.6 cd m^{-2}, and the mean luminance of the adapting field was 603 cd m^{-2}.

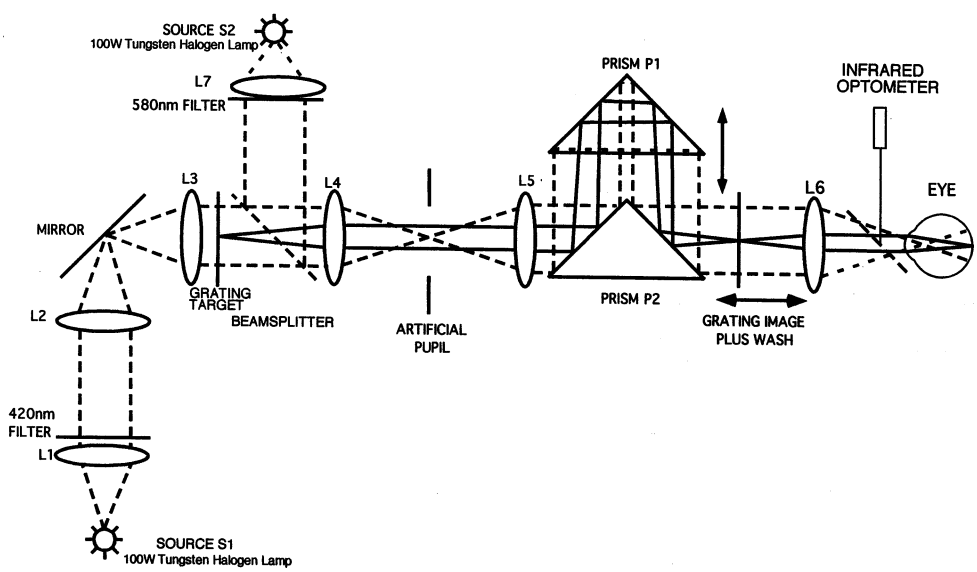

Fig. 1. Instrumentation for isolating the reflex accommodation response from S-cones. Light from source *S*1 was collimated by L1, and filtered by an interference filter (420 nm; 10 nm bandwidth) before illuminating the target (photographic transparency) from behind. Lens L4 focused the light at an artificial pupil and lens L5 re-collimated the illumination. After reflection at the mirrored surfaces of prisms P1 and P2, light from the illumination system was brought to focus in the pupil of the subject's eye by Badal lens L6, producing an image of the artificial pupil. A second illumination channel was provided by source *S*2. Collimated light from *S*2 was filtered (580 nm interference filter with10 nm bandwidth) and superimposed on the light path from *S*1, using a pellicle beamsplitter. Light from *S*2 provided a homogenous yellow field of light over the blue/black grating illuminated by *S*1. The target could be illuminated by white light by removing the 420 nm filter and eliminating source *S*2. Light from the target (3 cpd sine wave grating) was collimated by lens L4, and brought to a focus by lens L5 after reflection at prisms P1 and P2. An image of the target was formed in the focal plane of Badal lens L6, and collimated light reached the subject's eye. Movement of the prism P1 (as shown by the arrow) moved the target image towards or away from the eye and altered the vergence of light reaching the eye.

Table 1
Illumination conditions for experiment 1[a]

Conditions for S-cone experiment 1	Retinal illuminance (trolands)	L-cone modulation	M-cone modulation	S-cone modulation
'Blue' condition (420 nm grating + 580 nm adapting field)	Adapting field 4267 Grating 82	0.0082	0.0143	0.5289
'White' condition (Broadband white grating)	Grating 82	0.5300		0.5300

[a] L-, M- and S-cone contrasts are provided for the 'blue' and 'white' conditions.

Calibration of the accommodative response involved taking both subjective and objective measures of accommodation simultaneously. A high contrast Maltese cross served as the target for the calibration procedure to ensure a strong accommodative response. The subject was instructed to keep the target clear and the accommodative response was recorded to 0, 1, 2, 3, 4 and 5 D of accommodative demand. To provide a subjective measure of accommodation, the subject adjusted the focus of red and green limbs of a red–green vernier target that was superimposed on the Maltese cross (Lee et al., 1999). The simultaneous objective and subjective measures allowed an absolute calibration of the accommodation response.

2.1.4. Subjects

Eight subjects ranging from 21 to 31 years of age participated in the study. They gave informed consent and were paid for their participation. All subjects were optometry students, and all except subject *S*4 were naive to the purpose of the study. A clinical refraction was performed on all subjects including distance refractive states and near point of accommodation. All subjects had normal color vision (Nagel Anomaloscope, Farnsworth 100-hue test).

2.1.5. Procedures

The subject was positioned in the apparatus using an infrared video display to align Purkinje Image I with the center of the 3 mm artificial pupil. A bite plate and forehead rest kept the subject still, trial lenses before the eye compensated for the measured refractive error, and the right eye was patched. The room was dark and the target was the only visible stimulus. The subject adapted to the yellow field during the alignment procedure, for approximately 1 min.

Two experimental conditions were used: a 'blue' condition that reduced cone contrast for the L- and M-cones to a level where they did not contribute to the response, and a 'white' control condition that provided contrast for all three cone types. In the 'blue' condition the grating was illuminated from behind with collimated 420 nm light (10 nm bandwidth) and a monochromatic homogenous adapting field (580 nm; 10 nm bandwidth) was superimposed over the grating by means of a pellicle beam splitter (Fig. 1) creating a pink/yellow grating. In the 'white' condition the target was illuminated from behind with collimated white light (3207 K) from a tungsten source. In the 'white' condition the white/black grating was viewed without an adapting field. The experimental conditions are summarized in Table 1.

The grating target moved towards and away from the eye in a sum of sines motion, with a starting position of 2.0 D and a peak-to-peak amplitude of 3.5 D. Two different target motion paths were used (Table 2). The sum of sines motion consisted of a base temporal frequency at 0.195 Hz and two higher frequencies (0.638 and 0.557 Hz) which were used to mask the base frequency. The higher frequencies provided a relatively unpredictable stimulus path for the subject, reducing voluntary contribution to the reflex accommodation response. Reflex accommodation responds best to temporal frequencies of less than 0.2 Hz for spatial frequencies 0.98–10.5 cpd (Mathews & Kruger, 1994). As

Table 2
Base and masking frequencies for the sum of sines motion paths of the target[a]

	Base frequency	Mask frequency 1	Mask frequency 2
Motion path No. 1			
Temporal frequency (Hz)	0.195	0.638	0.557
Temporal phase (degrees)	152	−118	36
Amplitude (diopters)	1.5	1.0	1.0
Motion path No. 2			
Temporal frequency (Hz)	0.195	0.638	0.557
Temporal phase (degrees)	110	−80	70
Amplitude (diopters)	1.5	1.0	1.0

[a] Two motion paths were used to reduce predictability.

Table 3
L-, M- and S-cone contrasts for the three conditions in the control experiment[a]

Conditions for control experiment	Retinal illuminance (trolands)	L-cone modulation	M-cone modulation	S-cone modulation
Condition 1	Adapting field 4345 Grating 77	0.0075	0.0132	0.5289
Condition 2 (Adapting field luminance increased)	Adapting field 7661 grating 77	0.0043	0.0076	0.5281
Condition 3 (Target and adapting field luminance increased)	Adapting field 7661 grating 130	0.0072	0.0126	0.5289

[a] In condition 1 and 3, cone contrasts are the same as in the main experiment. In condition 2, cone contrasts for the L- and M-cones are reduced. In condition 3, the retinal illuminance is increased, but the cone contrasts are the same as in condition 1.

a result, the responses at the higher masking frequencies (0.638 and 0.557 Hz) were small compared to those at 0.2 Hz. Linear addition of the three temporal frequencies was not assumed, and only the responses at 0.195 Hz were used in the analysis.

Both target illumination conditions and target motion conditions were presented in random order. Six trials of 20.48 s duration were run for each condition with 2 min between trials. The subjects were instructed to 'keep the target clear as if you are reading a book'.

3. Control experiment

A control experiment was performed on two subjects (*S*4, and *S*5) who responded best in the main experiment. The control experiment used the methods described above, but with three different illumination conditions (Table 3). 'Condition 1' was the same as the 'blue' condition in the main experiment. 'Condition 2' further reduced the contrast of the L- and M-cones by increasing the retinal illuminance from the adapting field (7661 trolands). These conditions (Condition 1 and 2) controlled for the possibility that L- and M-cones contributed to the response in the 'blue' condition: they should give similar responses if the reflex accommodation response was mediated by S-cones without a contribution from L- and M-cones. In 'Condition 3' the luminance of the adapting field and the grating were increased so that the contrast for the L-, M- and S-cones remained the same as in 'Condition 1'. Both conditions (1 and 3) should give similar responses if the luminance of the blue grating is in the Weber region for S-cones.

3.1. Calculation of cone contrasts

Relative cone-excitations for the peaks and troughs of the grating were calculated by using the Smith–Pokorny cone fundamentals (Smith & Pokorny, 1975) for 420 nm and 580 nm light. Michelson cone-contrasts were then calculated for each cone class (L, M- and S-cones) using the formula: 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. The calculated cone modulations (contrasts) for the two stimulus conditions of the main experiment are shown in Table 2. In the 'white' condition the modulations of all cone types are 0.53. In the 'blue' condition L- and M-cone modulations are reduced to 0.008 and 0.014, respectively, while S-cone modulation remains high at 0.529. The modulations of the individual cone types have been computed for in focus images and the modulations will change as a result of defocus and the effects of LCA.

3.2. Analysis

An analysis software program written in the Asyst version 4 programming language (Keithley Instruments, Taunton, MA) removed the effects of blinks, and scaled the data according to the subject's calibration. A fast Fourier transform was performed on the data from each trial to determine gain and phase of the response at the base temporal frequency (0.195 Hz). Gain is the amplitude of the response relative to the stimulus amplitude, and phase is the delay in the response relative to the stimulus measured in degrees. Gain and phase lag for the six trials for each condition were vector averaged to provide mean gain and phase.

The two illumination conditions were compared for the group of eight subjects using a one-tailed t-test for matched samples. The correlation between the two conditions was calculated using the point biserial correlation coefficient (r_{pb}), for one continuous and one dichotomous variable. The value $(r_{pb})^2$ indicates how much the 'blue' testing condition contributed to the variability between the conditions and how much was due to other factors. For individual subjects, the responses in the different conditions were compared using a one-tailed randomization t-test using random permu-

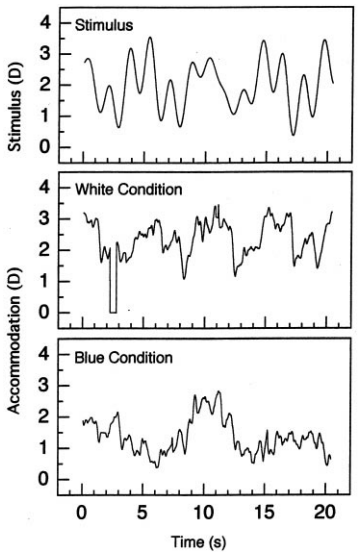

Fig. 2. Samples of the traces recorded by the polygraph recorder for the accommodation responses in the 'blue' and 'white' condition. In the 'blue' condition a 420 nm grating (1.9 log troland) was viewed with a 580 nm adapting field (3.6 log troland). The top trace shows the stimulus path. The target moved in an unpredictable sum of sines motion. The middle and bottom traces are the responses in the 'white' and 'blue' conditions.

tations (Edgington, 1997). This test is a powerful non-parametric test for single subject analysis that does not require any special assumptions of form or underlying distributions of the sampled population. A one-tailed test was used because a reduced response in the 'blue' condition was anticipated for several reasons: gain is usually reduced in monochromatic light (Kruger et al., 1993, 1997), there is reduced contribution of short wavelength light to the photopic luminosity function (Smith & Pokorny, 1975), and there is an absence of S-cones in the foveal center (Williams et al., 1981).

4. Results

4.1. Experiment 1

Fig. 2 shows an example of the polygraph traces for one subject. The upper trace shows the target motion towards and away from the eye in a sum-of-sines motion. The base frequency of 0.195 Hz is visible as the four broad peaks in the stimulus motion path, and the masking frequencies are the smaller fluctuations superimposed on the base frequency. In the 'white' condition (middle trace), the four broad peaks in the response can be clearly seen. In the 'blue' condition (bottom trace) the response is less accurate but still discernable.

The accommodative responses at the base frequency are summarized in Table 4. There was clear variability among the subjects' responses. Overall, the 'blue' condition reduced mean accommodative gain by approximately 50% compared to the white condition for the group of eight subjects (0.33–0.17).

The 'blue' and 'white' conditions were compared for each subject using a one-tailed randomization t-test (Edgington, 1997) using random permutations. The result showed a significant difference ($P < 0.012$) in response between the two conditions for three subjects ($S4$, $S5$, and $S6$). The group response in the 'blue' condition was also significantly different from the 'white' condition (one-tailed, t-test $P = 0.026$, Point biserial coefficient $r_{pb} = 0.52$ ($P < 0.05$), $(r_{pb})^2 = 0.28$). To summarize, the response in the 'blue' condition was statistically different from the 'white' condition. There was a moderate correlation between the gain of the response and the reduction in L-and M-cone contrast, 28% of the variability between the two conditions could be attributed to the loss of L- and M-cone contrast.

Because of the stringent nature of the test and the correspondingly reduced gains, it was important to

Table 4
Results for the experiment 1[a]

Subjects	White condition		Blue condition		Permutation test (Probability)	Principal axis regression (Standard deviation)
	Gain	Phase (Deg.)	Gain	Phase (Deg.)		
1	0.31	−64	0.22	−55	0.060	3.11
2	0.04	−177	0.06	−38	0.625	0.39
3	0.33	−54	0.14	−71	0.116	0.89
4	0.62	−44	0.23	−62	0.001	2.01
5	0.62	−46	0.24	−35	0.001	1.82
6	0.59	−57	0.26	−49	0.012	1.27
7	0.10	−69	0.15	−68	0.721	1.91
8	0.03	−93	0.09	−55	0.729	0.32
Mean	0.33	−76	0.17	−54		

[a] The gains in the 'blue' and 'white' conditions, and the Permutation test results, indicate the probability that the responses are the same in the 'blue' and 'white' conditions. An indication of the size of the mean response above noise in the 'blue' condition is expressed in standard deviations.

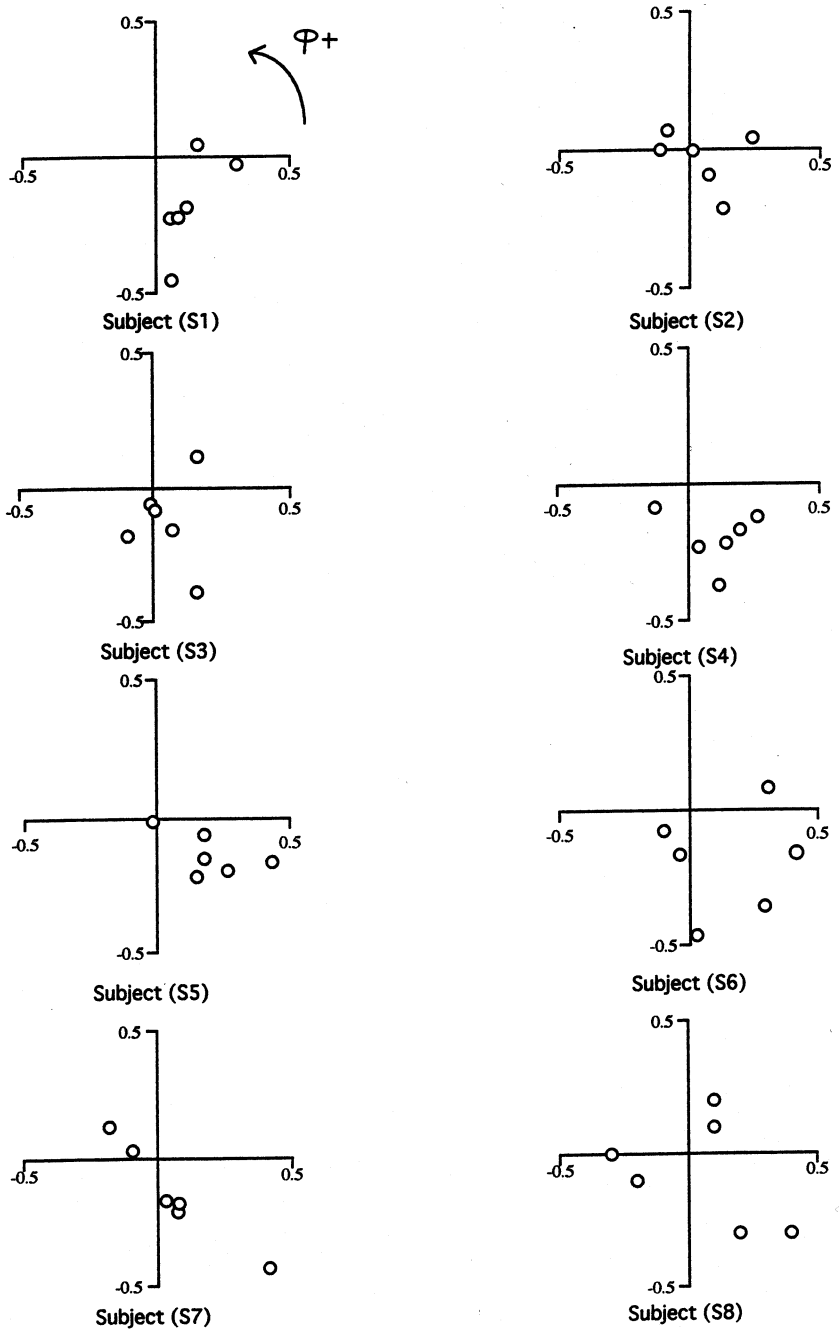

Fig. 3. Gain and phase at 0.195 Hz are plotted in polar co-ordinates for each subject (8) for the 6 trials, each of 20.48 s duration, carried out in the 'blue' condition. The distance of the data points from zero is a measure of the gain of the response. The position of the data points around zero is a measure of phase. Responses should cluster in a particular area to indicate a consistent response. Data points at random positions centered on zero indicate a response that is due to noise.

show that the response in the 'blue' condition was not due to noise or random changes of accommodation not related to the stimulus. To test for this, a procedure using principal axis regression was used to give a quantitative measure of the size of the response in the 'blue' condition in terms of standard deviations (Sokal & Rohlf, 1981). In this procedure the results of each individual's six trials were plotted in Cartesian co-ordinates (Fig. 3). Then the distance of the mean from zero (or noise) was calculated, in standard deviations, to give an estimate of the size of the response above noise.

The analysis showed that the response in the 'blue' condition was substantially greater than noise for four of the eight subjects. Two subjects ($S1$, $S4$) showed substantial responses in the 'blue' condition with mean responses that were 3.11 and 2.01 standard deviations greater than noise. Subjects $S5$ and $S7$ showed mean responses that were 1.82 and 1.91 standard deviations

Table 5
Results for the control experiment[a]

	Subject $S5$			Subject $S4$		
	Gain	Phase (Deg.)	Distance of bivariate mean from zero (S.D.)	Gain	Phase (Deg.)	Distance of bivariate mean from zero (S.D.)
Condition 1	0.21	−92	2.16	0.09	−89	1.07
Condition 2 (Reduced L- and M-cone contrast)	0.24	−63	2.73	0.26	−44	2.15
Condition 3 (Increased retinal illuminance: L- and M-cone contrasts as in condition 1)	0.26	−45	2.08	0.16	−86	1.84

[a] The mean gain and phase of the responses in each condition is shown. An indication of the size of the mean response is expressed in standard deviations, for each condition.

away from noise, respectively, which were still large responses. The mean responses for subjects $S3$ and $S6$, were 0.89 and 1.27 standard deviations above noise, and therefore may not have been due to S-cone stimulation. The remaining subjects ($S2$, $S8$) failed to respond in the 'blue' condition with the responses placed randomly around the zero point, indicating that the responses are most likely due to noise. Subjects that did not respond in the 'white' condition were not expected to respond in the 'blue' condition.

4.2. Control experiment

The size and variability of the responses were evaluated by calculating the gain and the distance of the mean response from zero (in standard deviations) as before, and the results are summarized in Table 5 for the two subjects. Subject ($S5$) gave consistent responses in all conditions (2.08–2.73 S.D.) with an average gain varying between 0.21 and 0.26 in the three conditions. Subject ($S4$) gave more variable responses (1.07–2.15 S.D.). The conditions were compared using a two tailed, randomization t-test using random permutations for individual subjects (Edgington, 1997). The P values are listed in Table 6 for the comparisons between the conditions. These values are all larger than $P = 0.05$, confirming that the responses in the three conditions are not statistically different.

5. Discussion

The results show that some subjects can accommodate using only S-cones, but there are large differences among individuals. Some subjects responded well in the 'white' condition with diminished responses in the 'blue' condition while others failed to respond in either condition. The r_{pb} value shows a moderate correlation (0.52) between the experimental condition and the gain value, and $(r_{pb})^2$ indicates that 28% of the variability between the conditions can be accounted for by the reduction of L- and M-cone contrast. It is possible that short wavelength cones are involved in the accommodation response in all subjects, but that the conditions of the present experiment were so stringent that some subjects were unable to respond, even in the 'white' condition. The factors that may have contributed to the variability can be divided into two groups: those associated with accommodation research and those related to S-cone research.

5.1. Comparison with other accommodation research

First, it is important to recognize that variations in sensitivity to blur have been found in many accommodation experiments (Fincham, 1951; Charman & Tucker, 1978; Owens, 1980; Kergoat & Lovasik, 1990; Kruger et al., 1993). In addition, the variability may be attributed to the variable sensitivity to defocus in monochromatic light (Fincham, 1951; Troelstra et al., 1964; Kruger & Pola, 1986; Kruger et al., 1993; Aggarwala et al., 1995b). Out of eight subjects, two responded equally in white and monochromatic light ($S3$ and $S7$), four gave reduced responses in monochromatic light ($S1$, $S4$, $S5$, $S6$), and two ($S2$ and $S8$) failed to respond in either white or monochromatic light. Further analysis indicates that the response of subjects $S1$, $S4$, $S5$ and $S7$ were substantially greater

Table 6
Results of the random permutation t-tests on individual subjects ($S4$ and $S5$) in the control experiment[a]

Conditions	Subject 4 probability (P)	Subject 5 probability (P)
1 and 2	0.175	0.58
2 and 3	0.3	0.575
3 and 1	0.528	0.3

[a] The P values are all larger than $P = 0.05$, confirming that the responses in the three conditions are not statistically different.

than noise, while $S6$ and $S3$ were not. The preferences and sensitivity of the S-cone accommodation mechanism are unknown and in the present experiment the stimulus provided may not have been ideal. However, the results of this experiment indicate that all three cone types mediate reflex accommodation to some degree.

A related factor was the stringent nature of the testing conditions. The target was limited to a monocular 6° field that moved towards and away from the eye, but the size of the target (spatial frequency) remained constant as a result of the Badal optical system. There was no perceptual awareness of target distance, reduced predictable motion due to the sum of sines motion of the target, and the effects of monochromatic aberrations were minimized with a 3 mm pupil (Walsh & Charman, 1985; Liang & Williams, 1997) and by the use of a 3 cpd grating. Thus all cues to accommodation were removed except for residual cues inherent in blur from defocus i.e. luminance contrast changes, chromatic contrast (as a result of LCA in white light), and information from the vergence of the incident light. Reducing the stimulus in this way can cause a significant reduction in the accommodative response in some subjects, but the stringent method was essential to isolate the reflex accommodation response from S-cones.

In summary, the variability in S-cone mediation of accommodation is in line with previous findings regarding the response to dioptric blur, in fact variability between individuals seems to be a hallmark of the accommodation system (Fincham, 1951; Charman & Tucker, 1978; Owens, 1980; Kergoat & Lovasik, 1990; Kruger et al., 1993).

5.2. S-cone research and the present experiment

There are several issues when conducting experiments on S-cones (Swanson, 1996). These include ensuring that the response is mediated only by S-cones, that there is sufficient S-cone contrast to provide a measurable response, and that the sensitivity of the S-cones is not markedly reduced by the testing conditions. The contributing factors that are relevant to the experiment are considered below.

In order to reduce the contrast of the L- and M-cones to a level where they will not contribute significantly to the measured response, the contrast of the L- and M-cones must be reduced below the minimum contrast level necessary for a reflex accommodation response. This level is about 0.8 log unit greater than the contrast detection threshold (Raymond, Lindblad, & Leibowitz, 1984). As a result, the reflex accommodation response decreases to the empty field level below 3–5% contrast (Bour, 1981; Raymond et al., 1984; Mathews & Kruger, 1989), unless voluntary accommodation is encouraged (Ciuffreda & Rumpf, 1985; Tucker, Charman, & Ward, 1986; Ward, 1987). The experiment was designed so that the calculated residual L- and M-cone contrasts were considerably below the threshold level for reflex accommodation (0.8% and 1.4%, respectively), and voluntary accommodation was discouraged by the low L- and M-cone contrast and sum-of sines target motion. However, the calculations of cone contrast do not allow for variations in macular pigment and the actual values may have differed. To test the validity of the calculations, the control experiment tested for an L- and M-cone contribution by comparing the response at two different contrast levels for the L- and M-cones. This was achieved by measuring the response at two different intensity levels for the long-wavelength adapting field. The results showed that the responses were not statistically different in the two conditions. It can be concluded that there was isolation of S-cone mediated reflex accommodation in the main experiment.

Another concern in S-cone accommodation research is the possibility that S-cone contrast may be reduced below the level that is required for a stable accommodation response. The reflex accommodation response to a black/white *sinusoidally moving* target reaches accommodation threshold at approximately 0.05 modulation, and the response increases linearly with contrast reaching a plateau at 0.5 (Mathews & Kruger, 1989). However, S-cones show a considerably higher detection threshold than L- or M-cones, requiring modulation of between 0.1 and 0.17 at 3 cpd (Humanski & Wilson, 1992). As a result the accommodation threshold may be increased proportionally. At 0.53 modulation the grating contrast was only three to six times above threshold and may have provided insufficient S-cone contrast for a reflex accommodation response. However, the choice of target contrast was limited by the need to keep L- and M-cone contrast below threshold for reflex accommodation.

S-cone contrast can also be reduced as a result of the S-cone quantal catch from the adapting field or increased lens density, which would preferentially reduce the S-cone quantal catch from the short-wavelength grating in comparison with the long-wavelength adapting field. Absorption of short-wavelength light by macular pigment would not affect the S-cone contrast as the peaks and troughs of the grating would be affected equally assuming even pigment coverage. The effect of these factors on S-cone contrast is minimal if the mean luminance of the target is in the Weber region (Swanson, 1996). S-cone contrast obeys Weber's law when retinal illuminance reaches 1.5–2 log td for short-wavelength cones (Hess et al., 1989; Swanson, Fellman, Lynn, & Starita, 1995). In the 'blue' condition target luminance was 11.6 cd m^{-2}, (1.9 log trolands) which suggests that the experiment was performed at retinal illuminance levels in the Weber region. Also, S-cone

contrast was only marginally reduced from 0.530 to 0.529 by the S-cone quantal catch from the adapting field. The control experiment measured the responses at two different intensity levels for the S-cones, to test the assumption that the experiment was performed in the Weber region. The responses were not statistically different for the two intensity levels, indicating that the retinal illuminance levels were in the Weber region, and suggesting that the density of the macular pigment and lens density variations had little effect on the responses of these subjects.

Reduction of S-cone contrast sensitivity as a result of second-site adaptation also may have contributed to the variability among subjects. Second-site adaptation occurs as a result of isolating S-cones with long wavelength adaptation, and depends on the ratio of S-cone excitation to the sum of L- and M-cone excitation (Krauskopf & Reeves, 1980; Yeh, Smith, & Pokorny, 1993). Strong chromatic adaptation of the L- and M-cones, within the opponent site, can decrease the sensitivity of S-cones (Yeh et al., 1993) and decrease the response of the cone-opponent mode (Pugh & Mollon, 1979; Polden & Mollon, 1980). Thus second-site adaptation might decrease the S-cone mediated accommodation response. In this experiment, the relative intensity of the short-wavelength target (82 td) to the long-wavelength adapting field (4267 td) was low, so that reduction in S-cone sensitivity was not expected (Pugh & Mollon, 1979; Polden & Mollon, 1980). The control experiment tested for a reduction in S-cone contrast sensitivity due to second-site adaptation by measuring the response at two different levels of adapting field intensity, thereby changing the ratio of S-cone excitation to the sum of L- and M-cone excitation. The responses were not statistically different in the two conditions and it can be concluded that second site adaptation did not affect the S-cone response.

5.3. The stimulus to accommodation in the present experiment

In the accommodation system several different types of information contribute to the response, including changes in luminance contrast (Phillips & Stark, 1977), chromatic contrast (Campbell & Westheimer, 1959; Smithline, 1974; Kruger & Pola, 1986, 1987; Kruger et al., 1993, 1995, 1997), perceived distance (Ittleson & Ames, 1950; Kruger & Pola, 1985, 1987; Takeda, Hashimoto, Hiruma, & Fukui, 1999) and voluntary contributions (Provine & Enoch, 1975). In addition, information from the vergence of light, may provide a signal to the reflex accommodation system (Fincham, 1951; Kruger et al., 1997). Clearly LCA was not involved in providing a signal, in the 'blue' condition, in this experiment. However, it is clear that S-cones can contribute to the reflex accommodation response and may extend the range of a signal from LCA in the 'white' condition. There were no distance or size cues, the 3 mm pupil and the alignment method minimized monochromatic aberrations and the contribution from voluntary accommodation was reduced by an unpredictable sum of sines target motion. Thus, the remaining cues to accommodation were changes in luminance contrast or S-cone contrast and potentially a signal from the vergence of light per se.

Several investigators have found that S-cones do not contribute to the luminance contrast signal (Schrödinger, 1925; Whittle, 1974; Tansley & Boynton, 1978; Eisner & MacLeod, 1980; Cavanagh et al., 1987). Others have demonstrated a small contribution during subjective brightness measurements (Marks, 1974), flicker and increment threshold measurements (Drum, 1983), spatio-temporal masks (Blythe, Bromley, Holliday, & Ruddock, 1986) and under high intensity adaptation conditions (Lee & Stromeyer, 1989; Stockman, MacLeod, & DePriest, 1991; Stockman, MacLeod, & Lebrun, 1993). If S-cones do contribute to luminance contrast, the results can be explained by the standard view of accommodative control, where the stimulus is an even error luminance contrast signal. On the other hand, if S-cones do not contribute to luminance contrast, it is possible that the system used negative feedback to maximize an S-cone contrast signal. A final possibility is that an unknown directional signal provided information about the vergence of light (Fincham, 1951; Kruger et al., 1997).

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