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CROSS-COUPLING BETWEEN ACCOMMODATION AND CONVERGENCE IS OPTIMIZED FOR A BROAD RANGE OF DIRECTIONS AND DISTANCES OF GAZE

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Abstract

Accommodation and convergence systems are cross-coupled so that stimulation of one system produces responses by both systems. Ideally, the cross-coupled responses of accommodation and convergence match their respective stimuli. When expressed in diopters and meter angles respectively, stimuli for accommodation and convergence are equal in the mid-sagittal plane when viewed with symmetrical convergence, where historically, the gains of the cross coupling (AC/A and CA/C ratios) have been quantified. However, targets at non-zero azimuth angles, when viewed with asymmetric convergence, present unequal stimuli for accommodation and convergence. Are the cross-links between the two systems calibrated to compensate for stimulus mismatches that increase with gaze-azimuth? We measured the response AC/A and stimulus CA/C ratios at zero azimuth, 17.5 and 30 degrees of rightward gaze eccentricities with a Badal Optometer and Wheatstone-mirror haploscope. AC/A ratios were measured under open-loop convergence conditions along the iso-accommodation circle (locus of points that stimulate approximately equal amounts of accommodation to the two eyes at all azimuth angles). CA/C ratios were measured under open-loop accommodation conditions along the iso-vergence circle (locus of points that stimulate constant convergence at all azimuth angles). Our results show that the gain of accommodative-convergence (AC/A ratio) decreased and the bias of convergence-accommodation increased at the 30 deg gaze eccentricity. These changes are in directions that compensate for stimulus mismatches caused by spatial-viewing geometry during asymmetric convergence.

Keywords

accommodation; asymmetric convergence; cross-coupling; phoria; viewing geometry; near response; iso-vergence circle; iso-accommodation circle

Introduction

The near response describes the coordination of several visual-motor systems that align the two eyes with convergence and focus the retinal images with accommodation. Convergence is stimulated by binocular disparity, and accommodation is stimulated by contrast reduction of the retinal image caused by defocus, and both systems respond to perceived distance (Schor, Alexander, Cormack, & Stevenson, 1992). In straight-ahead gaze (zero azimuth), targets in the

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midsagittal plane produce equal magnitudes of disparity and defocus when they are expressed in meter angles ($MA = 1/\text{viewing distance [m]}$) and diopters ($D = 1/\text{viewing distance [m]}$) respectively. However, when targets are viewed in asymmetric convergence (i.e., with some combination of horizontal version and convergence), conflicts arise between stimuli for accommodation and convergence as a consequence of three-dimensional spatial geometry.

Stimulus conflicts are illustrated in Figure 1 that compares a plan view of the iso-accommodation circle to the iso-vergence circle. The iso-accommodation circle describes the locus of points that subtend a constant average accommodation stimulus to the two eyes with increasing azimuth. This circle has a radius equal to the viewing distance from the cyclopean eye to the object of regard in any horizontal direction of gaze lying in a common visual plane. The iso-vergence circle passes through the fixation point and two centers of eye rotation (Luneburg, 1948). The distance of points along the circle to the cyclopean eye varies with both viewing distance and direction of gaze (azimuth). The circle has a radius that is equal to the inter-pupillary distance (PD) divided by twice the sine of the angle of convergence (α).

$$\text{Iso-vergence radius} = PD / (2 * \sin \alpha) \tag{1}$$

Note that in asymmetric convergence, the viewing distance to the fixation target is greater in the adducting than abducting eye such that the stimulus to accommodation is unequal for the two eyes, and this difference increases with gaze eccentricity (azimuth) and stimulus proximity (Marran & Schor, 1998). However this difference is normally very small because versional eye position rarely exceeds 15 degrees from straight ahead (Bahill, Adler & Stark, 1975).

The only spatial locations that present matched stimuli for accommodation and convergence lie in the midsagittal plane where the iso-vergence and iso-accommodation circles intersect (Figure 1). For points lying to the left or right of the mid-sagittal plane, the stimulus to accommodation is always greater than the stimulus to convergence. The average accommodation stimulus along the iso-vergence circle increases greatly while the convergence stimulus is invariant with increasing azimuth. Figure 2 plots the computed binocular accommodation (D) and convergence (MA) stimulus combinations for a 25 cm viewing distance from the baseline along the iso-vergence and iso-accommodation circles respectively. The Matlab algorithms for solving for MA and D with azimuth are available on request. The accommodation and convergence stimulus values were computed for a range of azimuth values from zero to 70 degrees. The convergence angle at all points on the iso-vergence circle is a constant 4.06 MA and the average binocular accommodative stimulus at all points on the iso-accommodation circle is a constant 3.97 D for a 6 cm inter-pupillary distance (Y axis intercepts at zero azimuth). The average stimulus to accommodation increases along the iso-vergence circle from 3.97 D at zero azimuth to 5.7 D at 45 degrees azimuth which corresponds to a change of 1.73 D. The convergence stimulus decreases along the iso-accommodation circle from 4.06 MA at zero azimuth to 3.1 MA at 45 degrees azimuth which corresponds to a change of 0.96 MA or 3.4 degrees of convergence.

The stimulus conflicts that increase with gaze azimuth pose problems for coordinating the cross-coupled accommodation and convergence components of the near response in asymmetric convergence. Typically, measurements of these ratios use targets placed straight ahead in the midsagittal plane. However, natural viewing conditions often include near responses to targets viewed to the left and right of straight ahead (i.e., asymmetric convergence), and the ideal cross-link ratios change markedly with gaze azimuth (Figure 3). The ideal responses of accommodation and convergence that would match the various stimulus combinations at different azimuths could be accomplished by changing the gains of the cross-link ratios, or by changing response biases from the values in the straight ahead direction. The ideal changes of bias and gain of cross-link interactions are predicted based on spatial geometry

of stimuli and they are not specific to any particular feedback model of cross-link interactions. Any model capable of recalibrating gain and/or static bias, could conform to these predictions.

Our description of ideal ratios for cross-link interactions assumes that either accommodation or convergence dominates the initial cross-link interactions of the near response. Studies of proximal convergence have investigated which motor system (accommodation or convergence) dominates the near response (Malmstrom & Randle, 1976; McLin & Schor, 1988; McLin, Schor & Kruger, 1988; Wick & Bedell, 1989). These studies open the visual-feedback loop for both disparity and defocus with monocular viewing through a pinhole pupil and the near response is stimulated with loom (target-size changes). The ratios of proximal convergence/proximal accommodation and proximal accommodation/proximal convergence (stimulated by loom) were compared to traditional measures of the AC/A and CA/C ratios to determine which cross-link ratio the proximal ratio most resembles. McLin et al. (1988) reported that accommodation orchestrated the near response to step and smooth changes in perceived target distance whereas Wick & Bedell (1989) reported that convergence was the dominant input for the proximal response to perceived depth. The main difference between these studies was that convergence was the dominant input when saccades were associated with convergence (Wick & Bedell 1989). These studies demonstrate that there are binocular conditions when either ratio can dominate the initial near response.

The ideal cross-couplings between accommodation and convergence that match convergence and accommodation responses to the stimulus combinations in asymmetric convergence have a three-dimensional spatio-topic dependence. Figure 3 plots the ideal AC/A (MA/D) and CA/C (D/MA) ratios as a function of gaze azimuth that would produce accommodation and convergence responses respectively that corresponded to stimuli viewed in asymmetric convergence along either the iso-accommodation circle or the iso-vergence circle. This figure is derived from the data in Figure 2 after it was normalized to a 1M viewing distance at zero azimuth. The ideal AC/A ratio decreases with azimuth and the ideal CA/C ratio increases with azimuth and the two ideal ratios are reciprocally related. Figure 4 is a plot of the ideal AC/A and CA/C ratios at a fixed azimuth angle of 40 degrees for viewing distances ranging from 0.1 to 1m. The ideal ratios change little with viewing distance because both stimuli to accommodation and convergence increase proportionally with the reciprocal of viewing distance, such that their ratio is invariant with viewing distance. Thus the ideal ratios change markedly with gaze azimuth but not appreciably with viewing distance along common azimuth lines described as iso-version lines (Luneburg, 1948).

Biases of convergence and accommodation could also be calibrated to compensate for changes in stimulus combinations in asymmetric convergence when the cross-link gains are invariant with azimuth. For example, the ideal convergence bias in meter angles along the iso-accommodation circle is an increase in exo-phoria (divergence bias) from gaze directed straight ahead. We have computed changes in bias that match accommodation and convergence responses to stimuli at different azimuths when the gains of the AC/A and CA/C ratios are invariant with azimuth. Equation 2 and Equation 3 compute the ideal static bias for convergence and accommodation respectively for designated azimuths along the iso-accommodation and iso-vergence circles. The ideal biases for convergence and accommodation, expressed in meter angles (MA) and diopters (D) respectively, is computed at the designated azimuth from the change in ideal cross-link gains, described in Figure 3, from straight ahead to the designated azimuth, times the stimulus along the iso-accommodation or iso-vergence curves. These biases are computed in equation 2 and equation 3, where AC/A_{az} and CA/C_{az} equal the ideal cross link gains at the eccentric gaze angle (azimuth) and the ideal gain is unity in straight ahead gaze.

$$\text{Convergence bias} = D \times (\text{AC/A}_{\text{az}} - 1) \quad (2)$$

$$\text{Accommodative bias} = MA \times (CA/C_{az} - 1) \tag{3}$$

For example, the ideal AC/A ratio along the iso-accommodation circle decreases from 1.0 in straight ahead gaze to 0.77 at 40 degrees azimuth. If the magnitude of the AC/A ratio did not change with azimuth, then the ideal convergence bias would be $-0.23 MA$ at 40 deg azimuth along the iso-accommodation circle for a 1D accommodation response. Similarly, the ideal gain of the CA/C ratio along the iso-vergence circle increases from 1.0 in straight ahead gaze to 1.31 at 40 degrees azimuth. If the magnitude of the CA/C ratio did not change with azimuth, then the ideal accommodation bias would be $+0.31D$ at 40 deg azimuth along the iso-vergence circle for a 1 MA convergence response. As indicated by the distance scalars (D and MA) in equation 2 and equation 3, these biases increase with the reciprocal of viewing distance. Figure 5 a,b plots the ideal biases for (a) accommodation and (b) convergence as a function of gaze azimuth, along iso-vergence and iso-accommodation circles respectively, for two viewing distances (1m and 0.25m). These biases would produce accommodation and convergence responses that matched stimulus combinations viewed in asymmetric convergence along the iso-vergence circle or the iso-accommodation circle respectively, with azimuth-invariant cross-link ratios. The ideal accommodation bias increases with azimuth and the ideal convergence bias decreases (increased divergence bias) with azimuth and the magnitudes of the biases increase with the reciprocal of viewing distance.

Biases that match the accommodative and convergence responses to stimuli at different azimuths can also be computed based upon the empirical measures of AC/A and CA/C ratios. The biases are computed in equation 4 and equation 5 from ideal (I) and empirical (E) measures of cross-link ratios at the designated azimuth.

$$\text{Convergence bias} = D \times (AC/A_I - AC/A_E) \tag{4}$$

$$\text{Accommodative bias} = MA \times (CA/C_I - CA/C_E) \tag{5}$$

Do empirically measured cross-coupling ratios between accommodation and convergence change with gaze azimuth to conform to the mismatched stimuli in asymmetric convergence, or do they have a fixed value that is a compromised solution to the commonly used range of version angles of approximately ± 15 degrees (Bahill et al., 1975)? Interestingly, the normal-empirical AC/A ratio measured at zero azimuth has a value of $4PD/D$ ($0.67MA/D$) (Ogle, Martens & Dyer, 1967). This is lower than the ideal ratio of $6PD/D$ ($1MA/D$) for symmetrical convergence but equals the ideal AC/A ratio for a gaze azimuth of approximately 50 degrees. It is possible that the normal low AC/A ratio for zero azimuth optimizes the range of gaze azimuths for clear and single binocular vision by not producing excessive accommodative-convergence in asymmetric convergence. If the empirical AC/A ratio equaled the ideal for symmetrical convergence, and was invariant with azimuth, then accommodation to targets viewed in asymmetric convergence would produce excessive accommodative-convergence (an eso-error of convergence) that would require fusional divergence to obtain binocular alignment. In contrast, if the normally low AC/A ratio at zero azimuth is associated with insufficient convergence (an exo-error of convergence), then fusional convergence is necessary to obtain binocular alignment. The latter condition is preferable since the range of fusional convergence (i.e., disparity vergence) is nearly three times the range of fusional divergence (Morgan, 1964). Thus an invariant AC/A ratio that is lower than the ideal value for symmetrical convergence greatly increases the range of azimuths over which single and clear binocular vision can be achieved with an azimuth-invariant AC/A ratio.

A similar argument can be made for having the empirical CA/C ratio equal to the ideal ratio for zero gaze azimuth. Normally the empirical CA/C ratio in symmetrical convergence is close to the ideal CA/C ratio in young adults ($1D/MA$) (Fincham & Walton, 1957; Kent, 1958; Schor & Narayan, 1982). However, the ideal CA/C ratio in asymmetric convergence increases with

azimuth. If the normal-empirical CA/C ratio was invariant with azimuth, then it would be lower than the ideal value for any amount of asymmetric convergence (eccentric gaze azimuth), and the convergence-accommodation responses would be less than the dioptric value of the accommodative stimulus. This would require additional optical-reflex accommodation to focus the retinal image (Heath, 1965). This in turn would stimulate more accommodative-convergence. However the additional accommodative-convergence would not produce an excessive convergence error (eso-phoria) because for most gaze eccentricities, the empirical AC/A ratio is lower than the ideal, such that it produces a divergence (exo) vergence error. This exo-phoria bias could serve as a buffer to absorb the additional accommodative-convergence produced by compensating for the lower than ideal CA/C ratio in asymmetric convergence. It is also possible that the AC/A and CA/C ratios do vary with azimuth to conform to the stimulus demands set by three-dimensional spatial geometry.

Finally, it is possible that the cross-link ratios do not change with azimuth, but the near response is augmented by variations in bias of accommodation and convergence (phorias) with gaze azimuth that is similar to variations of vertical phoria with gaze azimuth (Schor, Maxwell, McCandless & Graf, 2002). For example, a divergence or exo-phoria bias could increase with azimuth to match the convergence and accommodation responses to single targets (compare points B and D in Figure 1). The combination of a variable bias with invariant AC/A and CA/C ratios could produce optimal responses to targets viewed in asymmetric convergence at various gaze eccentricities.

Purpose and Rationale: Gain and bias variations of AC and CA with horizontal eye position cues

The AC/A and CA/C ratios may be calibrated to conform to three-dimensional spatial geometry, such that their magnitudes will be different in symmetric and asymmetric convergence. It is also possible that the two ratios might have fixed values that are a compromise between the stimuli to convergence and accommodation that vary differently with azimuth and that biases match their responses to the unequal stimuli. We have quantified the two ratios and their biases as a function of gaze azimuth to distinguish between these two possibilities.

We determined whether accommodative-convergence conforms to spatial geometry by measuring the AC/A ratio in different directions of gaze (azimuth) with a range of accommodative stimuli that step defocus from a constant target distance (1m) along the iso-accommodation circle while the convergence loop is opened by monocular occlusion. The iso-accommodation curve keeps the reference stimulus to accommodation fairly constant, so that any variations in the AC/A ratio with azimuth can not be produced by non-linearities of the accommodative response with magnitude (Miege & Deniuel, 1988). Similarly, we also determined whether convergence-accommodation conforms to spatial geometry by measuring the CA/C ratio in different directions of gaze (azimuth) with a range of disparity vergence stimuli that step disparity from a constant initial convergence angle (1MA) along the iso-vergence circle while the accommodative loop is opened with a low-pass filtered stimulus (Tsuetaki & Schor, 1987). The variations of empirically measured cross-coupling ratios were compared to predictions of the theoretical changes with azimuth of the ideal interactions between accommodation and convergence. Our results support a reduction of the AC/A ratio with azimuth and an azimuth-invariant CA/C ratio. Bias of convergence was azimuth-invariant whereas bias of accommodation increased with azimuth. These azimuth-dependent changes of accommodation and convergence responses help to compensate for stimulus mismatches caused by spatial-viewing geometry during asymmetric convergence.

Methods

AC/A ratios were derived from subjective measures of accommodation and convergence with the left eye occluded. The closed-loop stimulus to accommodation that was used to evoke accommodative-convergence was an illuminated text target (a paragraph). It was presented monocularly to the right eye at a 1m viewing distance along the iso-accommodation circle over a range of dioptric vergence produced with ophthalmic lenses from +0 to -5D in 1D steps. The subject fixated at the center of the paragraph (with letter size ~20/30). This stimulus provided monocular defocus feedback for accommodation (closed-loop response) and no disparity feedback for convergence (open-loop response). CA/C ratios were derived from subjective measures of accommodation while the eyes viewed a low-pass filtered Difference of Gaussian stimulus (DoG) presented binocularly with a center frequency of 0.2 cpd (Tsuetaki & Schor, 1987) over a range of disparities from -1MA to +4MA in 1MA steps. The disparities were introduced with ophthalmic prisms placed before the two eyes. The iso-vergence circle included a viewing distance of 1m at zero azimuth. This binocular fusion stimulus provided disparity feedback to convergence but no defocus feedback to accommodation.

Subjective estimates of accommodation were measured with a stigmascopes mounted before the right eye in a Wheatstone-mirror haploscope. The stigmascopes consists of a Badal lens system (Figure 6) that images a stigma (0.5 mm point source of light) to the right eye. The posterior focal point of the 10D Badal lens coincides with the entrance pupil of the eye to eliminate size changes of the stigma during measurement of accommodative response. The stigmascopes is mounted on right arm of the haploscope along an axis that passes through the right eye's center of rotation. The haploscope arms rotate about points that coincide with the eye's center of rotation, about 13 mm behind the corneal apices. This insures that there were only rotations and no translations of the stigma during rotation of the haploscope arms to different stimulus azimuth angles. The subject's head was held with an adjustable mouth bite that allows forward, lateral and rotational adjustments of the head for proper alignment. Precise alignment was confirmed by rotation of the haploscope arm 30 degrees and subjective perception of a 30 degree shift of the stigma that is optically superimposed with a beam splitter onto a calibration target, consisting of two vertical lines separated by 30 degrees. All ametropic subjects wore their spherical contact lens corrections during the experiment.

During measurement of accommodation, subjects were instructed to focus with accommodation on the center of the text viewed with their right eye, or to binocularly fuse the image of the vertical DoG and to focus the image of the right stigma with their hand by turning a knob to vary its image distance. Subjects were able to perform this task after a short training period. Subjects bracketed responses between near and far just-detectable blur limits of the stigma. The image location of the stigma represents the optical conjugate focus of the right eye. The accommodative response was calculated with reference to the entrance pupil of the eye. Pupil size variations between subjects usually range between 4 to 5.5 mm. Repeated measures have a standard error of 0.1 D which is comparable to the accuracy of most objective optometers.

Subjective measures of convergence were made to quantify the AC/A ratio with the Wheatstone-mirror haploscope using a dichoptic Vernier (Nonius) alignment criterion. Subjects rotated the left arm of the haploscope to change the perceived azimuth of the left stigma until it appeared in vertical alignment (i.e., at the same azimuth) as the fixated letter viewed by the right un-occluded eye. The left eye viewed the left stigma from a beam-splitter whose front surface was occluded. During measures of the CA/C ratio, the convergence response was assumed to equal the convergence stimulus as long as the subject could fuse the target. Fixation disparity is less than 0.25 degrees with this type of fusion stimulus (Schor, Wesson & Robertson, 1986).

Azimuth was varied pseudo randomly from 0 to 17.5 to 30 degrees (rightward) along the iso-accommodation circle for measures of the AC/A ratio and along the iso-vergence circle for measures of the CA/C ratio. The fixation distance at zero azimuth was 1M. Combinations of retinal stimuli of defocus and disparity were randomized at each azimuth and there were seven stimulus presentations for each condition. Randomization reduced the possibility of adapting the resting focus and convergence phoria to a given stimulus magnitude for either accommodation or convergence. Accommodative-convergence and convergence-accommodation responses were measured on separate days.

Analysis

To quantify the AC/A ratio, open-loop convergence responses were plotted as a function of closed-loop accommodation responses to a range of accommodative stimuli 0–5 D. Plots were of absolute values of accommodation and convergence. The cross-coupling ratios were expressed in units of diopters and meter angles which are independent of inter-pupillary distance. The AC/A ratio was calculated for each of the three azimuth locations from the slopes of the regression lines fit to these data. The data could be well fitted by a straight line for accommodative stimuli within the range of 1 to 5 D. Results for the three azimuth locations along the iso-accommodation circle were plotted separately. For the analysis of CA/C ratio, open-loop accommodative responses were plotted as a function of the convergence stimulated by five prism stimuli within the range of –1 to 4 MA. Linear regression analysis was performed on the linear portion of the data set, and the slope of the straight-line fit quantified the CA/C ratio. The linearity assumption was cross checked by fitting higher order polynomials to the data set. If higher order polynomials did not yield significantly better fits when compared to the linear model, the data set was considered adequately linear. Results for the three azimuth locations along the iso-vergence circle were analyzed separately. The biases equaled the Y intercepts of these straight line plots and they quantified the absolute values of open-loop accommodation and open-loop convergence responses when the closed loop stimulus to the cross-coupled system was zero.

Subjects

Eight subjects participated in the study. Their ages ranged from 21 to 32 years and their accommodative amplitudes, inter-pupillary distances and distance refractive corrections are shown in Table I. All had normal monocular amplitudes of accommodation, normal visual acuity of at least 20/20, binocular alignment, and stereopsis of at least 20 arc sec as measured on the RanDot™ test. Ametropic subjects' refractive errors were corrected with contact lenses. Subject selection and procedures conformed to the human subject IRB guidelines. Subjects participated in the study after signing an informed consent form approved by the Center for Protection of Human Subjects (CPHS), University of California at Berkeley.

Results

We have tested two models that predict the bias and gain of cross-coupling interactions between accommodation and convergence as a function of gaze azimuth. The gain-variant model predicts a decrease of AC/A ratio and an increase in CA/C ratio with azimuth and no change in bias of accommodation and/or convergence in asymmetric convergence. The bias-variant model predicts changes in the convergence bias and/or accommodation bias with azimuth to compensate for errors of accommodation and convergence associated with invariant cross-link ratios. Some combination of these two models might also be observed.

Figure 7 (a) is a bar graph that illustrates the slopes of the accommodative-convergence functions (AC/A ratio) for all subjects at the three tested angles of azimuth. Inspection of

individual data revealed that the AC/A ratio at 17.5 degrees decreased from the zero azimuth measure in 7 out of 8 observers. AC/A ratios were lower at 30 degree than at 17.5-degree azimuths in 7 of 8 subjects, while one subject showed slight increment at 30-degree azimuth. The mean AC/A ratio in units of MA/D was 0.92 ± 0.37 (SD) at zero azimuth, 0.77 ± 0.33 at the 17.5-degree azimuth angle, and 0.66 ± 0.27 at the 30-degree azimuth angle. These correspond to gain changes from 0 degrees of 0.15 at 17.5 deg and 0.26 at 30 degrees. Four out of the 8 subjects had lower AC/A ratios than the ideal 1MA/D at zero azimuth, and all 4 showed a slight decrease in the AC/A ratio at 17.5-degree azimuth relative to straight ahead position, and 3 showed lower AC/A ratios at 30 degrees than at 17.5 degree azimuth. This result is similar to the remaining 4 subjects who had high AC/A ratios ($> 1MA/D$) at zero azimuth. Both (sub) groups showed a decrease in AC/A ratio with azimuth, but the group with lower initial AC/A ratio (zero azimuth) demonstrated slightly lower average change in AC/A ratio with gaze azimuth. The combined data set was analyzed with non-parametric statistics owing to the small sample size ($n = 8$). The Friedman test for correlated samples showed that AC/A ratios vary with gaze angle ($\chi^2 = 12.25$, $df = 2$, $p < 0.01$). Post hoc tests with Wilcoxon signed ranks test (with Bonferroni correction ($\alpha = 0.05/n$, where $n = 3$)) showed lower AC/A ratios at 30-degree azimuth angle than at zero and 17.5-degree azimuths (p values ≤ 0.017), but the difference in AC/A ratios between zero and 17.5-degree azimuths did not reach statistical significance ($p > 0.017$). As illustrated by figure 3, the predicted change in AC/A ratio from zero azimuth to 17.5 deg eccentric gaze (0.0286 MA/D) is small, and since our data showed a clear trend of lower AC/A ratios at 17.5 degrees (7 of the 8 subjects), the absence of statistical significance here does not disprove our gain-variant model for the AC/A that predicts reductions in gain of AC with increasing azimuth.

Figure 7 (b) is a bar graph that illustrates the CA/C ratios measured at the three angles of azimuth in the same subjects. The mean CA/C ratio in units of D/MA was 0.34 ± 0.2 (SD) at zero azimuth, 0.38 ± 0.12 at 17.5-degree azimuth, and 0.39 ± 0.22 at 30-degree azimuth. Note that the mean empirical CA/C ratio at zero azimuth is low when compared to those reported by some studies (Fincham & Walton, 1957; Kersten & Legge, 1983), however, low CA/C ratios reported here are not unusual in normal adults (Bobier, Guinta, Kurtz & Howland, 2000).

On examining the inter-individual variation, we found that 5 of our 8 subjects had slightly lower CA/C ratios at 17.5 degrees than at zero azimuth, and the remaining three showed an increase at 17.5 degrees. Three of the 8 subjects showed lower CA/C ratios at 30-degree azimuth than at 17.5-degree azimuth, 4 subjects showed an increase and one subject showed no difference between the two gaze angles. Further, if the subjects were categorized as two subsets, one with high initial CA/C ratios at zero azimuth (> 0.50 D/MA, $n = 2$) and the other with low initial CA/C ratios (< 0.50 D/MA, $n = 6$), the pattern of changes in gain with azimuth could not be differentiated. The two subjects with high initial CA/C ratios (> 0.50 D/MA) showed a decrease in CA/C ratio as the azimuth angle increased to 17.5 degrees from straight ahead gaze. Three of the 6 subjects with low initial CA/C ratios (< 0.50 D/MA) also showed a slight decrease in CA/C ratio at 17.5 degrees from the zero azimuth ratio, while the remaining three showed an increase. Azimuth places larger demands on subjects with lower CA/C ratios, since the ideal CA/C ratio increases with azimuth. This suggests that in our sample, the pattern of gain changes of CA with increasing azimuth is independent of the initial CA/C ratio. Friedman test on the group data revealed that CA/C gain is statistically invariant with gaze angle ($\chi^2 = 1.75$, $df = 2$, $p > 0.05$).

We also analyzed possible changes in the open-loop convergence bias (phoria) and the open-loop accommodation bias with azimuth (these biases are indicated by the Y-intercepts of the AC/A and CA/C plots respectively). The open-loop convergence bias is the open-loop convergence response measured with the accommodative stimulus at zero diopter, i.e. the

distance heterophoria (Owens & Tyrrell, 1992; Jiang & Woessner, 1996). The open-loop accommodation bias is the open-loop accommodation response measured with the convergence stimulus at zero MA. These biases could compensate for errors of accommodation or convergence resulting from AC/A and CA/C ratios that do not conform to the spatial geometry of targets viewed in asymmetric convergence. Figure 8 plots the average open-loop accommodative bias in the zero convergence condition at the three azimuth locations along the iso-vergence circle. The same graph illustrates the open-loop convergence bias associated with closed-loop accommodation response to zero diopters at the three azimuth locations along the iso-accommodation circle. For comparative purposes, the theoretical functions for ideal biases are also depicted as a function of azimuth. Comparison of y-intercepts revealed that the open-loop convergence bias is constant across all three azimuths (Friedman test, $\chi^2 = 3.0$, $df = 2$, $p > 0.05$). In contrast, the open-loop accommodative bias changed with gaze angle (Friedman test, $\chi^2 = 10.75$, $df = 2$, $p < 0.05$). It was constant across the zero and 17.5-degree azimuths ($p > 0.017$) and invariant across 17.5 and 30 degree azimuths ($p > 0.017$). However, it was significantly higher at 30 degrees than at zero degree azimuth ($p = 0.012$). This increase at 30-degree azimuth was in a direction that would compensate for accommodative errors associated with eccentric gaze and an azimuth-invariant CA/C ratio. The bias (0.84D) is greater than the accommodative stimulus on the iso-vergence circle (0.15D) and may be an uncalibrated response to this unusually large gaze angle that exceeds the upper limit of the normal 15 degree range of gaze eccentricity by a factor of two.

To obtain a comprehensive picture of the results, we plotted the mean accommodative-convergence ratio, mean convergence-accommodation ratio and the theoretical functions for the ideal ratios as a function of azimuth (Figure 9). The deviation of the empirically measured ratios from no change (horizontal line) would indicate an influence of azimuth on cross-coupling gains. Comparison of the direction and magnitude of changes to those predicted by spatial geometry will indicate if horizontal gaze direction (azimuth) has any influence on the magnitude of cross-coupling between accommodation and convergence. Note that the empirical average accommodative-convergence gain (filled triangles) was lower at 30-degree gaze angle when compared with zero azimuth, keeping in line with the theoretical predictions of the gain-variant model for AC. In contrast, the convergence-accommodation gain (open squares) did not increase at the extreme gaze angle compared to the zero azimuth measure, indicating a mismatch between the empirical estimates and theoretical predictions of the gain-variant model. Instead, there was an increase in the empirical accommodative bias at thirty-degree azimuth than at straight ahead gaze (see Figure 8), keeping in line with the theoretical prediction of the bias-variant model for CA.

Taken together, our data provide evidence supporting both the gain-variant and bias-variant models that predict the cross-coupled interactions between accommodation and convergence during asymmetric convergence. As predicted by the gain-variant model, we found a decrease in the accommodative-convergence gain at thirty-degree gaze angle from the straight-ahead position, without any significant changes of convergence bias. As predicted by the bias-variant model, we found changes of accommodation bias that were consistent with compensation for errors of accommodation associated with an azimuth-invariant CA/C ratio.

Discussion

Because accommodation and convergence are cross-coupled and spatial geometry produces stimulus inequalities that increase with gaze azimuth, asymmetric convergence presents a cue conflict between stimuli for these two systems. How is the conflict resolved? Is the coupling adjusted to a compromised solution that is invariant with azimuth or does the coupling change with azimuth to conform to spatial geometry? If the gain of the coupling is invariant with azimuth, are there changes in the convergence and/or accommodation biases (phorias) that

compensate for stimulus mismatches produced by asymmetric convergence? Previously, we demonstrated that it was possible to train and adapt the convergence phoria to vary systematically with azimuth (Schor et al., 2002) and this is a highly plausible strategy that could compensate for azimuth-invariant cross-couplings between accommodation and convergence.

The normal low value for the AC/A ratio in symmetrical convergence would suggest that the AC/A ratio was calibrated to be invariant with azimuth. The normal value for the AC/A ratio measured with targets in the mid-sagittal plane is 0.67MA/1D (Ogle et al., 1967), while the ideal value is 1MA/1D. The normal AC/A ratio produces open-loop convergence responses that are smaller than the convergence stimulus. For example, a 2D accommodation response to a target at 0.50 m. is normally coupled with an open-loop convergence response to 1.33 MA. What is the advantage of having the AC/A ratio normally calibrated to a lower value than that which would adjust eye alignment and accommodation to a common distance at zero azimuth? Although the normal ratio is not ideal for targets in the mid-sagittal plane, it is ideal for some horizontal version angle in asymmetric convergence.

An invariant AC/A ratio can only be ideal for a single gaze eccentricity, and it will produce residual errors (phorias) at gaze eccentricities that are smaller or larger than the optimal azimuth. For gaze angles beyond the optimal azimuth angle, the fixed AC/A ratio is too high and produces eso-phoric (excessive convergence) residual errors and it is too low for smaller version angles and it produces exo-phoric (insufficient convergence) residual errors. The residual errors of convergence and/or accommodation are compensated by fusional (disparity) vergence and optical-reflex accommodation respectively. Fusional vergence has a much larger range in the convergence than divergence direction (Morgan, 1964), such that it is preferable for the AC/A ratio to produce residual errors that can be corrected with convergence rather than divergence (i.e., exo-phoria). Hence there is a larger penalty for high AC/A ratios that produce eso-phoria or excessive convergence than for low AC/A ratios that produce exo-phoria or insufficient convergence. Assuming that avoiding eso-phoria is a priority, then the range of version angles from straight ahead for which the normal AC/A ratio ($4/1 \Delta/D$ or $0.67/1 \text{ MA/D}$) will not produce eso-phoria is approximately ± 50 degrees.

Even though the low AC/A ratio would be ideal for an invariant cross-coupling, the empirical results of the present study showed that the gain of accommodative-convergence was significantly reduced as the gaze eccentricity exceeded 17.5 degrees from straight ahead gaze, while the convergence phoria did not change with increasing gaze eccentricity. Our subject sample showed inter-individual variation of the AC/A ratio. Interestingly, half of our subjects had AC/A ratios that were calibrated to a lower than ideal value for straight ahead gaze, whereas the remaining subjects had ideal or slightly higher than ideal ratios. Irrespective of the magnitude of the AC/A ratio in symmetrical convergence, both subsets of subjects showed an average decrease in AC/A ratio with increase in gaze eccentricity (asymmetric convergence), but the group with higher AC/A ratio showed slightly more decrease than in the other group. This is reasonable because, as described above, the excessive convergence penalty for high AC/A ratios is greater than for low AC/A ratios. The accommodation-convergence gain of subjects with high AC/A ratios measured in the mid-sagittal plane decreased to a greater extent with increasing azimuth, to match the accommodative and convergence stimulus demands occurring at eccentric gaze angles, in order to facilitate clear and single binocular vision.

The normal value for the CA/C ratio in young adults is similar to the ideal value for stimuli in symmetrical convergence (Fincham & Walton, 1957), suggesting that it should be calibrated to increase with azimuth. The effects of gaze azimuth on the CA/C ratio have been investigated previously by Kersten and Legge (1983). They describe raw data for the CA/C ratio of three subjects at three version (azimuth) angles of 0, 32 and -32 degrees, for convergence stimuli

ranging from 0 to 25 deg in 5 deg steps, and expressed the CA/C ratio in terms of Diopters/degree. The ideal CA/C ratio at zero azimuth for a person with a 6cm IPD would be 0.29D/deg and this would be expected to increase 20 percent to 0.35D/deg at 32-degrees azimuth. Kersten and Legge observed an average increase of the CA/C ratio of 20.6 percent for +32 deg and an average increase of 3 percent for -32 deg from zero azimuth. However, the changes in CA/C ratio with azimuth were not found to be significant. Kersten & Legge (1983) did not provide the data on the changes in accommodative bias with azimuth, so it is not clear from their study if subjects varied accommodation bias to compensate for the stimulus demands resulting from asymmetric convergence. Our results confirm their finding that the CA/C ratio does not change significantly with azimuth. However the open-loop accommodative bias does increase with azimuth to about 0.84 D at 30 degree (from zero azimuth), which will minimize errors of accommodation on targets viewed in lateral gaze.

Several other lines of evidence suggest that the AC/A ratio can be calibrated in response to stimulus conflicts between accommodative and convergence (Miles, Judge & Optican, 1987; Bobier & McRae, 1996; Jiang & Ramamirtham, 2005) similar to those that occur naturally in asymmetric convergence. For example, AC/A ratios can be adapted to increase in response to a tele-stereoscope which widens the inter-pupillary distance (IPD) (Judge & Miles, 1985; Bobier & McRae, 1996) or decrease in response to a similar device that optically reduces the IPD (Jiang & Ramamirtham, 2005). Another demonstration of adaptive regulation of the AC/A ratio comes from the studies on ageing. The AC/A ratio remains invariant with age until the onset of absolute presbyopia (Bruce, Atchison & Bhoola, 1995; Ciuffreda, Rosenfield & Chen, 1997) even though the lens gradually stiffens with increasing age, and without recalibration, the extra effort needed to accommodate the aging lens would increase the AC/A ratio.

Prior studies of the plasticity of the CA/C ratio are inconclusive. Adaptation studies with a tele-stereoscope that widens the inter-pupillary distance to increase the convergence stimulus independently of the accommodation stimulus illustrate that the gain of the CA/C ratios decreased after a short period of training (Miles et al., 1987). In contrast to these observations, studies on aging reveal that the CA/C ratio is not recalibrated with aging of the ocular lens and accommodation. Fincham and Walton (1957) reported that the CA/C ratio for straight ahead gaze was close to the ideal 1D/MA for young adults, but that the ratio became reduced as the accommodative amplitude declined with age. This shows that the convergence-accommodation gain does not adapt to age related bio-mechanical changes of the ocular lens. Based upon the lack of plasticity of the CA/C ratio with age and the high plasticity of the AC/A ratio with age, the AC/A ratio might be expected to conform more than the CA/C ratio to the stimulus conflicts in asymmetric convergence.

In addition to adjusting cross-link gains, another way that the near response could adjust for stimulus conflicts in asymmetric convergence is to independently calibrate the bias for accommodation and convergence. For example, as azimuth increases along the iso-vergence circle, the stimulus to accommodation increases while the stimulus to convergence remains constant. Similarly, as azimuth increases along the iso-accommodation circle, the stimulus to convergence decreases while the stimulus to accommodation remains constant. Responses to these two stimuli could be matched by increasing the accommodation bias or by increasing the divergence bias or phoria with azimuth without changing the cross-link gains. Bias shifts would also be useful to supplement partial changes in cross-link gain that did not fully respond to stimulus conflicts. Indeed, Miles et al. (1987) found that the gain changes of the cross-links between accommodation and convergence were associated with changes in respective biases. They showed that the AC/A ratios increased along with a vertical upward shift of the accommodative-vergence curves (increase in eso-phoria) to match the responses to the stimulus demands set by the tele-stereoscope. Similarly, they found a decrease in CA/C ratios along with a downward shift in the vergence accommodation curves (hyperopic shift) to overcome

the stimulus mismatches. The present results are in agreement with their results in that the AC/A ratios are not invariant. However, we observed that either gain changed or bias changed with azimuth but not both for a given cross-link direction. Our data reflect the greater plasticity of the AC/A ratio than the CA/C ratio in adapting to stimulus conflicts that vary with azimuth. The AC/A ratios varied with eccentricity but the open-loop convergence bias was invariant with gaze eccentricity. In contrast the gain of the CA/C ratio did not vary significantly with azimuth. However, we observed changes in bias of convergence-accommodation with increasing gaze azimuth that were consistent with stimulus combinations that change with azimuth. Our results are consistent with inability to adapt CA/C ratios and the ability to adapt AC/A ratios as indicated by studies of aging.

Summary

In general, our group results show that the AC/A ratios decrease with azimuth whereas the convergence bias remains invariant, as predicted by the gain-variant model. CA/C ratios were invariant with azimuth whereas the accommodative bias increased with azimuth as predicted by the bias-variant model. Our subject sample illustrates that these changes with azimuth compensate for the accommodation and convergence demands (see Figure 2) set by asymmetric convergence, along the iso-accommodation and iso-vergence circles, however generalization of these results requires testing with a larger sample size. Our results suggest that either direction of the cross-link interaction that dominates the initial near response (AC or CA) is calibrated for stimulus conflicts in asymmetric convergence by adjusting AC gain and CA bias.

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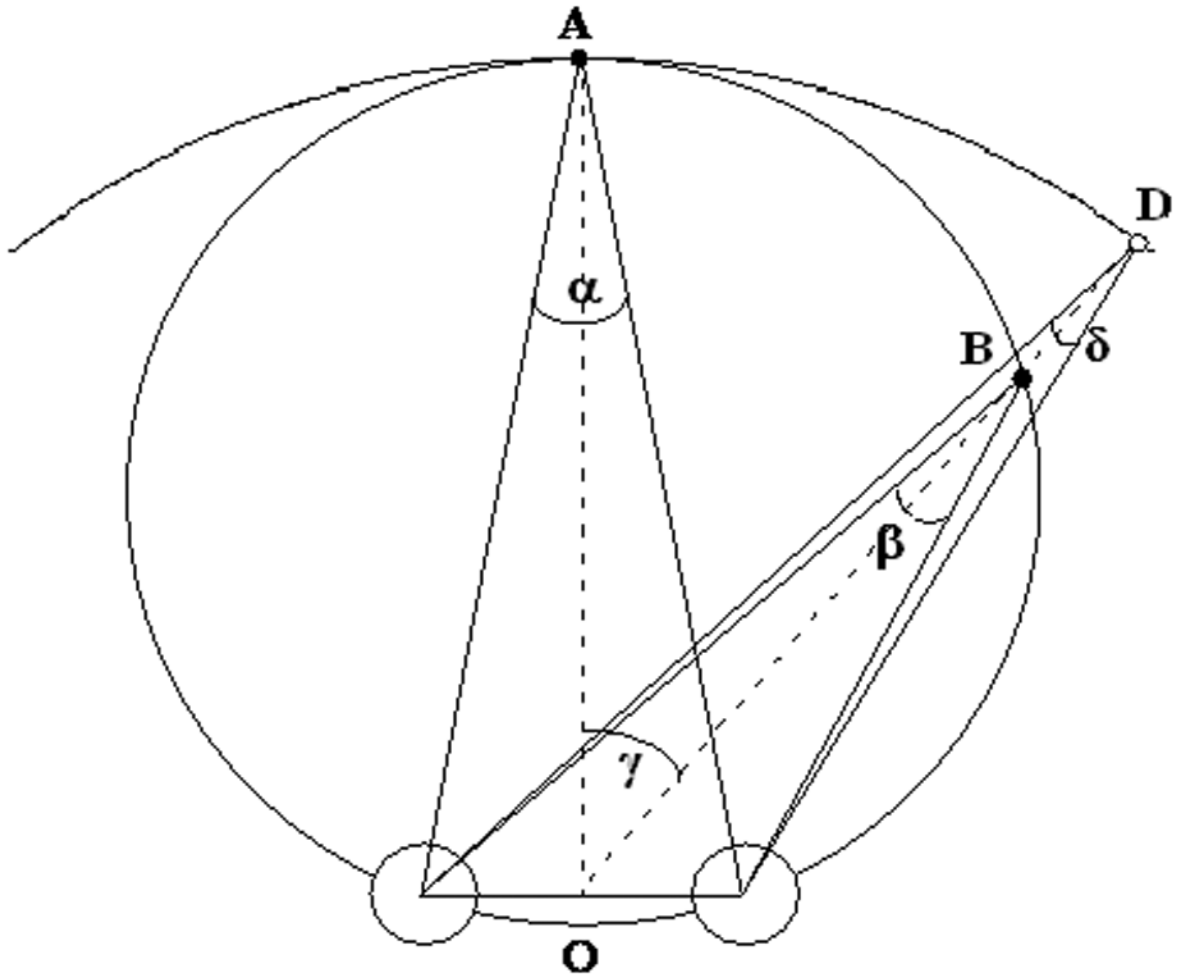


Figure 1. Plan view of iso-vergence circle (large complete circle), iso-accommodation circle (shown as an arc) and various azimuth angles. The two small circles represent the right and the left eye. The point A represents the spatial location that corresponds to matched stimuli for accommodation and convergence. α = convergence angle at point A (angle made by the intersection of two lines of sight), β = convergence angle at point B, and $\alpha = \beta$ along the iso-vergence circle. γ = lateral gaze angle. Note that at point D on the iso-accommodation circle, the convergence stimulus is lower than at point B by δ .

Accommodation along the iso-vergence circle Convergence along the iso-accommodation circle

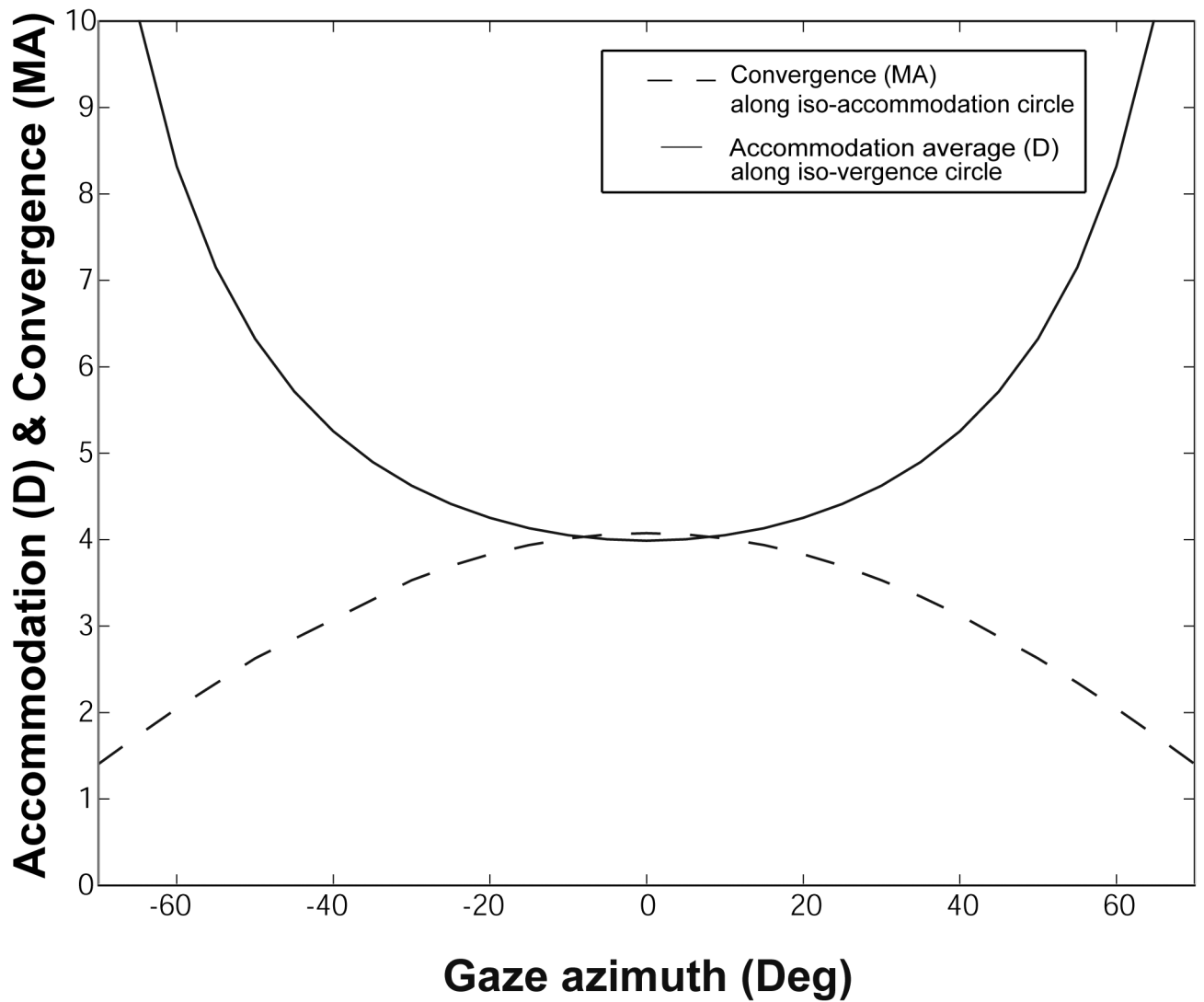


Figure 2. The binocular accommodation (D) and convergence (MA) stimulus combinations along the iso-vergence and iso-accommodation circles are shown respectively for a 25 cm viewing distance. X-axis shows the gaze azimuth from straight-ahead gaze (stimuli in the midsagittal plane).

Cross-coupling interactions and gaze azimuth

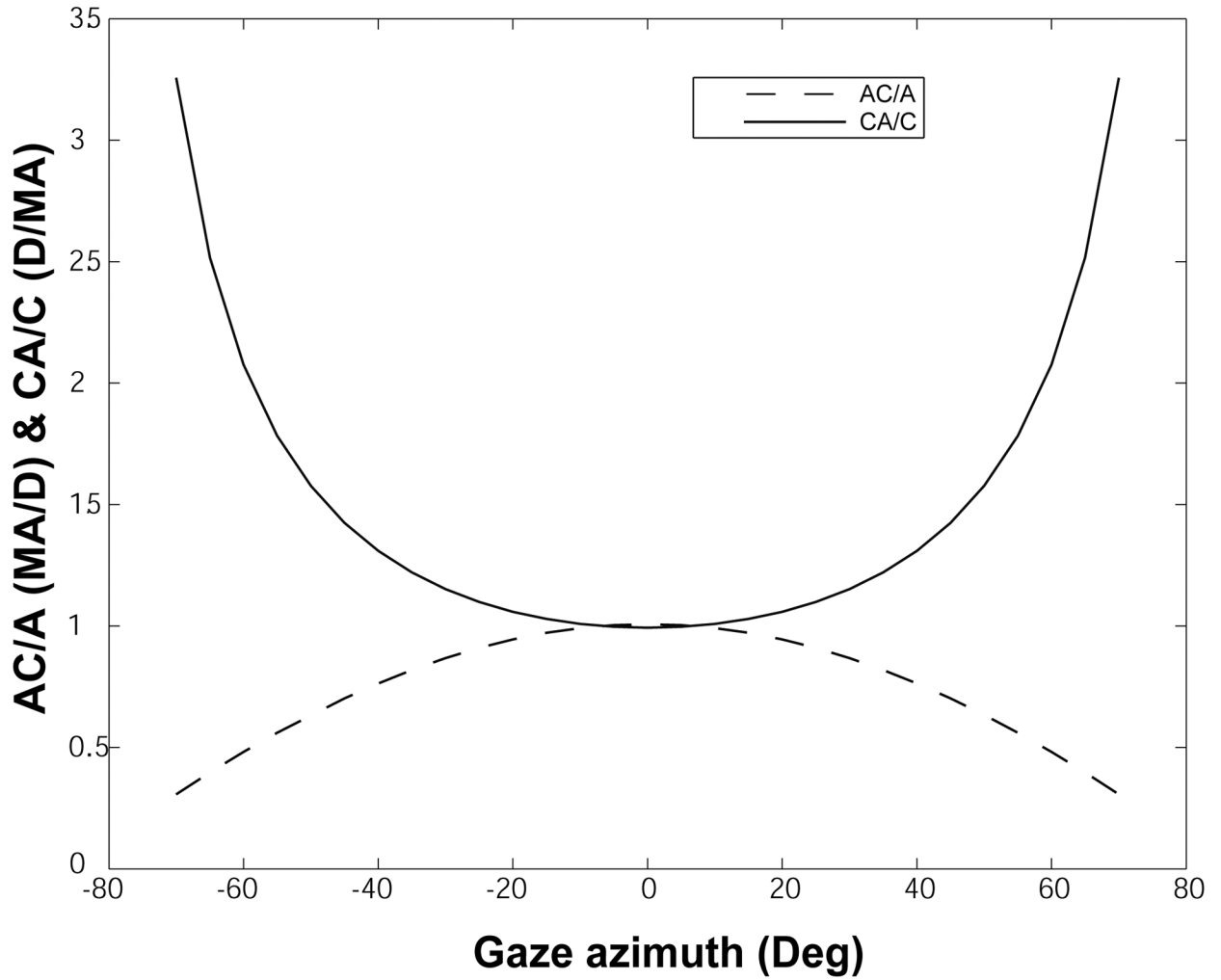


Figure 3. The ideal AC/A and CA/C ratios, plotted as a function of azimuth, that would produce accommodation and convergence responses that would match their stimuli during asymmetric convergence along the iso-accommodation circle or the iso-vergence circle respectively for a 1 m viewing distance at zero azimuth.

Optimal AC/A & CA/C ratios with convergence distance (40 deg azimuth)

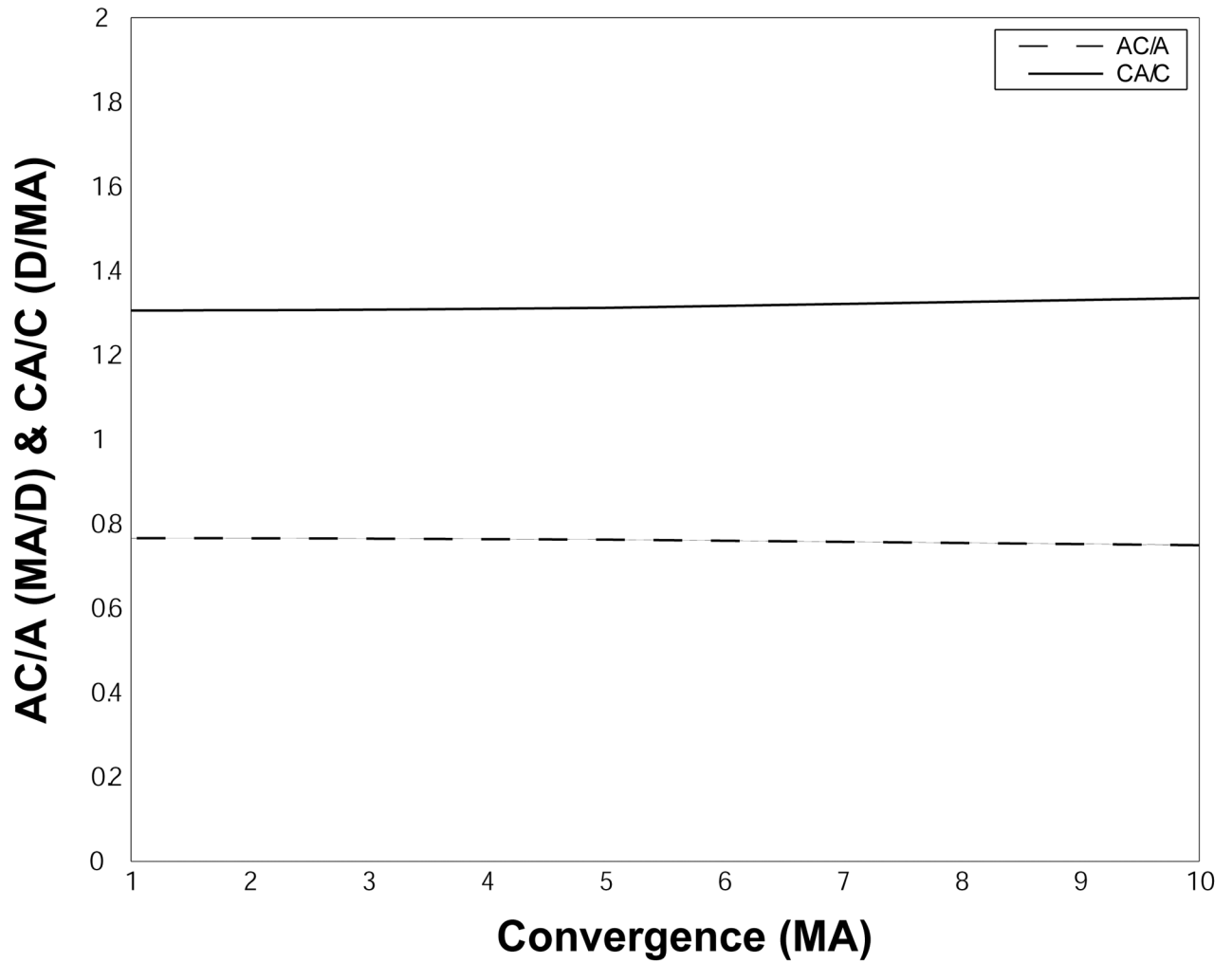
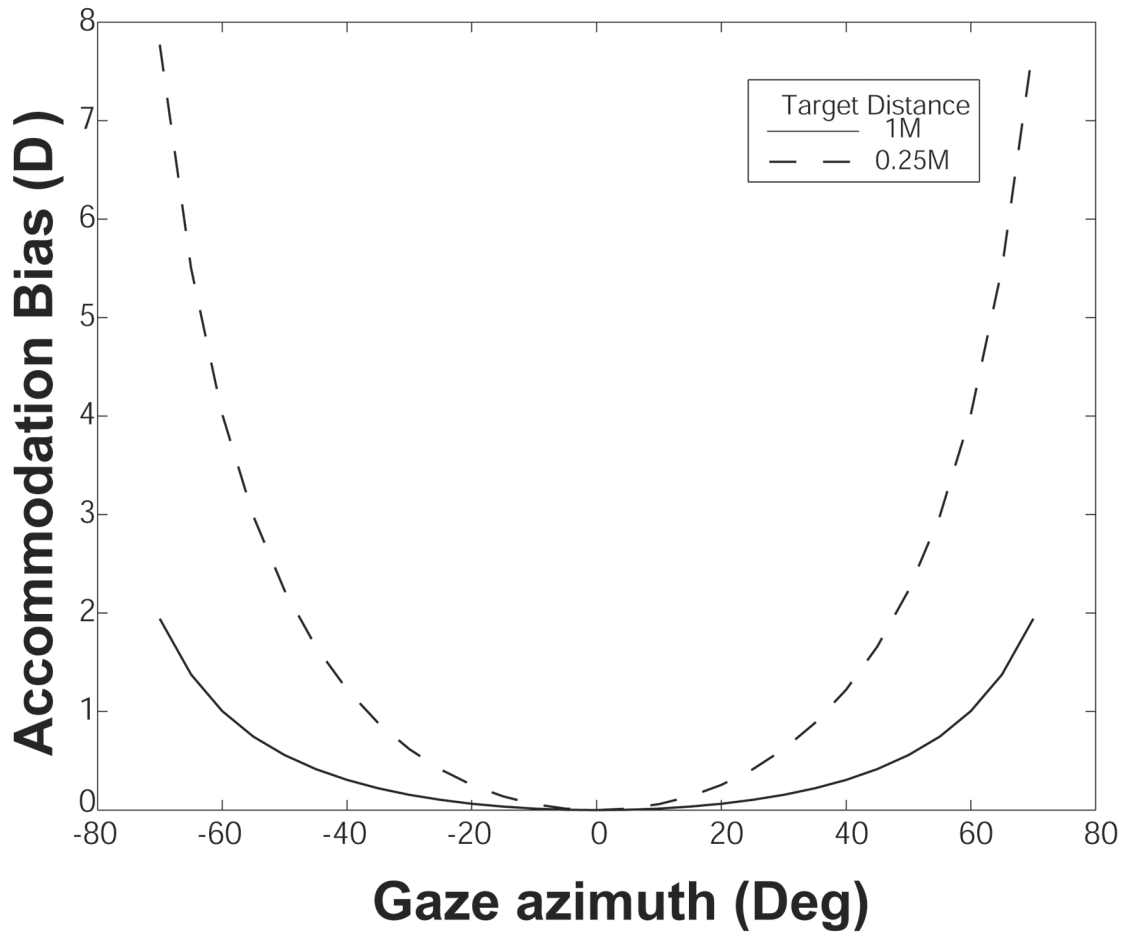


Figure 4. The ideal AC/A and CA/C ratios at an azimuth angle of 40 degrees for viewing distances ranging from 0.1m to 1m are shown. The flat lines indicate that the ideal ratios do not change with viewing distance.

Ideal accommodation bias along iso-vergence circle



Ideal convergence bias along iso-accommodation circle

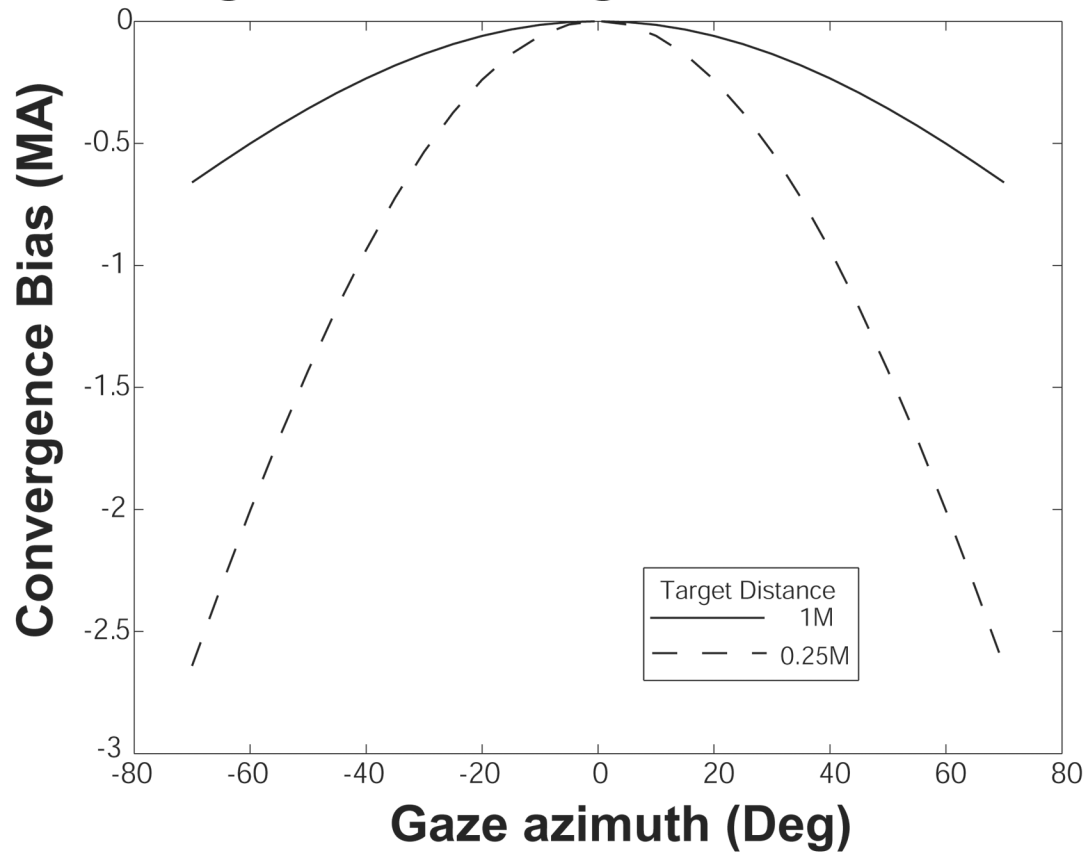


Figure 5. Ideal biases for convergence (MA) and accommodation (D) are plotted as a function of azimuth that would produce accommodation and convergence responses that would match their stimuli during asymmetric convergence along either the iso-vergence circle or the iso-accommodation circle at a 1m (solid line) and 0.25m (dashed line) view distances at zero azimuth.

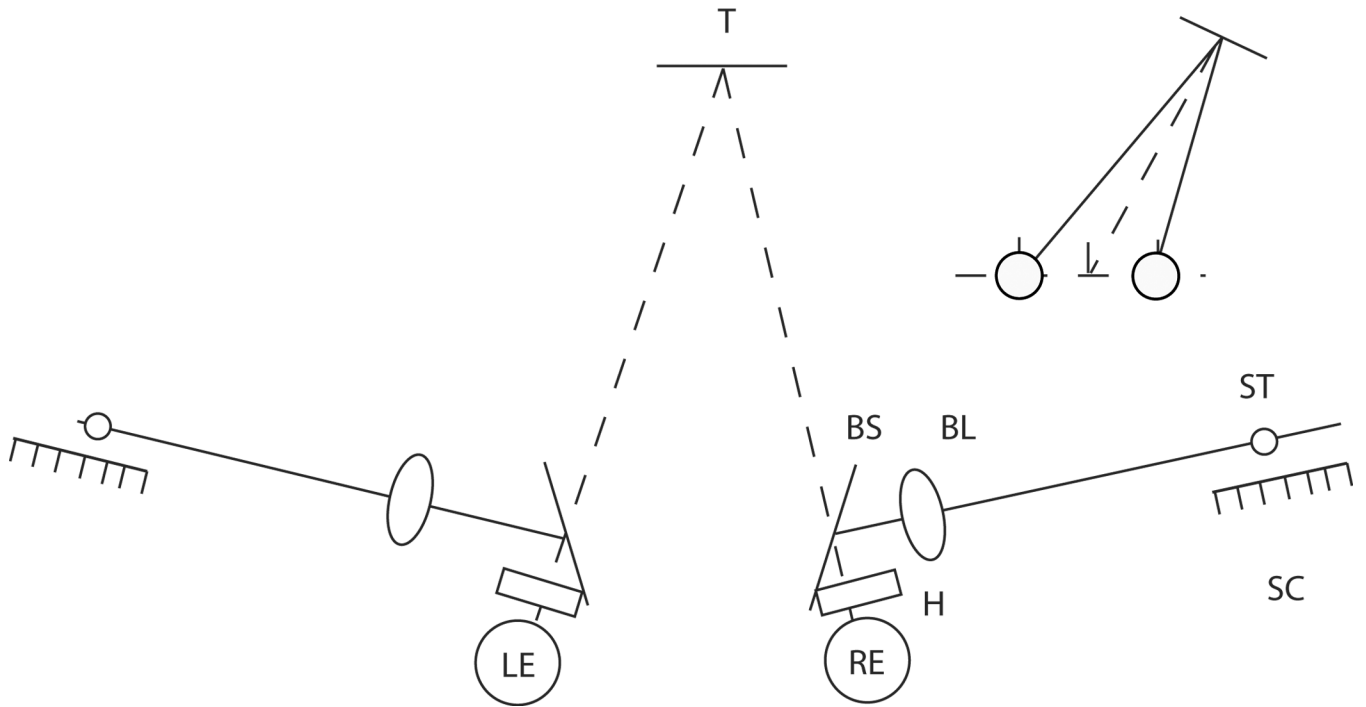


Figure 6. Schematic of two stigmascopes mounted on a Wheatstone-mirror haploscope to measure subjective accommodative response and convergence angle. The right stigma ST (point source of light) visible to the right eye (RE) was imaged on a target T viewed by that eye through a beam splitter (BS). The subject adjusted the focus of the stigma by moving it toward or away from the 10D Badal lens (BL), while fixating at target T. The stigma is focused when it is optically conjugate with the retina, and the scale reading (SC) is converted to accommodation in Diopters. For measuring convergence, the left stigma was made visible to the left eye (LE), but the view of target T by the left eye was occluded. Lenses of different powers were placed on the lens holder H, to induce a range of accommodative stimuli. The holder rotated with the arms of the haploscope to avoid off-axis prismatic effects at non-zero azimuths. Subjects moved the left haploscope arm in order to adjust the horizontal direction (azimuth) of the stigma so that it was aligned with the fixation target of the right eye. Inset shows the shift in target position and two lines of sight for a rightward gaze eccentricity.

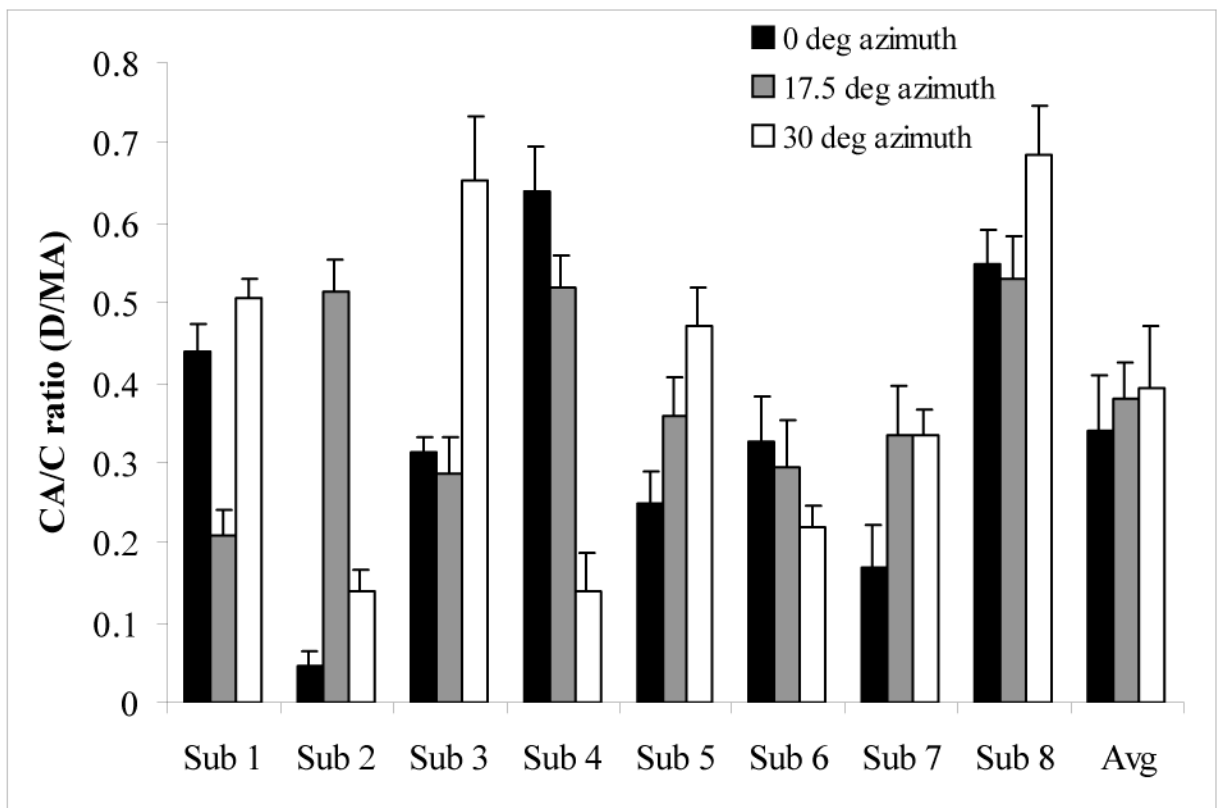
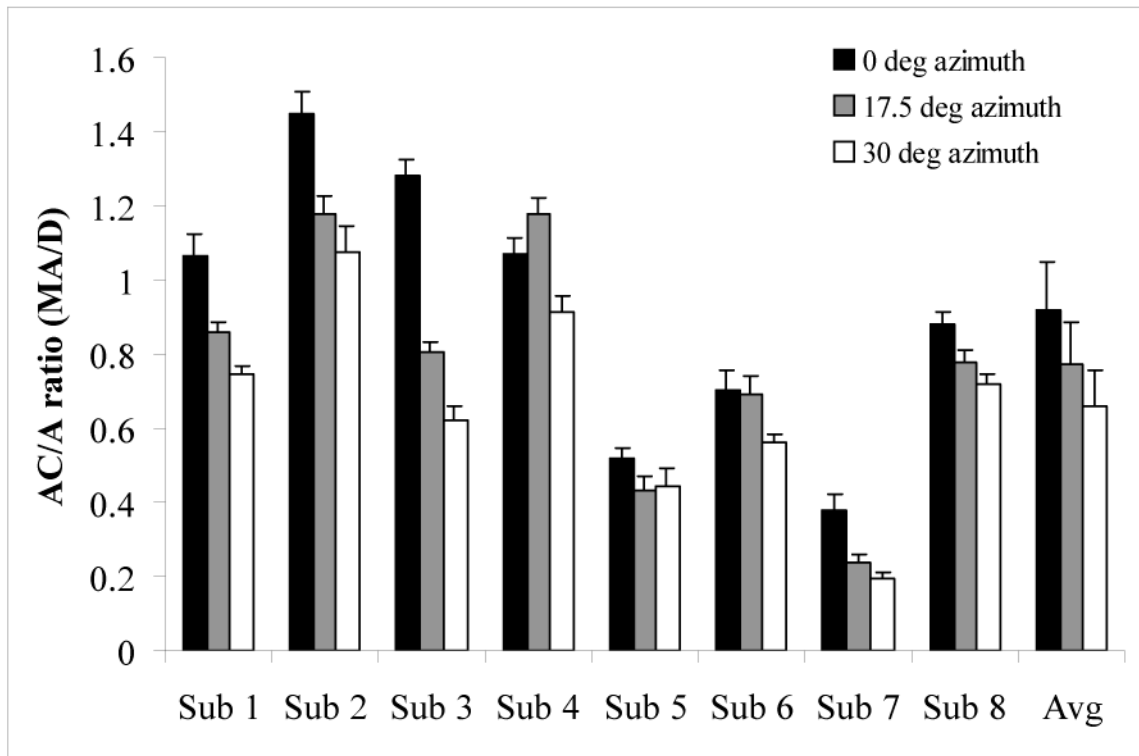


Figure 7.

Figure 7A: Individual response AC/A ratios are presented in bar graphs for the eight subjects. For each subject, the black solid bar represents response AC/A ratio at zero azimuth. The grey solid bar represents the AC/A ratio for 17.5-degree azimuth, and the vertical white solid bar represents the AC/A ratio for 30 degrees rightward azimuth angle. Error bars represent one standard error. The rightmost set of columns show the average data for the whole group of subjects.

Figure 7B: Individual CA/C ratios are presented in a bar graph for the eight subjects. For each subject, the first (black solid), second (grey solid) and third (white solid) bars represent the CA/C ratios measured at 0, 17.5 and 30-degree azimuth angles respectively. Error bars represent one standard error. The right-most set of columns (Avg) show the average data the whole group of subjects.

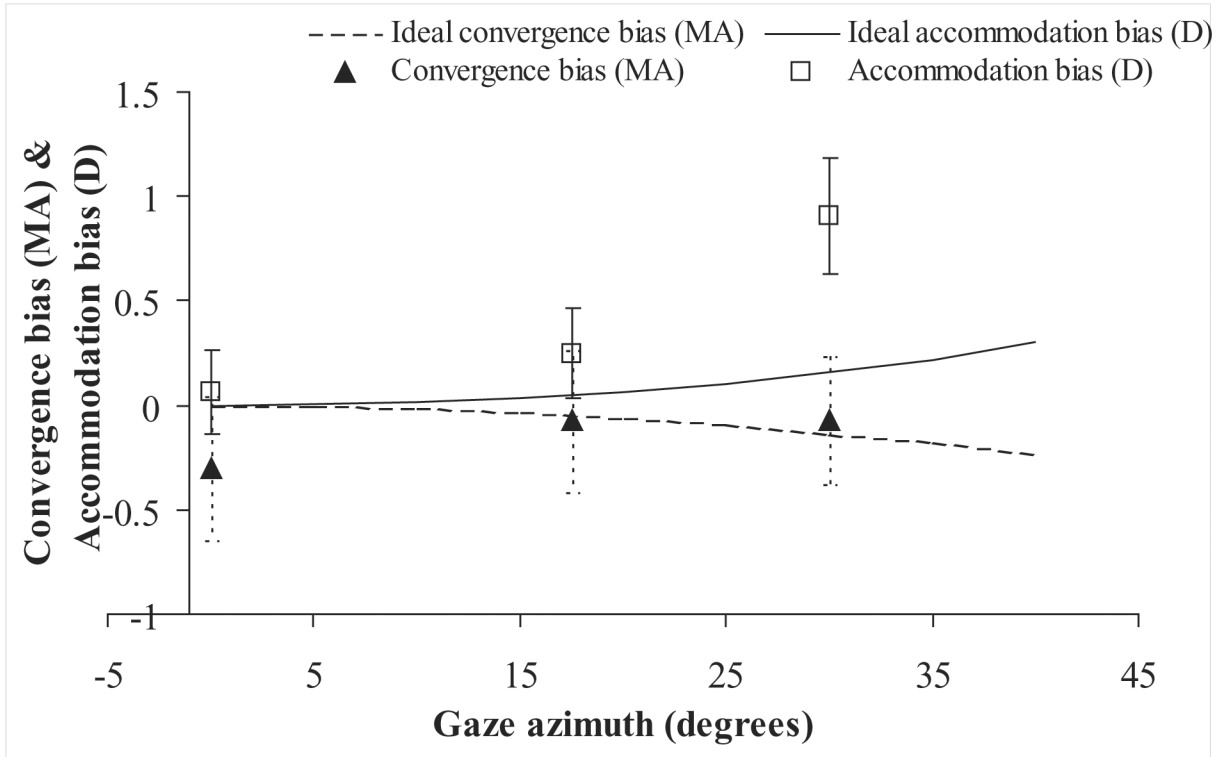


Figure 8.

The average accommodative bias (open squares), relative to a 0D reference, and convergence phoria (filled triangles), relative to zero convergence in primary position, are presented as a function of azimuth. Error bars represent one standard error of the mean. The dashed line and the solid line represent the ideal convergence bias and accommodation bias as a function of azimuth respectively for a 1m viewing distance at zero azimuth.

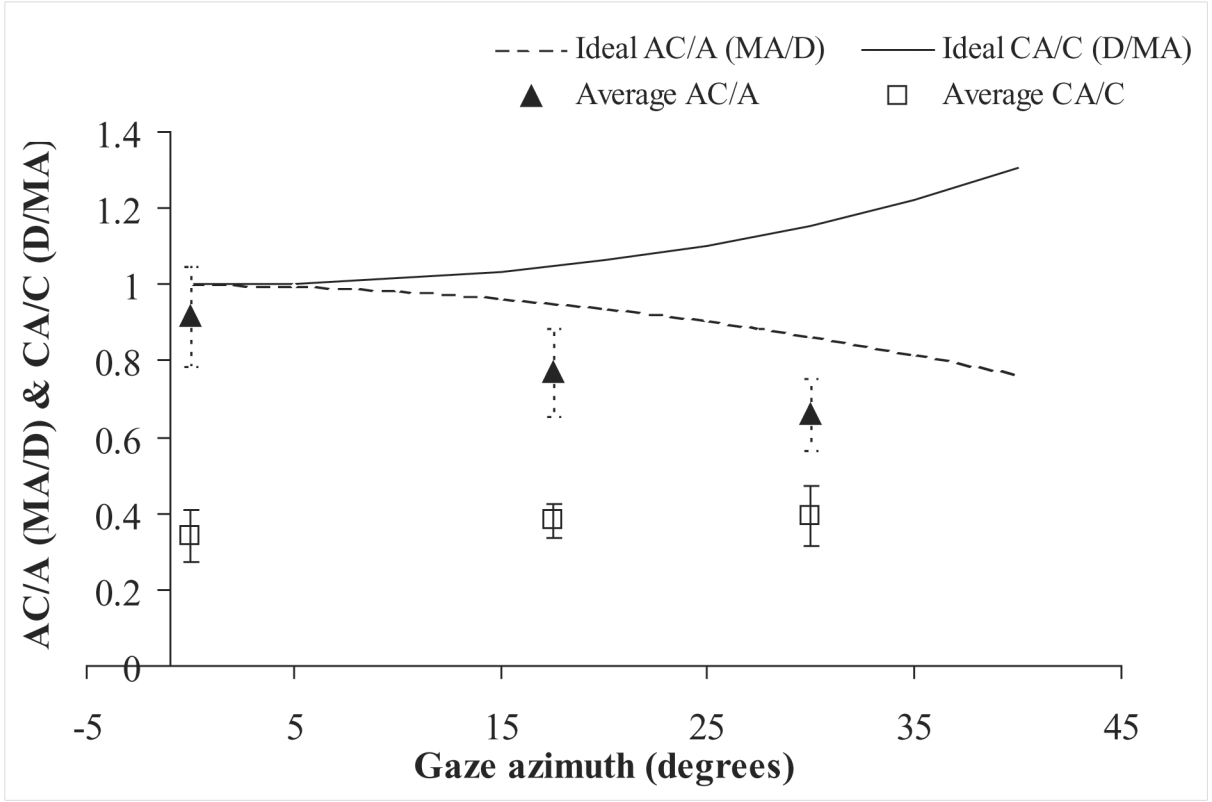


Figure 9. The average AC/A (\pm 1S.E.) and CA/C ratios (mean \pm 1S.E.) are presented as a function of rightward gaze angle. The dashed line and the solid line represent the ideal AC/A and CA/C ratios as a function of azimuth, respectively.

Table 1

Subjects ages, IPD (inter-pupillary distance in centimeters measured in primary position), and amplitudes of accommodation (measured by the push up technique) and distance refractive contact lens correction.

Subject number	Age (years)	IPDd (cm)	Accommodation Amplitude (D)	Right eye Refractive error	Left eye Refractive error
1	27	6.4	6.9	-6.5 DS	-8.25 DS
2	23	5.9	8	-8.25 -0.75 × 175	-7.25 -0.75 × 165
3	31	5.8	12.0	-3.25 DS	-3.25 DS
4	24	6.0	8	0.0	0.0
5	31	5.9	8.3	-3.5 DS	-3.5 DS
6	30	6.3	9	0.0	0.0
7	26	5.8	10	-3.25 DS	-3.75 DS
8	27	5.8	10	+2.0 DS	+0.50 DS