Accommodation Responds to Optical Vergence and Not Defocus Blur Alone

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Purpose. To determine whether changes in wavefront spherical curvature (optical vergence) are a directional cue for accommodation.

Methods. Nine subjects participated in this experiment. The accommodation response to a monochromatic target was measured continuously with a custom-made adaptive optics system while astigmatism and higher-order aberrations were corrected in real time. There were two experimental open-loop conditions: vergence-driven condition, where the deformable mirror provided sinusoidal changes in defocus at the retina between −1 and +1 diopters (D) at 0.2 Hz; and blur-driven condition, in which the level of defocus at the retina was always 0 D, but a sinusoidal defocus blur between −1 and +1 D at 0.2 Hz was simulated in the target. Right before the beginning of each trial, the target was moved to an accommodative demand of 2 D.

Results. Eight out of nine subjects showed sinusoidal responses for the vergence-driven condition but not for the blur-driven condition. Their average (±SD) gain for the vergence-driven condition was 0.50 (±0.28). For the blur-driven condition, average gain was much smaller at 0.07 (±0.03). The ninth subject showed little to no response for both conditions, with average gain <0.08. Vergence-driven condition gain was significantly different from blur-driven condition gain ($P = 0.004$).

Conclusions. Accommodation responds to optical vergence, even without feedback, and not to changes in defocus blur alone. These results suggest the presence of a retinal mechanism that provides a directional cue for accommodation from optical vergence.

Keywords: accommodation, defocus blur, vergence, adaptive optics, dynamic accommodation

Accommodation refers to the ability of young eyes to actively bring into focus objects that are at different distances. For nonpresbyopic eyes with no disabilities, accommodation is fast and precise.[1–4] Apart from binocular cues like disparity, the visual system has access to a number of monocular cues for accommodation[5] both from context (e.g., apparent distance and size[6–8] and interposition of objects),[8] and from optics of the eye itself since the projected image can be different depending on whether it is formed in front or behind the retina.[9] Among optical cues, chromatic aberration has been shown to provide a strong reliable directional cue for accommodation.[10] Monochromatic aberrations,[11–15] microfluctuations of accommodation,[3,4,16] and the Stiles-Crawford effect[17] may also provide cues for accommodation.

Even when all these cues are removed, many eyes still accommodate. It has long been thought that correct accommodation is achieved by using a trial-and-error strategy.[18–21] Nevertheless, the correct and fast response of the eye to variations in the accommodative demand over time[11,12,15] cannot be explained[4] by such a simple trial-and-error strategy. A provocative alternate explanation proposed by Fincham[22] is that the visual system is able to detect or infer the sign of defocus directly from wavefront spherical curvature, or optical vergence. Trial and error requires that the eye obtain feedback from changes in accommodation, a role attributed to microfluctuations.[23–27] Yet, evidence has been found that the eye can accommodate correctly even without feedback,[28] an observation against the trial-and-error hypothesis for accommodation.

The aim of this work was to test directly the theory that the human visual system infers directly the sign and magnitude of defocus from optical vergence and does not function by trial and error. To test this hypothesis, two types of blurred images were formed on the retina to drive accommodation: (1) naturally out-of-focus images that are a consequence of inaccurate focus of the eye on the object (i.e., accommodative lead or lag); and (2) artificially produced computer-generated images of an object that is itself blurred but perfectly focused on the retina. In the first condition, optical vergence of a target changed sinusoidally without feedback from changes in accommodation. In the second condition, the stimulus was always imaged clearly on the retina but the target itself changed its blur sinusoidally, also without feedback from changes in accommodation. Thus, the stimulus projected onto the retina had defocus blur in both experimental conditions. However, in the first condition but not in the second condition, there were also changes in optical vergence.

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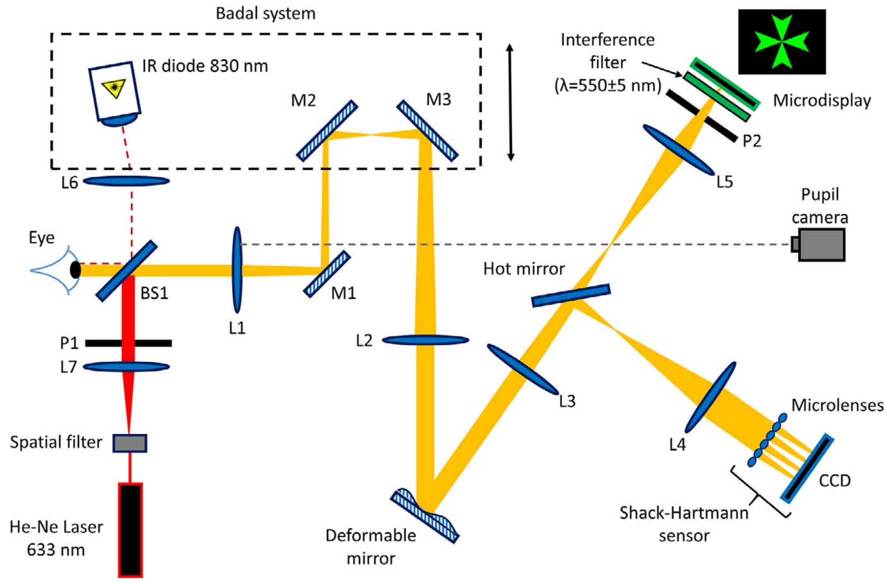

FIGURE 1. Schematic diagram of the adaptive-optics system. Lenses L1, L2, L3, and L5 are achromatic doublets; lenses L4, L6, and L7 are singlets; M1, M2, and M3 are flat mirrors; P1 is an artificial pupil; P2 is the 4-mm pupil; and BS1 is a pellicle beam splitter.

METHODS

Subjects

Nine subjects, who were known from a preliminary experiment to accommodate effectively under monochromatic light, were enrolled to participate in this study. The participants had an average (±SD) age of 27 (±6) years and their refractive errors ranged from −5.0 to +0.5 diopters (D), with a mean spherical refractive error of −1.44 (±1.89) D. None of the participants had astigmatism greater than 1 D. Subjects presented no ocular pathologies and no accommodation anomalies. Informed consent was obtained from all the subjects after explanation of the nature and possible consequences. The study adhered to the tenets of the Declaration of Helsinki.

Apparatus

The custom-made adaptive optics system used to perform the accommodation experiments is illustrated in Figure 1. The system consists of a Shack-Hartmann aberrometer (HASO4 First; Imagine Eyes, Orsay, France), a 52-actuator deformable mirror (Mirao 52e, Imagine Eyes), a motorized Badal optical system and a microdisplay (800 × 600 pixels). The target was a narrow bandwidth green Maltese cross (550 ± 5 nm) with a luminance of about 20 cd/m^2 and spanning a 1.95° visual angle. The target was seen through a fixed circular artificial pupil of 4 mm in diameter at the entrance pupil plane of the subject.

A dental mold (bite-plate) was made for each subject and it was used to reduce their head movements during the experimental trials. The dental mold was mounted on a three-dimensional linear stage used for alignment between the subject's eye and the optical system. The pupil was monitored in real time using an infrared pupil camera (Fig. 1).

All measurements were taken using custom-made software in MATLAB (MathWorks, Inc., Natic, MA, USA), based on the analysis and simulation software library and software development kits provided by the manufacturer (Imagine Eyes).

Experimental Procedure

Preliminary trials were run to ensure that the subjects who volunteered to participate in the experiment were able to accommodate in monochromatic light. These preliminary trials consisted of a monochromatic green Maltese cross target moving sinusoidally between 1 and 3 D at a temporal frequency of 0.2 Hz and run under typical closed-loop conditions with accommodation feedback present, and with the habitual monochromatic aberrations of the eye left intact. Only subjects with gain equal to or greater than 0.2 were selected, where gain is defined as response amplitude divided by stimulus amplitude (see "Data Analysis" for details on how gain is calculated).

Before starting the experimental trials, subjects were asked to find their far point using a fogging methodology with the help of the Badal system. More precisely, participants were instructed to move a visual acuity chart far enough away from them beyond their far point, so they could not see it clearly. Then, they were asked to move the target slowly toward the eye until it first became clear, thus avoiding unintentional use of their accommodation. The average of three repetitions was taken as the subject's far point.

Experimental Conditions

Two different stimulus conditions were part of this experiment. In both conditions, monocular depth cues such as apparent distance and change in size were absent because optical vergence (target distance) was changed using a Badal lens. Cues from chromatic aberration were removed in real time by using a narrow-band color filter. Lower-order astigmatism and higher-order aberrations (HOAs) were compensated with the deformable mirror in real time at 20 Hz. The deformable mirror also compensated for changes in defocus produced by changes in accommodation including microfluctuations, thus opening the accommodation feedback loop so that the eye could not use trial and error to determine the correct direction of accommodation. In the vergence-driven condition, the deformable mirror also generated sinusoidal changes in defocus that varied between −1 and +1 D at 0.2 Hz, centered at 2 D of accommodative demand, that is, a vergence of 2 D closer than the far point of the subject. Thus, all known cues except defocus blur and optical vergence were removed in addition to any feedback from accommodation. In the blur-driven condition, defocus blur was simulated with the Fourier optics calculator[29] and displayed on a microdisplay (Fig. 1). Sinusoidal defocus blur between −1 and +1 D at 0.2 Hz was added to the Maltese cross. Unlike the vergence-driven condition, in the blur-driven condition the sinusoidally blurring and clearing target was always imaged accurately in focus on the retina. Therefore, cues from changes in optical vergence were absent, and only defocus blur was present. Supplementary Movie S1 shows one cycle of the sinusoidal changes for the two conditions with a duration of 5 seconds. The upper row shows the wavefront, vergence, and simulated retinal image for the vergence-driven condition. The lower row shows the same for the blur-driven condition.

Six trials of 25 seconds of duration for each condition were presented in random order. The initial direction of the sinusoidal defocus induced optically in the vergence-driven condition or simulated in the blur-driven condition was also random. All measurements were taken monocularly while the other eye was occluded.

Data Analysis

The Shack-Hartmann sensor measures accommodative error (lag or lead) of the eye with respect to the defocus generated with the deformable mirror. Therefore, the minimum root mean square (RMS) accommodative response[30] was obtained by subtracting the accommodative lead or lag measured with the wavefront sensor from the defocus generated by the deformable mirror, as in Chen et al.[15] (see Fig. 2 of Ref. 15).

A sinusoidal function with a temporal frequency of 0.2 Hz was fitted to the accommodative responses recorded over the 25 seconds of each trial. Gain, defined as the ratio between the amplitude of the response and the amplitude of the demand, was calculated from the amplitude of the fitted sinusoidal.

The appropriateness of the adaptive-optics system in correcting aberrations and inducing the required level of optical spherical defocus during the trials was assessed as follows. The RMS error for astigmatism and HOAs was computed for a 4-mm pupil in all the trials to ensure that the deformable mirror was compensating accurately for the ocular aberrations. For all but 2 trials for all conditions and subjects, the medians for uncorrected low-order astigmatism and HOAs RMS were around or below 0.1 μm. For the other two trials RMS error was between 0.1 and 0.2 μm. For the vergence-driven condition, a sinusoidal function with temporal frequency of 0.2 Hz was fitted to the accommodative error measured with the wavefront sensor. The minimum and maximum amplitudes obtained were 0.93 and 1.04 D, very close to the desired amplitude of 1 D. For the blur-driven condition, for which the goal was to have an optical defocus of 0 D at all times, the median of the accommodative errors measured with the sensor were always lower than 0.03 D for all trials. The median absolute deviation was always lower than 0.09 D. The root mean square error of the sinusoidal (vergence-driven condition), or the linear fit (blur-driven condition), was smaller than 0.15 D in all trials (not to be confused with the RMS of the residual wavefront shown above), confirming that the deformable mirror was providing the desired level of defocus at the retina.

Data were first tested for normality using a Shapiro-Wilk test and since the data were found not to be normally distributed, a Wilcoxon signed rank test was performed, which is the nonparametric version of the paired *t*-test. The significance level was set at 0.05.

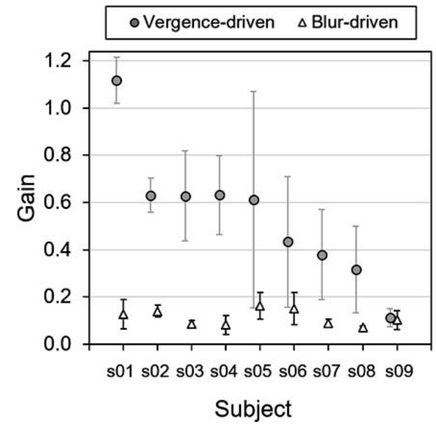

FIGURE 2. Mean gain of each subject over six trials for the two experimental conditions. *Error bars* are ± SD.

RESULTS

The mean gains in both conditions are shown in Figure 2. All subjects except one (s09) were able to accommodate and follow the target when changes in optical vergence were present with no feedback from accommodation, but not when changes in optical vergence were absent. The mean (±SD) gain for the vergence-driven condition over all subjects was 0.50 (±0.28), whereas for the blur-driven condition it was much smaller at 0.07 (±0.03). Gains in the vergence-driven condition were greater than the gains obtained in the blur-driven condition for all subjects, except subject s09, whose average gains were <0.08 in both conditions. Only 1% of the responses were found to be in counter-phase with the demand in the vergence-driven condition, and only for the subject with negligible average gains (s09). In contrast, about 46% of the responses were in counter-phase in the blur-driven condition, which showed that subjects could not follow the sinusoidal blur pattern when optical vergence was not present. Gains were significantly different between conditions ($P = 0.004$).

Figure 3 shows examples of accommodation responses for the two conditions for the most responsive subject (s01). Solid gray curves represent the optical vergence provided by the deformable mirror at the retina during the vergence-driven condition and the simulated blur of the target during the blur-driven condition. This subject showed large and relatively accurate sinusoidal accommodation responses in the vergence-driven condition when real sinusoidal changes in optical vergence were presented. Even though this subject could not follow the simulated sinusoidal blur of the target, some accommodative activity clearly exists, erratic nonetheless. Figure 4 shows responses for the two conditions for the least responsive subject (s09). The difference in the behavior of accommodation for these two subjects between the two conditions is quite noticeable. Subject s09 seemed to repeat the same accommodative behavior regardless of the experimental condition, The subject increased the accommodative response up to a level that could be the tonic state of accommodation—the intermediate resting position, where the eye accommodates passively when there is insufficient light or when the stimulus is a uniform background with no spatial frequency content.[31] In contrast, subject s01 could follow the sinusoidal change remarkably well in the vergence-driven condition, with a small temporal lag. This subject could not follow the sinusoidal change in the blur-driven condition, even if the subject made every effort to search for the correct direction in which to accommodate.

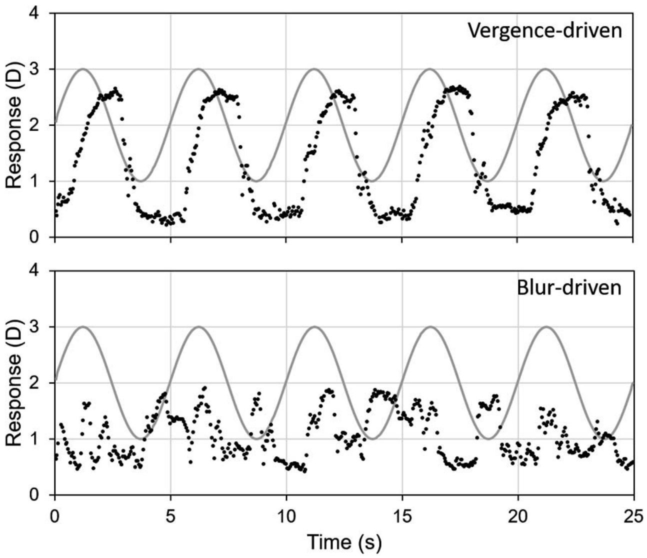

Figure 3. Responses in the first trial for each condition for a responsive subject (s01). *Black dots* represent the accommodative response, calculated with the minimum RMS metric. *Grey solid curves* show the optical vergence that the deformable mirror provided over time (vergence-driven condition) or the changes in simulated blur of the target (blur-driven condition).

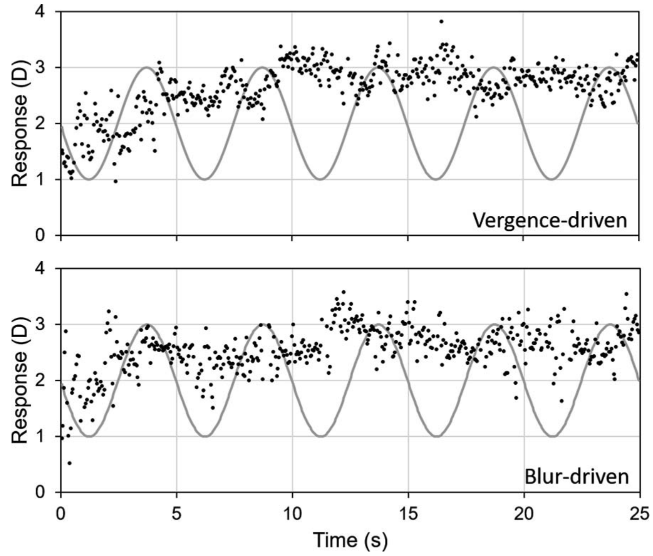

Figure 4. Responses in the first trial for each condition for nonresponsive subject (s09). Details are as for Figure 3.

Discussion

The present experiment is the first to use optical vergence to drive accommodation in the absence of all the other potential directional cues for the sign of defocus. The main conclusion of this study is that the visual system is able to detect the global wavefront spherical curvature, caused by an error in the correct focus of the image at the photoreceptor plane.

In this study, the fundamental accommodation cue that is caused by inaccurate focus, called defocus blur, was carefully isolated from any other potential cue. For this purpose, binocular and monocular depth cues were eliminated by viewing targets monocularly in a Badal optical system, directional cues from chromatic and monochromatic aberrations of the eye were eliminated by viewing the target in monochromatic light and using adaptive optics to remove astigmatism and HOAs in real time, and ongoing oscillations of accommodation were excluded by a high speed adaptive optical system operating at 20 Hz. In addition, the subject's natural pupil was replaced with a round artificial pupil so that the irregular shape of the natural pupil would not provide blurred images that were different for positive and negative defocus.[9]

The main potential limitations of this study are set by how well the adaptive-optics system compensated for the low-order astigmatism and HOAs of the subjects and, more importantly, how accurately it provided the required level of defocus at the retina at each moment in time. The median values of the errors in generating the necessary defocus were always lower than 0.03 D, and the median absolute deviation was always below 0.09 D, as shown in the "Data Analysis" section. Curd et al.[32] showed that for pulses with duration of 100 ms or less, the accommodation response was absent or was very small in magnitude. Subjects who responded to these fast pulses showed responses around 0.2 D for both 1 and 2 D of accommodative demand. Since these pulses were more than 10 and 20 times larger than the errors introduced by the deformable mirror, and the correction lag was only 50 ms, it is highly unlikely that these tiny errors could elicit any response or provide effective cues for accommodation.

The size of the target in the present experiment (1.95°) is not expected to limit the accommodation response, since targets that subtend more than approximately 0.25° (15 min arc) provide the same dynamic gain as a much larger Maltese cross target.[33]

The 2-D midpoint was chosen because it is an intermediate distance (50 cm in an emmetropic or corrected eye), it is not too large an accommodative demand and so allows measurement in middle-aged subjects, and it is large enough to prevent the accommodative response from reaching 0 D. The majority of previous studies on dynamic accommodation have also used 2 D as the midpoint of accommodative demand,[28,34,35] so the results are directly comparable.

Defocus, low-order astigmatism and HOAs were measured and compensated at 20 Hz. Since microfluctuations of accommodation that are greater than 5 to 6 Hz are quite small in magnitude,[4,36] a correction speed of 20 Hz is more than fast enough to eliminate any nonnegligible cues from microfluctuations. This speed was also sufficient for the simulated blur of the target to appear to change smoothly in the blur-driven condition.

Subjects were not included in the experiment if they were unable to accommodate in preliminary trials under typical monochromatic and monocular closed-loop conditions, where feedback was available from changes in accommodation. They were excluded because they were unlikely to respond in the two more stringent experimental conditions without feedback, and thus not useful to test the present hypothesis. Therefore, the hypothesis here cannot be generalized to the minority of the population that cannot accommodate in monochromatic light.

From previous experiments[12,15,22] (Marín-Franch I, et al. *IOVS* 2016;57:ARVO E-Abstract 3952) it can be estimated that from approximately 65% to 85% of subjects can accommodate to optical vergence in monochromatic light. In Marín-Franch et al. (*IOVS* 2016;57:ARVO E-Abstract 3952), the study with greater number of subjects, 5 out of 14 subjects (35%) could not accommodate in monochromatic light. In Chin et al.,[12] the number of subjects who could not accommodate in monochromatic light was 1 out of 5 (20%), and in Chen et al.,[15] 1 out of 6 (17%). It is not possible to extrapolate the results of this study to the 15% to 35% of subjects who do not accommodate in monochromatic light. But it is reasonable to speculate that in white light, some or all of these subjects use optical vergence to compute differences in the amount of defocus between long-, medium-, and short-wavelength-sensitive cone photoreceptors.[35,37,38]

The gain values obtained for the open-loop vergence-driven condition were not systematically greater or smaller than for the normal closed-loop condition with feedback and without correcting any aberrations, as in the preliminary experiment. However, subjects generally showed greater temporal lag in the open-loop condition than in the closed-loop condition of the preliminary experiment. These results are also in agreement with those obtained by Kruger et al.[28] in an open-loop dynamic accommodation experiment.

The results of this study present further evidence in support of the hypothesis that accommodation responds directly to optical vergence, not indirectly via defocus blur.[22,39] In the vergence-driven condition, eight out of nine subjects showed clear sinusoidal responses, whereas in the blur-driven condition, where no changes in optical vergence occurred and only defocus blur was present, the accommodation response was negligible. Response gains did not depend on the spherical refractions of the subjects. The coefficient of determination between spherical refraction of subjects and gain for the vergence-driven condition was very small (0.003; $P = 0.884$).

Since blur from defocus alone is an even-error cue with amplitude but no sign, the gains in the blur-driven condition are expected to be zero. Yet, the experimentally obtained gains were not exactly zero for two reasons. First, many eyes continue to have microfluctuations in accommodation even if these are compensated by the adaptive optics system and feedback is removed. Thus the energy of the microfluctuations at 0.2 Hz is added to the amplitude of the accommodative response. Second, amplitudes that are fitted to noisy response data seldom will be zero, and because gain is a positive-defined parameter, the average over repetitions is bound to be greater than zero. Since defocus blur is an even-error cue, the effect of optical vergence in the retinal image was the only directional cue in the vergence-driven condition that could have informed the eye that the image was focused behind or in front of the retina.

Beside the implications for everyday focusing of the eye (accommodation), there may be consequences for the long-term focusing process termed emmetropization,[40,41] which is the coordinated growth and development of the optical components of the eye (cornea and lens) and its axial length, which prevents the development of myopia. Myopia is a significant public health problem,[42] and a leading cause of blindness from diseases secondary to the development of high amounts of myopia.[43] Research on the eyes of fishes, chicks, kestrels, squirrels, rabbits, guinea pigs, tree shrews, cats, marmosets and monkeys shows that the vertebrate eye compensates for positive and negative optical vergence by altering its axial length.[44,45] Negative optical vergence produced by placing negative lenses in front of the animal's eye, increases the rate of elongation of the eye by thinning the choroids of chicks, while myopic defocus from positive lenses slows the rate of elongation and thickens the choroid. Two decades of animal research have failed to uncover the fundamental monochromatic directional signal that provides the sign of defocus. While blur, contrast, spatial frequency, and color signals from chromatic aberration all play a role, the present findings suggest that the eye must have an internal mechanism to detect or infer the optical vergence of light.

How the retina can detect or infer directly the sign of defocus without odd-error blur cues and without feedback from microfluctuations remains unknown. Fincham[22] suggested that the average Stiles-Crawford effect (from many directionally sensitive cones) might be used to determine the sign of defocus, but two experiments disproved this hypothesis.[17,46] A more recent proposal is that the waveguide property of retinal cones, which act as antennas,[47] produces different patterns of photopigment bleaching in individual cones and small groups of cones when the image is formed in front of the retina than when it is formed behind.[48] Another possibility, which can be complementary to the waveguide theory or not, is that retinal blood vessels including small capillaries in the macular region of the retina produce shadows on the photopigment layer of the retina that interact with the details of the retinal image (Lopez-Gil N, et al. *IOVS* 2016;57:ARVO E-Abstract 3958). The pattern of shadows cast due to the vessels is different whether the image is formed behind or in front of the retina, producing an odd-error cue for accommodation. Neither of these two hypotheses has been tested experimentally.

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