

Human eyes do not need monochromatic aberrations for dynamic accommodation

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Abstract

Purpose: To determine if human accommodation uses the eye's own monochromatic aberrations to track dynamic accommodative stimuli.

Methods: Wavefront aberrations were measured while subjects monocularly viewed a monochromatic Maltese cross moving sinusoidally around 2D of accommodative demand with 1D amplitude at 0.2 Hz. The amplitude and phase (delay) of the accommodation response were compared to the actual vergence of the stimulus to obtain gain and temporal phase, calculated from wavefront aberrations recorded over time during experimental trials. The tested conditions were as follows: Correction of all the subject's aberrations except defocus (C); Correction of all the subject's aberrations except defocus and odd higher-order aberrations (HOAs); Correction of all the subject's aberrations of the subject's eye, i.e., the adaptive-optics system only corrected the optical system's aberrations (N); Correction of all the subject's aberrations except defocus and fourth-order spherical aberration (SA). The correction was performed at 20 Hz and each condition was repeated six times in randomised order.

Results: Average gain (± 2 standard errors of the mean) varied little across conditions; between 0.55 \pm 0.06 (SA), and 0.62 \pm 0.06 (AS). Average phase (± 2 standard errors of the mean) also varied little; between 0.41 \pm 0.02 s (E), and 0.47 \pm 0.02 s (O). After Bonferroni correction, no statistically significant differences in gain or phase were found in the presence of specific monochromatic aberrations or in their absence.

Conclusions: These results show that the eye's monochromatic aberrations are not necessary for accommodation to track dynamic accommodative stimuli.

Introduction

Accommodation is the mechanism used by the pre-presbyopic eye to produce clear images on the retina of objects at different distances. This reflexive mechanism^{1,2} is initiated by signals that activate the ciliary muscle, changing the shape of the crystalline lens and thus the power of the eye. These signals should include the needed focus direction, whether positive or negative. Given that the eye is capable of accommodating effectively under monocular viewing conditions, binocular cues cannot be the only signals that stimulate accommodation.

During monocular viewing, many factors can serve as directional cues for the visual system, such as apparent distance and size,³ chromatic aberration of the eye^{1,4,5} and microfluctuations of accommodation.^{6–8} Monochromatic

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aberrations also may be used to determine the direction of defocus, since even-order aberrations such as astigmatism and spherical aberration form a different point spread function (PSF) depending on the sign of defocus (whether images are formed behind or in front of the photoreceptors layer).⁹ *Figure 1* shows example images computed for a monochromatic Maltese cross stimulus.

Several studies have examined the potential value of monochromatic aberrations on accommodation. A summary of the various studies and their conclusions are listed in *Table* 1.

Among all the monochromatic aberrations, astigmatism is the most common even-order aberration besides defocus, and spherical aberration (SA) is the aberration that changes substantially with accommodation. Thus these two aberrations are most likely to be used by the visual system for accommodation.¹⁸ The impact of fourth-order spherical aberration (SA) on accommodation has been studied previously (see Table 1), but its effect in isolation on dynamic accommodation has not been addressed. Astigmatism is an even-order aberration that has not been taken into account in previous experiments probably because it is easily corrected with spectacles or contact lenses. Only one investigation studied the effect of astigmatism on the accommodation response to a sinusoidally moving stimulus.¹⁹ Miège, in his thesis, studied both the static and dynamic characteristics of accommodation and presbyopia. He found a significant reduction in the accommodation response of two subjects when they viewed through cylindrical lenses that added from 0.0 to 1.5 D in 0.5 D steps of vertical or horizontal astigmatism.¹⁹ On the other hand, Campbell & Westheimer⁵ concluded that astigmatism can act as an odd-error cue to accommodation; but their subjects had learned the shape of the PSF for positive and negative defocus before the measurements were made. Moreover, Miège and Campbell & Westheimer performed their studies without correcting the rest of the natural aberrations of the eye. New technologies now allow us to study each aberration of the eye objectively and individually.

In this context, the aim of the present study was to determine whether human accommodation uses cues provided by the eye's own monochromatic aberrations to respond to dynamic accommodative stimuli. Accommodation was measured when all aberrations were removed by optical corrections, and when astigmatism, SA, and either odd or even aberrations remained.

Methods

Subjects

Nine naïve subjects were recruited for this experiment after they passed a preliminary test of their ability to accommodate in monochromatic light. Unfortunately, one of the nine selected subjects was clearly fatigued and could not accommodate at all in any of the aberration conditions of the main experiment. Since the goal of this study was to look for differences in response due to aberrations, this subject was removed from the study.

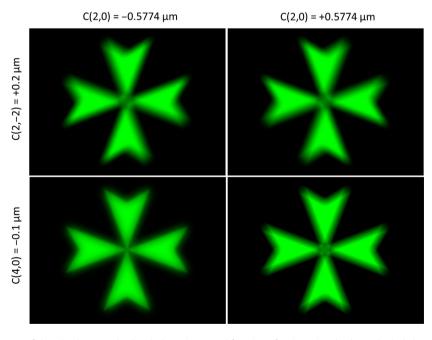


Figure 1. Simulated images of the stimulus convolved with the point spread function of astigmatism (top) or spherical aberration (bottom), and 1 D of negative (left) or positive (right) defocus for a 4 mm pupil. The reader should recognize that the images in the left and right columns are different providing a potential odd-error cue to accommodation.

Table 1. Summary of previous studies that examine	ed the potential value of monochromatic aberrations for the control of accommodation
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Study (year)	Number subjects	of	Age (years)	Aberrations corrected	Stimulus movement	Conclusions (does the eye use aberrations?)
Fincham (1951) ¹	55		17–25	None, SA	Step	60% subjects use LCA, SA is used
Campbell (1959) ⁵	4		Not provided	Defocus and astigmatism	Step	75% subjects use LCA, astigmatism and SA are cues for accommodation
Stark (1965) ¹⁰	6		Not provided	None	Step	Defocus blur alone is the effective signal for accommodation
Smithline (1974) ¹¹	4		Early twenties	None	Step	Defocus blur alone is not a sufficient stimulus
Phillips (1977) ¹²	9		Not provided	Defocus and astigmatism	Step	Defocus blur alone is a sufficient stimulus
Wilson (2002) ¹³	8		23–35	None	Step	Monochromatic aberrations are cues for accommodation
Fernández (2005) ¹⁴	2		29 and 40	Up to 3rd order	Step	Monochromatic aberrations may play a role in driving the accommodation response
Chen (2006) ¹⁵	6		27–37	All	Step	For most subjects, HOAs do not seem to be cues for accommodation
López-Gil (2007) ⁹	10		23–37	None, induced 3rd order HOAs	Sinusoidal	Third-order aberrations are not cues for accommodation
Chin (2009a) ¹⁶	4		24–34	All, inverted	Step	Accommodation in humans appears to derive a cue from the even-order aberrations
Chin (2009b) ¹⁷	5		24–34	All, SA, only even, only odd	Sinusoidal	Astigmatism and HOAs are not cues for accommodation

SA, spherical aberration; LCA, longitudinal chromatic aberration; HOA, higher-order aberrations.

The remaining eight subjects ranged in age from 21 to 40 years old, with a mean \pm standard deviation of 28 \pm 6 years. The refractive error of the subjects was between -5.00 and +0.50 D, and all subjects had at least 3.00 D of amplitude of accommodation measured in the preliminary test. None had a history of ocular disease. The subject's right eye viewed the target while the left eye was patched. The position of the tested eye was monitored on a video display. A dental bite bar was used to minimise head movements. The study adhered to the tenets of the Declaration of Helsinki and all participants gave written informed consent before participating in the study.

Experimental system

The experiments were performed using a customised adaptive optics system. A schematic diagram is shown in *Figure 2*. Aberrations were measured with a Hartmann-Shack wavefront sensor (HASO4 FIRST, www.imagine-eye s.com) at a rate of 20 Hz for the natural pupil, while the subject viewed the target through a 4-mm circular artificial pupil (P2 in *Figure 2*). An artificial pupil was used to provide the same target viewing conditions and retinal illuminance for all subjects. The size of the artificial pupil was large enough to ensure that the effects of aberrations were present, while making sure that it was always smaller than the subject's natural pupil during the experiment. An

electromagnetic deformable mirror (MIRAO 52-e, www. imagine-eyes.com) with 52 actuators was used to modify the aberration pattern of the eye in real time. The deformable mirror also compensated for all internal aberrations of the optical system in the stimulus path. Custom software was developed in MATLAB (www.mathworks.com), based on the analysis and simulation software library and software development kits provided by the manufacturer (www.imagine-eyes.com), to allow the mirror to do the partial corrections of Zernike aberrations in real time, which were necessary for the experiments. Drift artefacts associated with these types of partial corrections were prevented with a simple drift-control algorithm as described in Marín-Franch et al.²⁰ The stimulus was viewed on a monochromatic microdisplay (DSVGA OLED-XL, www. eMagin.com) through an interference filter ($\lambda = 550 \pm$ 5 nm). A Badal optical system mounted on a motorised linear motion stage (PLS-85, Micos, Germany) was used to compensate for the spherical refractive error of the subjects and induce 2 D of accommodative demand with respect to the subjects' calculated far point (see next section).

Procedures

The far point of each subject's eye was determined before starting the dynamic accommodation

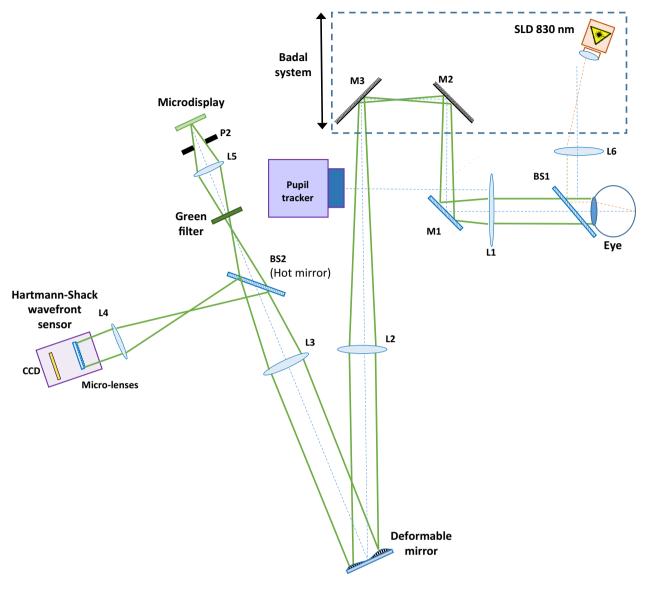


Figure 2. Schematic diagram of the customised adaptive optics system. All lenses, except L6, are achromatic doublets. P2 is an artificial pupil located at a plane conjugate with the eye's pupil plane. Green lines show the optical path of two marginal rays.

measurements. The astigmatic errors were always <1 D and were corrected in some tested conditions explained in "Experimental conditions" section. Each subject was asked to move the Badal system (*Figure 2*) away from the eye, which also moved the target away from the eye, until the target appeared very blurry, and then to move the target back towards the eye until the target first became clear. This procedure was designed to avoid unintentional use of accommodation and it was repeated three times per subject. The average value was used as the vergence of the subject's far point. Before the start of the experimental trials, participants were instructed to try to keep the target clear using the same effort as if they were reading a book.

Stimulus

During the experiment, the subject viewed the green Maltese cross subtending 1.95 degrees of visual angle at a luminance of 20 cd/m². The target was moved sinusoidally toward and away from the eye at 0.2 Hz with 1 D of amplitude centred on an accommodative demand of 2 D. The sinusoidal vergence change was generated using the deformable mirror.

Experimental conditions

The accommodation response of the subjects was measured under six different experimental conditions. The tested conditions were as follows: (1) Correction of all the subject's aberrations except defocus, i.e., except the defocus error to the moving stimulus (C); (2) Correction of all the subject's aberrations except defocus and habitual second-order astigmatism (AS); (3) Correction of all the subject's aberrations except defocus and odd HOAs (O); (4) Correction of all the subject's aberrations of the subject's eye, i.e., the adaptive-optics system only corrected the system's aberrations except defocus and fourth order spherical aberration (SA).

The correction was performed at 20 Hz, and each condition was repeated six times in a randomised order. The initial direction of the sinusoidal movement was also randomised. Each trial lasted 25 s. Measurements were performed in one session lasting between 30 and 60 min, including measurement time and rest breaks. Subjects were allowed to rest whenever they needed.

Analysis

From the aberrations measured during each trial, the accommodation response (AR) in dioptres was calculated as:

$$AR = \frac{4\sqrt{3}c_2^0}{r^2}$$

where c_2^{0} is the difference in the Zernike defocus coefficient between the refractive state and the refractive error (computed at the far point), and *r* is the radius of the subject's pupil. A sinusoidal function was then fitted to each AR and characterized by the gain, defined as the amplitude of the response of the eye to the stimulus movement divided by the amplitude of the stimulus demand; and by the temporal phase lag, defined as the difference in seconds between the peak locations of the stimulus and the AR. *Figure 3* shows the AR of a subject over time for one trial of the natural aberrations condition together with the sinusoidal movement of the stimulus. This subject showed typical gain and phase values for all conditions. During the preliminary testing of each subject's accommodation ability, a minimum gain of 0.2 was established as necessary to classify the subject as capable of accommodating in monochromatic light.

Paired *t*-tests were performed with the values of gain and phase obtained from the AR, to look for statistical differences between conditions, using a significance level of 0.003 after Bonferroni correction (0.05/15, 15 being the number of paired *t*-tests). Bonferroni correction is used to counteract the problem of multiple comparisons. With 15 tests being considered, there is around a 54% chance of observing at least one significant result, when actually there is no significance. Bonferroni correction prevents this error.

Results

The mean gain and the mean phase difference, calculated as the average value of the six trials for each subject and condition, are shown in *Figure 4*. Average gains for astigmatism were greater for two out of eight subjects (mean differences with the natural aberration condition were 0.07 and 0.15 for s03 and s04, respectively). Average phases for odd HOAs also were greater for two out of eight subjects (mean differences with the natural aberration condition were 0.14 and 0.29 s for s01 and s03, respectively).

The standard error of the mean (SEM) for mean gains varied from 0.01 to 0.10. SEM for phase varied from 0.01 to 0.12 s. *Figure 5* shows average gain (a) and phase difference (b) across subjects for each aberration condition.

Table 2 shows the mean difference in gain between all aberrations corrected (C) and the rest of the conditions, along with the lower and upper bounds of the 95% confidence intervals. The differences in gain were very small, the largest being 5% of gain between C and AS. In fact, average gain for all conditions varied little from 0.55 (SA) to 0.62

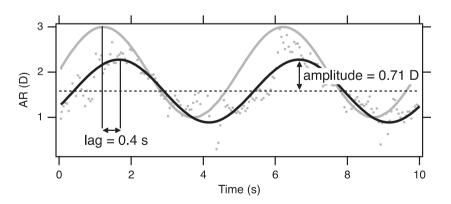


Figure 3. Accommodation response (AR in Dioptres D) measured (dots) and sinusoidal function adjusted (black line) for one subject under the natural aberrations condition. Accommodative demand (grey line) and graphic definitions for amplitude and lag are also shown.

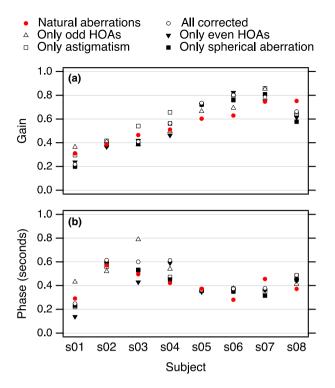


Figure 4. Mean gain (a) and phase difference (b) for each subject and condition.

(AS). Average phase also varied little from 0.41 s (E) to 0.47 s (O).

Multiple paired *t*-tests were performed for gain and for phase between pairs of conditions. After Bonferroni correction, none of the comparisons were statistically significantly different.

Discussion

This experiment tested the hypothesis that the eye takes advantage of the directional cues to defocus that astigmatism and some HOAs of the eye provide when viewing a dynamic monochromatic stimulus.

Sinusoidally moving targets have been used routinely in accommodation research 8,21,22 because they provide a

Table 2. Mean difference in gain between all aberrations corrected and the rest of the conditions, and confidence intervals

Condition	Gain mean difference	Standard deviation	Lower bound	Upper bound
AS	-0.05	0.06	-0.08	-0.008
0	0.005	0.08	-0.05	0.06
E	0.02	0.04	-0.008	0.05
Ν	0.02	0.10	-0.05	0.09
SA	0.02	0.03	-0.001	0.04

stringent method of examining the stimulus to accommodation. It has been argued that the predictable rhythmical change in the appearance of the target that accompanies sinusoidal changes in optical vergence can evoke anticipation that increases response gain and decreases phase lag.^{8,23,24} If that is the case, and since the stimulus started moving in a random direction at the start of each trial, the first cycle is less predictable than the last one, and so gain ought to be smaller and phase larger. Average gain over trials and subjects decreased only by about 0.03, while average phase lag increased by 0.08 s, from the first to the last sinusoidal cycle. Learning effects, where a subject improves the performance of accommodation with training²³ also could impact the results. Average gain over trials and subjects decreased by about 0.01, while average phase lag decreased by 0.04, from the first to the last trial of each condition. Thus our results do not seem to be affected by learning or fatigue. The present trials lasted about half the time of two previous dynamic accommodation experiments,^{3,4} where the subjects had to complete many more trials and conditions. Thus, in this experiment a possible fatigue effect was minimised. We did not find evidence that the predictability of the sinusoidal movement increases gain.

We were able to examine the role of the subject's own natural aberrations as cues for accommodation. Our results agree with both optical theory and previous experimental findings⁹ that there is no statistical difference in dynamic gain between defocus alone and defocus with odd HOAs present, suggesting that odd HOAs do not improve dynamic accommodation.

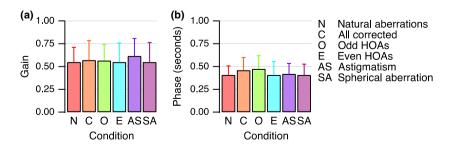


Figure 5. Mean gain (a) and phase difference (b) for each condition across subjects. Vertical bars represent standard deviation.

Chin *et al.* tested the role of SA by removing it, while we corrected all aberrations and then left the natural SA and defocus intact. Our results are, on average, in good agreement with those of Chin *et al.* (compare *Figure 5* against *Figure 3* in¹⁷): that is, no statistical differences were found between conditions. Although there are studies that have shown that SA expands the depth of field,^{25–27} this effect did not seem to influence accommodation response gain in our subjects.

Miège found that astigmatism decreased gain and did not affect phase, and that accommodation depended neither on the quantity of astigmatism nor on its axis. His results could have been affected by the natural aberrations of his subjects and the large amounts of astigmatism that were used. When the natural astigmatism of our subjects was left uncorrected, our results indicate that this aberration did not affect response gain or phase.

The result of this experiment that monochromatic aberrations are not universally used to guide dynamic accommodation, positively indicates that the eye may have another mechanism, not related to the aberrations of the light while going through the optical media of the eye (i.e. a retinal mechanism), that guides dynamic accommodation. Although they have not been tested experimentally, two theories have emerged recently. One proposes that retinal cones, acting as waveguides, produce individually and in small groups of cones, different patterns of photopigment bleaching depending whether the image is formed in front of or behind the retina.²⁸ The other novel theory proposes that the eye may obtain an odd-error cue for accommodation from the shadows of the blood vessels on the photopigment layer of the retina.²⁹

This knowledge of the accommodation mechanism and its stimulus could improve our understanding of the emmetropisation mechanism, since studies on animals and humans show that the process of long-term growth and development of the eye (emmetropisation) responds to the direction of defocus, i.e., the same optical signals that control short term defocus adaptation (dynamic accommodation) also could control long-term emmetropisation.^{1,11,30–34}

Conclusions

We have found no clear evidence that monochromatic aberrations are used universally by the human eye to guide dynamic accommodation. Young adults are able to accommodate to a dynamic monochromatic accommodative stimulus with or without the eye's astigmatism and/or its higher-order aberrations. These data reveal that sign appropriate accommodative responses can be produced in the absence of any defocus sign information in the blurred images, suggesting that another mechanism provides the signed signal to guide the accommodative responses.³⁵

Disclosure

The authors report no conflicts of interest and have no proprietary interest in any of the materials mentioned in this article.

Acknowledgements

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References

- 1. Fincham EF. The accommodation reflex and its stimulus. *Br J Ophthalmol* 1951; 35: 381–393.
- 2. Heath GG. Components of accommodation. *Am J Optom Arch Am Acad Optom* 1956; 33: 569–579.
- Kruger PB & Pola J. Dioptric and non-dioptric stimuli for accommodation: target size alone and with blur and chromatic aberration. *Vision Res* 1987; 27: 555–567.
- 4. Kruger PB, Nowbotsing S, Aggarwala KR & Mathews S. Small amounts of chromatic aberration influence dynamic accommodation. *Optom Vis Sci* 1995; 72: 656–666.
- Campbell FW & Westheimer G. Factors influencing accommodation responses of the human eye. *J Opt Soc Am* 1959; 49: 568–571.
- Charman WN & Heron G. Fluctuations in accommodation: a review. Ophthalmic Physiol Opt 1988; 8: 153–164.
- Charman WN & Heron G. Microfluctuations in accommodation: an update on their characteristics and possible role. *Ophthalmic Physiol Opt* 2015; 35: 476–499.
- Kruger PB, Mathews S, Aggarwala KR & Sanchez N. Chromatic aberration and ocular focus: Fincham revisited. *Vision Res* 1993; 33: 1397–1411.
- Lopez-Gil N, Rucker FJ, Stark LR *et al.* Effect of third-order aberrations on dynamic accommodation. *Vision Res* 2007; 47: 755–765.
- Stark L & Takahashi Y. Absence of an odd-error signal mechanism in human accommodation. *IEEE Trans Biomed Eng* 1965; 12: 138–146.
- 11. Smithline LM. Accommodative response to blur. J Opt Soc Am 1974; 64: 1512–1516.
- Phillips S & Stark L. Blur: a sufficient accommodative stimulus. Doc Ophthalmol 1977; 43: 65–89.
- Wilson BJ, Decker KE & Roorda A. Monochromatic aberrations provide an odd-error cue to focus direction. J Opt Soc Am A Opt Image Sci Vis 2002; 19: 833–839.

- 14. Fernandez EJ & Artal P. Study on the effects of monochromatic aberrations in the accommodation response by using adaptive optics. *J Opt Soc Am A Opt Image Sci Vis* 2005; 22: 1732–1738.
- Chen L, Kruger PB, Hofer H, Singer B & Williams DR. Accommodation with higher-order monochromatic aberrations corrected with adaptive optics. J Opt Soc Am A Opt Image Sci Vis 2006; 23: 1–8.
- Chin SS, Hampson KM & Mallen E. Role of ocular aberrations in dynamic accommodation control. *Clin Exp Optom* 2009; 92: 227–237.
- Chin SS, Hampson KM & Mallen EA. Effect of correction of ocular aberration dynamics on the accommodation response to a sinusoidally moving stimulus. *Opt Lett* 2009; 34: 3274– 3276.
- 18. Lopez-Gil N & Fernandez-Sanchez V. The change of spherical aberration during accommodation and its effect on the accommodation response. *J Vision* 2010; 10: 12.
- Miège C. Étude de la fonction accommodative de l'oeil humain: application à la correction de la presbytie, Université de Technologie de Compiègne: Compiègne, 1988.
- Marín-Franch I, Del Águila-Carrasco AJ, Levecq X & López-Gil N. Drifts in real-time partial wavefront correction and how to avoid them. *Appl Opt* 2017; 56: 3989–3994.
- Campbell FW & Westheimer G. Dynamics of accommodation responses of the human eye. J Physiol 1960; 151: 285– 295.
- 22. Brodkey J & Stark L. Accommodative convergence an adaptive nonlinear control system. *IEEE Trans Syst Sci Cybern* 1967; 3: 121–133.
- 23. van der Wildt GJ, Bouman MA & van de Kraats J. The effect of anticipation on the transfer function of the human lens system. *Opt Acta* 1974; 21: 843–860.
- 24. Kruger PB, Mathews S, Aggarwala KR, Yager D & Kruger ES. Accommodation responds to changing contrast of long, middle and short spectral-waveband components of the retinal image. *Vision Res* 1995; 35: 2415–2429.

- 25. Rocha KM, Vabre L, Chateau N & Krueger RR. Expanding depth of focus by modifying higher-order aberrations induced by an adaptive optics visual simulator. *J Cataract Refract Surg* 2009; 35: 1885–1892.
- 26. Benard Y, Lopez-Gil N & Legras R. Subjective depth of field in presence of 4th-order and 6th-order Zernike spherical aberration using adaptive optics technology. *J Cataract Refract Surg* 2010; 36: 2129–2138.
- Benard Y, Lopez-Gil N & Legras R. Optimizing the subjective depth-of-focus with combinations of fourthand sixth-order spherical aberration. *Vision Res* 2011; 51: 2471–2477.
- Vohnsen B. Directional sensitivity of the retina: a layered scattering model of outer-segment photoreceptor pigments. *Biomed Opt Express* 2014; 5: 1569–1587.
- 29. Lopez-Gil N, Jaskulski MT, Vargas-Martin F & Kruger PB. Retinal blood vessels may be used to detect the sign of defocus. *Invest Ophthalmol Vis Sci* 2016; 57: 3958–3958.
- Park TW, Winawer J & Wallman J. Further evidence that chick eyes use the sign of blur in spectacle lens compensation. *Vision Res* 2003; 43: 1519–1531.
- Smith EL 3rd, Hung LF & Harwerth RS. Effects of optically induced blur on the refractive status of young monkeys. *Vision Res* 1994; 34: 293–301.
- Smith EL 3rd & Hung LF. The role of optical defocus in regulating refractive development in infant monkeys. *Vision Res* 1999; 39: 1415–1435.
- Wildsoet CF & Schmid KL. Emmetropization in chicks uses optical vergence and relative distance cues to decode defocus. *Vision Res* 2001; 41: 3197–3204.
- 34. Lee JH, Stark LR, Cohen S & Kruger PB. Accommodation to static chromatic simulations of blurred retinal images. *Ophthalmic Physiol Opt* 1999; 19: 223–235.
- Del Águila-Carrasco AJ, Marín-Franch I, Bernal-Molina P et al. Accommodation responds to optical vergence and not defocus blur alone. *Invest Ophthalmol Vis Sci* 2017; 58: 1758–1763.