Optics and neural adaptation jointly limit human stereovision

Cherlyn J. Ng[a,b], Randolph Blake[c], Martin S. Banks[d,1], Duje Tadin[a,b,e], and Geunyoung Yoon[a,b,1]

[a]Flaum Eye Institute, University of Rochester, Rochester, NY 14642; [b]Center for Visual Science, University of Rochester, Rochester, NY 14627; [c]Department of Psychology, Vanderbilt University, Nashville, TN 37203; [d]School of Optometry, University of California, Berkeley, CA 94720; and [e]Department of Brain and Cognitive Sciences, University of Rochester, Rochester, NY 14627

Contributed by Martin S. Banks, April 1, 2021 (sent for review January 4, 2021; reviewed by Pablo Artal and Jenny C. A. Read)

Stereovision is the ability to perceive fine depth variations from small differences in the two eyes' images. Using adaptive optics, we show that even minute optical aberrations that are not clinically correctable, and go unnoticed in everyday vision, can affect stereo acuity. Hence, the human binocular system is capable of using fine details that are not experienced in everyday vision. Interestingly, stereo acuity varied considerably across individuals even when they were provided identical perfect optics. We also found that individuals' stereo acuity is better when viewing with their habitual optics rather than someone else's (better) optics. Together, these findings suggest that the visual system compensates for habitual optical aberrations through neural adaptation and thereby optimizes stereovision uniquely for each individual. Thus, stereovision is limited by small optical aberrations and by neural adaptation to one's own optics.

stereovision | adaptive optics | adaptation | interocular difference | optical aberrations

Many of us have refractive errors that degrade the quality of the images formed on our retinas, the most common errors being myopia, hyperopia, and astigmatism. If uncorrected, these optical defects can compromise everyday activities such as visually guided behavior and reading. Collectively known as lower-order aberrations, these defects are easily corrected with spectacles or contact lenses. In addition, we all have other optical aberrations that cannot be so easily corrected. These defects—higher-order aberrations—also degrade retinal images (1). We are not aware of these residual native aberrations because everyday experience provides no basis for knowing what the world would look like if those aberrations were eliminated. This conundrum raises a fascinating, albeit modest version of Molyneux's problem (2): What would the world look like if a person were able to see the world through eyes with perfect optics? Answering this question will specify the degree to which the higher-order aberrations limit human visual function and, in turn, reveal the extent to which the visual nervous system can utilize spatial information never before encountered.

This question can be answered using adaptive optics (AO). AO is a technique that measures optical wavefront distortions through the pupil of the eye and compensates by setting a complementary shape on a deformable mirror that reflects visual stimuli into the eye to achieve nearly perfect, diffraction-limited retinal images (3). Previous work has shown that removing higher-order aberrations yields significant improvements in visual acuity and contrast sensitivity (4–7). That work dealt with monocular vision, but humans are intrinsically binocular, so the question remains as to how aberrations of both eyes affect binocular vision. Expanding on technical advances by Fernandez et al. (8, 9), we developed a binocular AO system to examine the impact of higher-order aberrations on binocular depth perception, an aspect of vision that exploits tiny positional differences between locations of features in the two eyes' retinal images (10–12). These positional disparities are registered by binocular neurons that possess pairs of receptive fields, one for each eye. Activity within those neurons plays a crucial role in mediating the compelling sense of three dimensionality termed stereopsis (13, 14).

Stereopsis, like other visual functions, is adversely affected by blur (15–17), particularly when the images to the two eyes differ in optical quality (18–20). It is not uncommon that the two eyes have different spherical refractive errors [anisometropia and monovision are examples (21, 22)] and astigmatism of different magnitudes and axes. Even in well-focused eyes, higher-order aberration profiles are seldom the same in the two eyes (23). The profiles often exhibit some bilateral symmetry, which causes the blur patterns in the two eyes to differ by reflection about the midline (23).

Are there consequences from living with chronic and conventionally uncorrectable aberrations? We know that monocular images appear sharpest when they are presented with a person's native aberrations rather than other aberrations of the same magnitude. This observation strongly suggests that people adapt to the blur caused by their own optics (24–26). Binocular adaptation to habitual optics also biases the cyclopean percept of blurriness (27). Plausibly, stereopsis would capitalize on such adaptation too and thereby improve depth perception under habitually experienced conditions. This explanation was cited in an earlier paper (28) as a reason for not observing improvement in stereo vision when optical aberrations were corrected.

With these points in mind, we investigated whether stereopsis is limited by the optics of the two eyes, and, as a follow up, whether the neural mechanisms underlying stereopsis become adapted to

Significance

Humans, and other animals, have eyes laterally displaced on the head that view the world from slightly different vantage points to create small differences in the left and right images. These differences are utilized for depth perception (stereovision). Retinal images are also subject to optical imperfections, often different in the two eyes. Using advanced optical techniques, we show that even the smallest imperfections escaping clinical detection affect stereovision. Our data also suggest that neural processes become acclimated to a person's own optics. Hence, stereovision is directly affected by the eyes' optics and indirectly via neural adaptation. Because the optics change over the lifespan, the implication is that the adult binocular system is adaptable, pointing to the potential for binocular rehabilitation.

Author contributions: C.J.N., M.S.B., and G.Y. designed research; C.J.N. performed research; C.J.N. and D.T. analyzed data; and C.J.N., R.B., M.S.B., D.T., and G.Y. wrote the paper.

Reviewers: P.A., Universidad de Murcia; and J.C.A.R., Newcastle University.

The authors declare no competing interest.

[1]To whom correspondence may be addressed. Email: martybanks@berkeley.edu or gyoon@ur.rochester.edu.

This article contains supporting information online at https://www.pnas.org/lookup/suppl/doi:10.1073/pnas.2100126118/-/DCSupplemental.

Published May 31, 2021.

NEUROSCIENCE

an individual's degraded retinal images. We pursued this by measuring stereo acuity when all optical aberrations were eliminated by AO correction, in comparison to measurements with native optics when the familiar lower- and higher-order aberrations were in place. Improvement in AO-assisted stereopsis would be noteworthy because it would show that the brain can exploit greater image sharpness than ever experienced before (Fig. 1).

Results

Visual Acuity Follows Optical Quality. We first wanted to confirm that correcting the optical aberrations using our AO system yields improvement in monocular visual acuity where improvement was expected. We focused on monocular letter acuity because others had shown significant improvement in that task when aberrations are corrected by AO (4–6, 29).

Fig. 2*A* shows examples of an individual's aberrated wavefront pattern, the AO-corrected pattern, and the associated retinal images. Fig. 2*B* plots monocular visual acuity with and without AO correction. Note that the native optics in our study always included the best conventional refractive correction (sphere and cylinder). The average acuities for the left eye improved with AO correction from 20/18 to 20/12.3 (an improvement of 31.7%) and for the right eye from 20/17 to 20/11 (35.3% improvement). The improvements were statistically significant ($t_{13} = 10.0$, $P < 10^{-7}$, one-tailed, all eyes combined). Indeed, the corrected acuities approached limits set by photoreceptor spacing at the fovea (30, 31). Participants reported that stimuli viewed with AO correction appeared unusually sharp. These results confirm that our AO correction substantially improves retinal-image quality.

Visual acuity with the native optics was highly correlated with a quantitative measure of image quality (see *Materials and Methods* for description; Fig. 2*C*; Pearson $r_{12} = -0.92$; $P = 0.003$). This was entirely expected as it simply shows that those individuals with better native optics have better visual acuity. Surprisingly, we also found a similar degree of individual variability in the acuities measured under AO correction even though participants had essentially the same (near-perfect) image quality in that condition (Fig. 2*B* and *SI Appendix*, Fig. S1). Notably, the acuities with corrected optics were correlated with image quality before AO correction (Fig. 2*D*; Pearson $r_{12} = -0.90$; $P = 0.006$): those with poor native optics also exhibited relatively poor visual acuity under AO correction. Hence, there was no significant association between native image quality and how much visual acuity improved (*SI Appendix*, Fig. S2*A*). This is in contrast to what one would predict if photoreceptor sampling were the only factor that limited vision during AO correction (*SI Appendix*, Fig. S2*B*). Comparing the actual improvements with predictions, we observed that people with poorer native optics had far less improvement in their corrected visual acuity than expected, as compared with those who had good optics (*SI Appendix*, Fig. S2*C*). This suggests not only the presence of limiting factors other than photoreceptor sampling but also that these factors are more pronounced in people with poorer

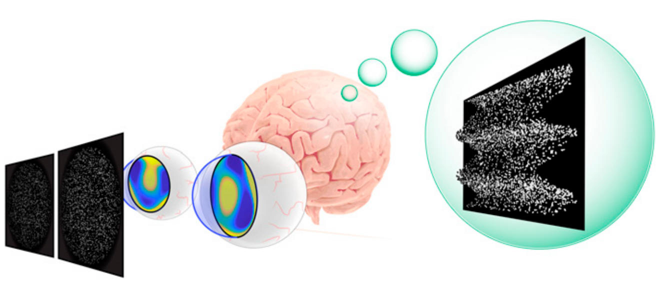

Fig. 1. Schematic of the paradigm. The aim of the study was to elucidate the interplay between optics and neural adaptation in determining stereoacuity.

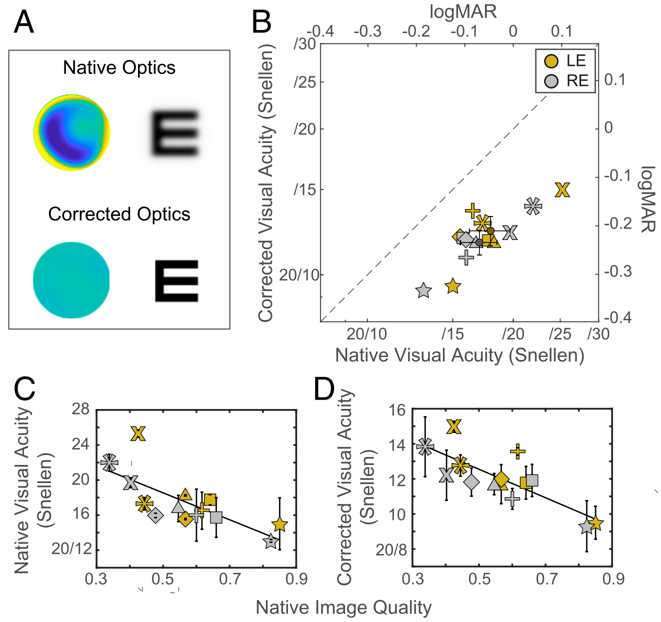

Fig. 2. Visual acuity and optical correction. (*A*) Wavefronts and retinal images from the right eye of a representative participant (S6). On the left are maps of the wavefront drawn in the same color scale in the native and corrected conditions. The color variation represents the distortion of the wavefront. On the right are simulations of the retinal images of a 20/20 Snellen letter E in the two conditions. (*B*) Monocular visual acuity with native and corrected optics. Visual acuity with AO-corrected optics is plotted against acuity with native optics for both eyes of all participants. Gold and silver symbols indicate the acuities for the left and right eyes, respectively. The left and bottom axes are acuity in Snellen notation. The right and top axes are the equivalent in logMAR units (logarithm of minimal angle of resolution in minutes of arc). The small circles are the average values for the left and right eyes. (*C*) Native and (*D*) corrected visual acuity as a function of native retinal-image quality, simulated by convolving individual eyes' PSFs with a 20/20 Snellen E (see *Materials and Methods*). Error bars indicate ±1 SD. Different symbols represent data from different participants as shown in *SI Appendix*, Fig. S1.

optics. Neural adaptation had been cited as a reason in a similar previous observation where patients with large higher-order aberrations due to corneal disease also show deficits in AO-corrected visual acuity (29). In the sections below, we examine the implications of these intriguing observations.

Stereo Acuity Improves with Optical Correction. We next turn to the main topic of investigation: How do the eyes' optics affect the precision of stereopsis? To answer that question, we measured the smallest disparity that allowed participants to identify the orientation of a disparity-defined depth corrugation (refs. 32 and 33 and Eqs. **1** and **2**) with their native optics and AO-corrected optics (Fig. 3*A*). Stereo acuity was measured at three corrugation frequencies: 1, 2, and 3 cpd.

As can be seen in Fig. 3*B*, there was a clear improvement in stereo acuity with AO correction at all three corrugation frequencies. The average improvement (small dark circles with error bars) was 30.0%, a statistically significant improvement ($F_{1,36} = 4.08$, $P = 0.050$; two-way repeated randomized-block ANOVA) and similar in magnitude to the improvement in visual acuity with AO correction (Fig. 2). Stereo acuity decreased (i.e., disparity at threshold increased) with increasing corrugation frequency ($F_{2,36} = 14.96$, $P < 10^{-4}$), but the improvement with AO-corrected optics relative to the native optics was similar at all frequencies (frequency × correction interaction: $F_{2,36} = 0.21$, $P = 0.81$).

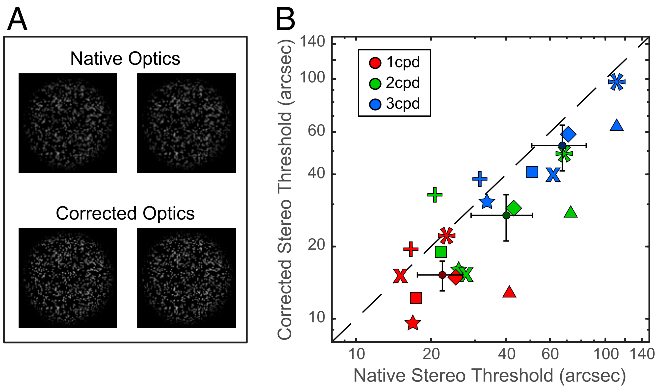

Fig. 3. Stereo thresholds and optical correction. (*A*) Simulated retinal images, one for each eye of the random-dot stimulus, are depicted for the native- and AO-corrected-optics conditions. The reader can cross-fuse to observe the depth corrugation. (*B*) Stereo thresholds with native and AO-corrected optics. The smallest discriminable disparity with correction is plotted against the smallest discriminable disparity with native optics for each participant and corrugation frequency (red for 1 cpd, green for 2 cpd, and blue for 3 cpd). The small circles are the average values for each frequency. Errors bars are SDs. Different symbols represent data from different participants as shown in *SI Appendix*, Fig. S1.

Most participants did substantially better in the stereo test with corrected optics. However, as with visual acuity (Fig. 2*D*), we found considerable individual differences in AO-corrected stereo acuity even though the retinal-image quality was essentially the same for all of them in that condition. One participant actually performed slightly worse with AO correction than with native optics (the three cross data points above the identity line in Fig. 3*B*), which we will discuss later.

What Causes Individual Differences in Stereo Threshold? Previous studies have found significant individual differences in stereo acuity (34, 35); we observed this with the native optics too (horizontal spread in Fig. 3*B*). Why do people differ in this task? To tackle that question, we investigated whether peoples' native optical aberrations determined the individual differences. There are two possibilities. First, some people simply have better optics than others. Consequently, those with minimal higher-order aberrations, and hence better image quality, are able to perform better. This hypothesis is consistent with the observation that stereo acuity is better with sharp images in the two eyes than with blurred images (16, 36). Our results show this too, because stereo acuity with AO correction was generally better than acuity without AO correction (Fig. 3*B*). Second, alternatively, individual differences in stereo acuity might largely derive from interocular differences in the aberrations. This hypothesis is suggested by the blur paradox (16), i.e., stereo acuity is actually better when both eyes' images are equivalently blurred compared to when only one eye's image is blurred and the other eye's image is not blurred. The blur paradox implies that the binocular matching required to see depth from disparity is dependent on having images of equivalent contrast energy and spatial-frequency content in the two eyes. We next sought to determine which of the two hypotheses is the better predictor of stereo acuity across individuals.

We simulated what the left and right retinal images for each participant would be by convolving their point-spread functions (PSFs) with our random-dot stimuli (*SI Appendix*, Fig. S3). From the resulting images, we quantified binocular image quality in two ways: the average image quality (ImQ_{Mean}; Eq. **4**) and the interocular difference in image quality (ImQ_{IOD}; Eq. **5**). Note that our metric of interocular difference incorporated the difference in both magnitude and the pattern of blur between the eyes. Results from those simulations are summarized in Fig. 4.

Fig. 4*A* plots stereo acuity with native optics as a function of average image quality; they do not covary systematically (Pearson's $r_5 = -0.13$, -0.30, and -0.43 at 1, 2, and 3 cpd; all $P > 0.34$). Fig. 4*B* plots native stereo acuity as a function of the difference in optical quality between the two eyes. Here we see a clear association: There were significant positive correlations for corrugation frequencies of 2 and 3 cpd (Pearson $r_5 = 0.89$ and 0.91, respectively; $P < 0.01$ in both cases) and a positive trend for 1 cpd (Pearson $r_5 = 0.55$; $P = 0.13$). In other words, participants with similar native aberration patterns in the two eyes exhibit better stereo acuity than participants with larger interocular differences. These results reveal that the blur paradox is not specific to lower-order aberrations (such as defocus) but generalizes to interocular differences in higher-order aberrations.

Individual differences in stereo acuity under native optics were expected. However, we also found similarly large intersubject variability under AO correction (vertical spread in Fig. 3*B*). That is, there were still notable individual differences when optical quality was essentially the same in all eyes because the optical imperfections had been corrected. Interestingly, participants' stereo acuity with AO-corrected optics was significantly correlated with their stereo acuity with their native optics at the higher corrugation frequencies (1 cpd: Pearson's $r_5 = -0.048$, $P = 0.92$; 2 cpd: $r_5 = 0.80$, $P = 0.032$; 3 cpd: $r_5 = 0.86$, $P = 0.013$).

NEUROSCIENCE

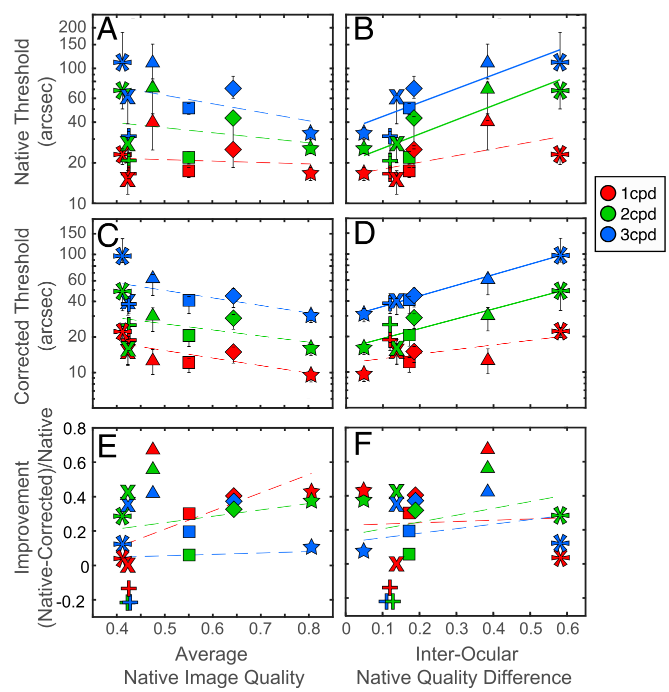

Fig. 4. Stereo thresholds and image quality. (*A* and *B*) Stereo threshold with the native optics as a function of the average (ImQ_{Mean}; Eq. **4**; *A*) and interocular difference (ImQ_{IOD}; Eq. **5**; *B*) in the native image quality. The smallest discriminable disparity was plotted for each participant and corrugation frequency against the average image quality for the two eyes. Different symbols represent data from different participants as shown in *SI Appendix*, Fig. S1. Error bars indicate ±1 SD. Solid lines are conditions that yielded significant correlations with each image-quality metric. Dashed lines are conditions that did not yield significant correlations. (*C* and *D*) Stereo threshold with AO-corrected optics as a function of the same two image-quality metrics. (*E* and *F*) Improvement in stereo acuity during AO correction. Improvement in stereo acuity was calculated using the formula (*Native*−*Corrected*)/*Native*, where *Native* and *Corrected* represent stereo thresholds measured with native optics and AO-corrected optics, respectively. Positive values indicate better performance with AO correction.

Similar to our observations of stereo acuity with native optics, overall image quality was not significantly correlated with AO performance. (Fig. 4*C*; 1 cpd: Pearson's $r_5 = -0.73$, $P = 0.06$; 2 cpd: $r_5 = -0.43$, $P = 0.33$; 3 cpd: $r_5 = -0.50$; $P = 0.25$). However, interocular difference in native image quality was well correlated with AO-corrected stereo acuity even though the optical aberrations had been eliminated (Fig. 4*D*; 1 cpd: Pearson's $r_5 = 0.63$, $P = 0.13$; 2 cpd: $r_5 = 0.93$, $P = 0.0024$; 3 cpd: $r_5 = 0.99$, $P < 0.0001$). Like monocular visual acuity (*SI Appendix*, Fig. S2*A*), we did not observe greater or lesser improvement in stereo acuity in people whose optics were bad to begin with (Fig. 4 *E* and *F*; average optical quality 1 cpd: Pearson's $r_5 = 0.54$, $P = 0.21$; 2 cpd: $r_5 = 0.21$, $P = 0.65$; 3 cpd: $r_5 = 0.05$; $P = 0.91$; interocular difference 1 cpd: Pearson's $r_5 = 0.048$, $P = 0.92$; 2 cpd: $r_5 = 0.28$, $P = 0.54$; 3 cpd: $r_5 = 0.22$; $P = 0.64$). Taken together, our results suggest that other factors also affect stereovision such that people with poorer native optics do not show greater improvement than people with good optics when corrected (within the typical range of the native optics, as tested in the present study).

In summary, individuals who have had large interocular differences in optical quality during everyday viewing had poorer stereo acuity with their native optics but also with AO-corrected optics (*SI Appendix*, Fig. S1). The finding with corrected optics is paradoxical because the people who received the greatest improvement in interocular image-quality difference had the poorest stereo acuity with AO-corrected optics. Why would people with larger interocular differences have poorer stereopsis than people with smaller differences, when the differences had been eliminated? We explore that question next.

Adaptation to Native Optics. The inability of individuals with poorer native optics to achieve greater improvement in stereo acuity implies that neural circuits subserving stereopsis have been shaped by the visual experience delimited by their habitual optics. To examine this, we replaced the optics of one person with those of another and measured the effect on stereo acuity (Fig. 5*A*).

We measured the wavefront aberrations of both eyes in six participants (*SI Appendix*, Fig. S3). Fig. 5*B* shows average native image quality and interocular difference in quality for each of them. We zeroed in on participant S5, who had the best average quality and the smallest interocular difference in quality. Then, as indicated in Fig. 5*A*, we used the AO system to fully correct the native optics and simultaneously impose the optics of S5 on participants S1, S2, S3, and S4. By doing so, we made the retinal images the same for all participants and made the quality of the retinal images better than those people were used to experiencing. We then examined stereo acuity when S1 through S4 viewed the stimuli with the improved but unfamiliar optics. Based on optical quality alone, we would expect that all four participants viewing the stimuli with the same optics would have the same stereo acuity and that that acuity would be the same as S5's.

Fig. 5*C* shows the results. The horizontal axis plots stereo thresholds for S5 for corrugation frequencies of 1, 2, and 3 cpd. The vertical axis plots thresholds for the other four participants when given the optics of S5. We emphasize that S1 through S4 now had the same optics and therefore the same retinal images. The four participants with unfamiliar optics performed more poorly than S5, who was tested with his native optics. Remarkably, S4 had the largest decline in performance even though her image quality (average and interocular difference) was most similar to S5. Although her optical quality was similar to S5's, the patterns of blur from her aberrations were quite different from his (*SI Appendix*, Fig. S3). The fact that she did relatively poorly with S5's optics indicates that familiarity with one's optics is important for fine stereopsis.

We also compared stereo thresholds in participants S1 through S4 with their native optics and with the improved but unfamiliar optics of S5. There was no systematic difference (Fig. 5*D*). This

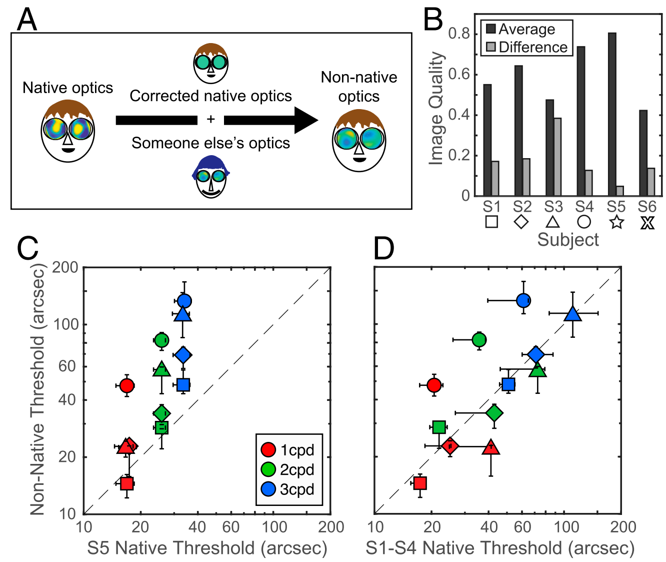

Fig. 5. Stereo thresholds with nonnative optics. (*A*) Experimental paradigm. (*B*) Image quality for each participant. Average quality (black) and interocular difference in quality (gray) are plotted for each of the six participants. We imposed the optics of S5 on the eyes of S1, S2, S3, and S4. We also imposed the optics of S1 on the eyes of S6, and vice versa. (*C*) Stereo thresholds with nonnative optics. The smallest discriminable disparity is plotted for S1, S2, S3, and S4 compared with S5, whose optics were imposed. As in *B*, ■ represents S1, ♦ S2, ▲ S3, and • S4. Colors represent measurements at different corrugation frequencies (red for 1 cpd, green for 2 cpd, and blue for 3 cpd). (*D*) Comparisons of the stereo thresholds of S1 through S4 with their native optics and with S5's optics. Error bars indicate SDs.

finding suggests that there are two offsetting factors that determine how optics affects stereopsis: a benefit from improving optical quality and a detriment from having unfamiliar optics. Notably, the one participant whose stereo acuity did not improve with AO correction (Fig. 3*B*) was among the best performers with the native optics. It was plausible that the optical improvement provided by AO was insufficient to counteract the negative adaptation effects as a result of unfamiliar optics.

To further investigate the importance of familiarity, we swapped the optics between the two participants with comparable interocular difference in optical quality: S1 and S6. Both participants performed significantly more poorly when given the other person's optics (particularly at high corrugation frequencies). S1's thresholds went from 17.4 arcsec with her own optics to 19.2 arcsec with S6's optics at 1 cpd (a 10.3% increase), from 21.9 to 48.6 arcsec at 2 cpd (122%), and from 50.7 to 94.7 arcsec at 3 cpd (87%). S6's thresholds exhibited even more dramatic changes. His thresholds went from 15.2 arcsec with his own optics to 64.9 arcsec with S1's optics at 1 cpd (270%), from 25.3 to 158 arcsec at 2 cpd (525%), and from 56.2 arcsec to unmeasurable at 3 cpd. These results again illustrate that stereopsis is significantly poorer when viewing stimuli with someone else's optics even when the optical quality of the participants is equivalent in magnitude. This again strongly suggests that the binocular visual system adapts to particular aspects of retinal images experienced in everyday life.

Discussion

Everyone's visual system has operated for years with the optics unique to the individual. The optics of our two eyes have inscribed their uniqueness on the distributions of light formed on the two retinae, i.e., their metaphorical, unique optical signature. The information embodied in those two images, in turn, is transcribed into neural representations that are utilized in mediating every aspect of visual perception including stereopsis. The present study sheds light on the consequences of manipulating those optical signatures using AO. Our results reveal that those consequences can be advantageous (i.e., improve stereo acuity) or deleterious (i.e., impair stereo acuity), depending on how closely AO correction conforms to the uniqueness of a given individual's native optics. The following sections consider these two consequences and their implications for understanding human binocular vision.

AO-Mediated Improvement in Vision. When aberrations in the habitual optics are corrected in the laboratory using AO, the world temporarily looks noticeably different (26). Accompanying those changes in visual appearance are significant improvements in visual acuity and contrast sensitivity (5, 25, 37–39). These improvements are not surprising given the well-documented, deleterious impact that blur has on resolution (3, 5, 6, 39–43). Indeed, participants with full AO correction in our experiments exhibited high visual acuity that approached the limit imposed by the sampling frequency of the photoreceptor lattice. Similarly, we found that correcting higher-order aberrations, which are not visually conspicuous in well-corrected eyes, improves stereo acuity, especially with higher-frequency modulations in disparity.

The improvement we observed in stereo acuity with AO-corrected optics stands in contrast to results from an earlier study out of our laboratory (28) that suggested that higher-order aberrations have essentially no impact on stereo acuity. We believe that procedural differences were responsible for the difference in findings. The earlier study used optical phase plates to achieve static correction of the higher-order aberrations, whereas the present study used real-time AO correction which, unlike static phase plates, compensates for eye movements and thus mitigates optical effects of pupil/image misalignment that can happen when viewing with a static correction. By constantly updating the correction profile, AO also compensates for other small sources of dynamic fluctuations in the aberrations brought about by the tear film and microfluctuations in accommodation from breathing and heartbeat. We are thus confident that the improved AO device and testing procedures employed in this study are responsible for revealing a genuine improvement in stereo acuity attributable to elimination of higher-order aberrations. This, in turn, raises the following question: How does this improvement come about?

AO Improves Stereopsis. Our results reveal that the precision of stereopsis achieved with AO exceeds that measured when viewing with normal optics. This achievement is remarkable given that the limits of human stereopsis assessed with natural optics already qualifies as a form of hyperacuity, i.e., disparity resolution that exceeds the sampling frequency of the photoreceptor mosaic (16, 36, 44–47).

What is the basis of this improvement in stereopsis with AO correction? It is natural to wonder whether the improvement might arise from more stable, accurate vergence fixation prompted by the enhanced clarity of edge information in the AO-corrected retinal images (48). We doubt, however, that more stable vergence accounts for our results because earlier work showed that 1) vergence accuracy is unaffected by bandpass spatial-frequency filtering of texture stereograms, a maneuver that mimics blur (49), and 2) fixation disparity [a proxy for vergence error that affects stereopsis (50)] is essentially the same when viewing stereo gratings ranging in spatial frequency from 0.5 to 8 cpd (51). Instead, we are inclined to attribute the improved stereopsis with AO-corrected images to neural processes involved in cortical disparity computation per se. To investigate this, we first need to consider the nature of the disparities arising from viewing conditions simulating three-dimensional objects (in our case, a corrugated textured surface) seen from two viewpoints. There are various ways to conceptualize the nature of those disparities (52, 53). One is in terms of positional disparities between pairs of matching features. A convenient means for extracting that information would be with location-specific cortical receptive fields that function as spatial-frequency-selective neural filters (54). Another complementary view concerns disparity in the phase domain (55). An impetus for this view comes from neurophysiological studies showing that binocular cortical neurons are sensitive to different phase shifts within pairs of monocular images (56, 57). Several groups have made the case for the joint involvement of both forms of disparity in mediation of stereopsis (58, 59). Our aim here is not to critique the different models of stereopsis but rather to surmise how AO, through the elimination of higher-order aberrations ordinarily embedded in each eye's retinal image, might augment the luminance distribution information defining those images.

Higher-order aberrations of the eye's optics degrade retinal images in three ways: 1) They reduce contrast over a range of spatial frequencies, 2) they eliminate very high spatial frequencies altogether, and 3) they alter phase relationships among spatial frequencies that crucially define spatial information portrayed within images. The disruption of this phase congruency causes a significant loss in key structural elements such as sharp edges that make features hard to match accurately between the eyes. In that way, estimating fine positional disparities becomes difficult. Correcting the aberrations with AO recovers the phase spectra of low spatial frequencies. Adding the phases of high-frequency components that were unavailable before correction enables phase disparity computation from a larger set of channels. It is plausible that this improvement in both contrast and phase congruency in a broadband stimulus, like the random-dot stereogram, allows the visual system to detect even smaller disparities than those resolved with well-focused normal optics. Further investigation is required to learn whether the binocular system can compensate for the phase disruption through long-term adaptation to the eyes' native optics and, if so, the extent to which the improvement in human stereopsis with perfect optics is compromised by phase adaptation (60, 61).

Putting aside those speculations about the bases of AO's contribution to improved stereo acuity, we next turn to a second intriguing feature of our results: the consequence of viewing the world through someone else's optics that was unexpectedly not beneficial despite ocular improvements relative to the participant's own optics.

Individual Differences in the Impact of AO Viewing. As noted earlier when discussing the blur paradox, differences in the patterns of blur and the sharpness of images viewed by the two eyes adversely affect stereo acuity (62), suggesting that having similar optical quality in the eyes is critical for fine stereopsis. We found that stereo acuity measured with AO was related to an individual's interocular difference in their native, habitually experienced optics. Why would that be the case?

Perhaps over the long period of natural viewing the visual nervous system adapts to the optical profile unique to the individual. This neural adaptation to one's own optics would support "normal" vision, including stereopsis, under natural, everyday viewing (63), but in a manner specific to the aberrations present in the optics of each eye (27). However, would the visual system not have to adapt to constantly changing aberrations due to changes in pupil size and accommodation? Previous work has shown that such changes in aberrations are small; specifically, aberration patterns remain fairly constant, except for magnitude, when pupil size changes (29). Hence, viewing with AO correction could disrupt the previously stable relation between optical profile and the visual nervous system, with the degree of disruption presumably being greater for individuals with more pronounced aberrations. Indeed, this is just what we found for both visual acuity and stereopsis (Figs. 2*D* and 4*D*): People with poorer native optical quality also had poorer performance during AO correction. Also consistent with this conjecture is our finding that individuals tested

NEUROSCIENCE

while viewing with the optics of another person exhibited poorer stereo acuity even though the nonhabitual optics were similar to or even better than their own. This kind of adaptation to blur is not limited to the laboratory. In the eye clinic, it is a common practice not to prescribe full eyewear correction (e.g., for astigmatism) so as to avoid short-term visual discomfort.

We conclude that visual performance with improved but unfamiliar optics is affected by two opposing factors: 1) improvement brought about by better optics and 2) disrupted neural adaptation that counteracts the effect of optical improvement.

Implications for Neural Plasticity and Clinical Relevance. The visual circuitry underlying stereovision was traditionally thought to reach maturity during childhood, beyond which little plasticity remains (64, 65). However, there have been anecdotal instances of post-pubertal recovery: "Stereo Sue" (14) and, more recently, Bruce Bridgeman (66). Using more controlled training paradigms, stereoblind people can also recover stereovision to certain extents (67, 68), implying that the binocular system is more plastic than previously thought. We assume that people adapt because the optics changes gradually throughout the lifespan (69, 70), yet there appears to be a benefit when viewing with their own native state at the time of testing. We found that thresholds with AO correlate with interocular image-quality difference presumably due to long-term adaptation, but less so with the average image quality in the native optics. It is conceivable that the effects are even more substantial in participants with highly aberrated eyes such as those of patients with keratoconus. Keratoconus is a disease that causes an irregular corneal surface profile and emerges in otherwise normal-sighted individuals during the second or third decade of life. Their large aberrations are usually quite different in the two eyes. We observed that these patients, even with AO correction, have no or very poor stereopsis. Various advanced vision correction methods (71, 72) that provide supernormal vision are currently available or under development. It is of scientific and clinical interest to determine if normal binocular function can be recovered by having the visual system become readapted to the new, improved optics over time and, if so, how quickly this readaptation can occur.

Materials and Methods

Participants. Eight adults participated, including C.J.N. and G.Y. The gender, age, and eyewear prescription of each individual are provided in *SI Appendix*, Table S1. The participants had eye examinations within the past year and had normal vision while wearing their usual prescription, if any: 20/20 Snellen acuity or better and 40 arcsec stereo threshold or better (Randot stereo test). The human participants' protocol was approved by the University of Rochester Research Review Board. All participants signed an informed consent form before participating. Prior to testing, 1% tropicamide solution was administered to both eyes to produce short-duration mydriasis (pupil dilation) and cycloplegia (paralysis of accommodation).

Apparatus. The binocular AO system used in this study has been described in detail elsewhere (43). The apparatus can measure and completely correct and/or manipulate lower- and higher-order optical aberrations while visual performance is measured with images projected separately to the two eyes. The apparatus consists of two identical systems, one for each eye. Each has a Shack–Hartmann wavefront sensor that measures the eye's aberrations from the retinal reflections of a superluminescent diode at 850 nm (Inphenix Inc.). Each wavefront sensor communicates with a deformable mirror (DM-97-15; ALPAO) that controls the amount and type of optical aberration by conforming its shape to yield the desired wavefront for each eye in real time at 12 Hz.

Aberrations were corrected for 6-mm pupil diameters while the actual pupil sizes during testing were restricted to 5.8 mm using artificial apertures placed at the pupil-conjugate planes. Participants rested their heads on a chin rest and a pair of temple mounts. The rest and mounts were translated by a three-axis motorized stage to center both pupils as monitored by a pair of pupil cameras. The same pair of pupil cameras monitored eye movements throughout the experiments to make sure that the visual axes were always aligned to the optical axes of the system. Interpupillary distance was set for each participant using a translation stage. Left- and right-eye stimuli were projected on to the retinae by two digital light-processing projectors (DLPDLCR4710EVM-G2; Texas Instrument Inc.), one for each eye. The stimuli were 8.4° wide by 4.7° high, spanning 1,920 × 1,080 pixels. Each pixel subtended 0.26 arcmin. RMS wavefront errors as well as image quality during AO correction of individual eyes are provided in *SI Appendix*, Fig. S1.

Visual Acuity. Monocular visual acuity was measured with the Tumbling E task (73). The black letter E was presented for 250 ms in one of four orientations on a white background of 120 cd/m^2. Participants indicated the perceived orientation in a four-alternative, forced-choice (4-AFC) response (*SI Appendix*, Fig. S4*A*). Auditory feedback was provided for each correct response. Letter size in terms of stroke width ranged from 0.3 to 50 arcmin (Snellen 20/6 to 20/1,000) and was varied over a 40-trial sequence according to the QUEST+ adaptive staircase method (74). The procedure was repeated three times (120 trials total) to obtain the letter size associated with 72.4% correct using the best-fitting cumulative Weibull function and Bayesian estimation provided by QUEST+.

Stereo Acuity. Binocular stereo thresholds were measured using random-dot stereograms that portrayed a densely textured surface with disparity-defined sinusoidal depth corrugations (Figs. 1 and 3, *SI Appendix*, Fig. S4*B*, and ref. 33). We used such stimuli because they allow one to eliminate monocular cues and because blur significantly affects the ability to see the depth corrugation (75). A trial started with the presentation of a fixation target consisting of a small dot and four diagonal lines seen by both eyes, along with vertical and horizontal nonius lines seen by one or the other eye. The parts that were seen by both eyes aided accurate alignment of the eyes. The parts seen only by one eye or the other allowed the participant to assess the accuracy of alignment. When the fixation target was properly fused and aligned, it looked like one dot and eight lines. Once fusion was achieved, participants initiated stimulus presentation with a key press.

Each dot in the random-dot stereogram was a small bright square (83.5 × 83.5 arcsec) on an otherwise dark background. The dot pattern was generated by first populating a hexagonal grid at nodal points spaced 110 arcsec apart. Each dot was then randomly displaced from the nodal point with a direction drawn from a uniform distribution ranging from 0 to 2π and a distance from 0 to 55 arcsec. Dot density was 180 dots per degree^2 in a super-Gaussian window (W):

$$W = e^{\left(-\left(\frac{(x-x_0)^2}{2\cdot\sigma^2}+\frac{(y-y_0)^2}{2\cdot\sigma^2}\right)^P\right)}, \quad [1]$$

where $P = 5$ and $\sigma = 0.5°$. The values $[x_o, y_o]$ are nodal points and $[x, y]$ are horizontal and vertical screen coordinates. Edges of the circular window were blended into the background so that the only fusion cues were the random dots themselves.

Left and right images were created from the random-dot pattern by displacing each dot in opposite directions in the two eyes:

$$Disparity(x, y) = \frac{A}{2}\cos(2\pi f(y\cos\theta - x\sin\theta) + \phi), \quad [2]$$

where A, f, ϕ, and θ are the peak-to-trough disparity amplitude, spatial frequency, phase, and orientation of the disparity-defined sinusoidal corrugation, respectively. Thresholds (the smallest discriminable disparity) were measured for corrugation frequencies of 1, 2, and 3 cpd. The corrugation presented on each trial had a random phase between 0 and 2π and an orientation of either +10° (slightly anticlockwise) or −10° (slightly clockwise) from horizontal. Participants indicated which of the two orientations were presented on each trial, guessing if necessary (2-AFC). Each stimulus was displayed for a maximum of 10 s, but participants were instructed to respond as soon as they were confident of their judgment. Most responses were completed under 1 s. The disparity amplitude was varied from trial to trial according to the method of constant stimuli. Five amplitudes (determined for each person in pilot testing) were each presented 40 times for a total of 200 trials per condition. More trials with large disparities were sometimes added to obtain the full psychometric function. We did not present disparity amplitudes that exceeded the disparity-gradient limit (75, 76). Auditory feedback was provided when a correct response was made. Data for each corrugation frequency were fitted with a cumulative Weibull function using psignifit (77). Stereo thresholds were defined as disparity amplitudes that produced 81.6% correct responses. Individual psychometric functions are provided in *SI Appendix*, Fig. S5.

Retinal-Image Quality. The PSF represents how a point source of light is blurred by the eye's aberrations on the retina. PSFs were calculated for the left (PSF_{LE}) and right eyes (PSF_{RE}) of each participant when their lower-order (spherical and cylindrical) refractive errors were corrected (using clinically prescribed eyewear), but their higher-order aberrations were not. The resultant PSFs were a combination of the higher-order aberrations as well as any residual lower-order ones. We quantified retinal-image quality in the following ways. For the visual-acuity experiment, we first generated simulated retinal images by convolving a 20/20 Snellen E with the eye's PSF. We then correlated the obtained images with the original perfect images. Specifically, we calculated the two-dimensional cross-correlation and took the maximum to avoid image translations as being judged of lower quality (78). The metric values can range from −1 to +1, where +1 would mean perfect image quality, unadulterated by aberrations and diffraction limited, and −1 would indicate anticorrelated image quality. This process was repeated for all four orientations of the E used in the experiment. The average of the four coefficients was used as the image-quality value associated with the monocular acuity stimuli.

We used the same approach for the stereo experiment, but by convolving a random-dot pattern presented to an eye with the eye's PSF. We did this for 10 different instances of random-dot patterns. Left-eye image quality (ImQ_{LE}) is

$$ImQ_{LE} = \frac{\sum_{i=1}^{n} \max((PSF_{LE} * RDP_i) \star RDP_i)}{n}, \quad [3]$$

where RDP is the random-dot pattern, $n = 10$ represents the 10 instances of RDPs, $*$ is the two-dimensional (2D) convolution, $\star$ is the 2D cross-correlation, and $\max(\star)$ provides the maximum of the 2D cross-correlation matrix. Right-eye quality (ImQ_{RE}) was calculated the same way. Comparisons of the left- and right-eyes' image quality are shown in *SI Appendix*, Fig. S6.

We also calculated the average image quality (ImQ_{Mean}) defined as the mean of the two eyes' quality indices across the 10 presentation instances:

$$ImQ_{Mean} = \frac{ImQ_{LE} + ImQ_{RE}}{2}. \quad [4]$$

Finally, an index of the interocular difference in image quality (ImQ_{IOD}) was derived by cross-correlating the left and right retinal images and then subtracting the resultant from unity:

$$ImQ_{IOD} = \frac{1 - \sum_{i=1}^{n} \max((PSF_{LE} * RDP_i) \star (PSF_{RE} * RDP_i))}{n}. \quad [5]$$

In doing so, differences in the magnitude and patterns of blur between the eyes were incorporated.

Data Availability. Anonymized visual threshold and eye aberration data have been deposited in Zenodo at https://doi.org/10.5281/zenodo.4776439.

ACKNOWLEDGMENTS. We thank Gregory DeAngelis for helpful comments on the manuscript. This work was supported by NIH grants EY014999 and P30 EY001319 and funding from Research to Prevent Blindness.

1. J. Liang, D. R. Williams, Aberrations and retinal image quality of the normal human eye. *J. Opt. Soc. Am. A Opt. Image Sci. Vis.* **14**, 2873–2883 (1997).
2. M. J. Morgan, *Molyneux's Question: Vision, Touch and the Philosophy of Perception* (Cambridge University Press, ed. 1, 1977).
3. J. Liang, D. R. Williams, D. T. Miller, Supernormal vision and high-resolution retinal imaging through adaptive optics. *J. Opt. Soc. Am. A Opt. Image Sci. Vis.* **14**, 2884–2892 (1997).
4. S. Marcos *et al.*, Vision science and adaptive optics, the state of the field. *Vision Res.* **132**, 3–33 (2017).
5. G. Y. Yoon, D. R. Williams, Visual performance after correcting the monochromatic and chromatic aberrations of the eye. *J. Opt. Soc. Am. A Opt. Image Sci. Vis.* **19**, 266–275 (2002).
6. S. Marcos, L. Sawides, E. Gambra, C. Dorronsoro, Influence of adaptive-optics ocular aberration correction on visual acuity at different luminances and contrast polarities. *J. Vis.* **8**, 1.1–12 (2008).
7. P. Artal, S. Manzanera, P. Piers, H. Weeber, Visual effect of the combined correction of spherical and longitudinal chromatic aberrations. *Opt. Express* **18**, 1637–1648 (2010).
8. E. J. Fernández, P. M. Prieto, P. Artal, Binocular adaptive optics visual simulator. *Opt. Lett.* **34**, 2628–2630 (2009).
9. E. J. Fernández, P. M. Prieto, P. Artal, Adaptive optics binocular visual simulator to study stereopsis in the presence of aberrations. *J. Opt. Soc. Am. A Opt. Image Sci. Vis.* **27**, A48–A55 (2010).
10. B. G. Cumming, G. C. DeAngelis, The physiology of stereopsis. *Annu. Rev. Neurosci.* **24**, 203–238 (2001).
11. R. Blake, H. R. Wilson, Neural models of stereoscopic vision. *Trends Neurosci.* **14**, 445–452 (1991).
12. H. B. Barlow, C. Blakemore, J. D. Pettigrew, The neural mechanism of binocular depth discrimination. *J. Physiol.* **193**, 327–342 (1967).
13. C. Wheatstone, Contributions to the physiology of vision.—Part the first. On some remarkable, and hitherto unobserved, phenomena of binocular vision. *Philos. Trans. R. Soc. Lond.* **128**, 371–394 (1838).
14. S. R. Barry, *Fixing My Gaze: A Scientist's Journey into Seeing in Three Dimensions* (Basic Books, New York, 2009).
15. I. C. Wood, Stereopsis with spatially-degraded images. *Ophthalmic Physiol. Opt.* **3**, 337–340 (1983).
16. G. Westheimer, S. P. McKee, Stereoscopic acuity with defocused and spatially filtered retinal images. *J. Opt. Soc. Am.* **70**, 772–778 (1980).
17. N. V. Odell, S. R. Hatt, D. A. Leske, W. E. Adams, J. M. Holmes, The effect of induced monocular blur on measures of stereoacuity. *J. AAPOS* **13**, 136–141 (2009).
18. R. Nabie, D. Andalib, S. Amir-Aslanzadeh, H. Khojasteh, Effect of artificial anisometropia in dominant and nondominant eyes on stereoacuity. *Can. J. Ophthalmol.* **52**, 240–242 (2017).
19. C. Schor, T. Heckmann, Interocular differences in contrast and spatial frequency: Effects on stereopsis and fusion. *Vision Res.* **29**, 837–847 (1989).
20. E. J. Fernández, C. Schwarz, P. M. Prieto, S. Manzanera, P. Artal, Impact on stereo-acuity of two presbyopia correction approaches: Monovision and small aperture inlay. *Biomed. Opt. Express* **4**, 822–830 (2013).
21. B. J. Evans, Monovision: A review. *Ophthalmic Physiol. Opt.* **27**, 417–439 (2007).
22. C. Schwarz, S. Manzanera, P. M. Prieto, E. J. Fernández, P. Artal, Comparison of binocular through-focus visual acuity with monovision and a small aperture inlay. *Biomed. Opt. Express* **5**, 3355–3366 (2014).
23. J. Porter, A. Guirao, I. G. Cox, D. R. Williams, Monochromatic aberrations of the human eye in a large population. *J. Opt. Soc. Am. A Opt. Image Sci. Vis.* **18**, 1793–1803 (2001).
24. L. Sawides *et al.*, Dependence of subjective image focus on the magnitude and pattern of high order aberrations. *J. Vis.* **12**, 4 (2012).
25. R. Sabesan, G. Yoon, Neural compensation for long-term asymmetric optical blur to improve visual performance in keratoconic eyes. *Invest. Ophthalmol. Vis. Sci.* **51**, 3835–3839 (2010).
26. P. Artal *et al.*, Neural compensation for the eye's optical aberrations. *J. Vis.* **4**, 281–287 (2004).
27. E. Kompaniez, L. Sawides, S. Marcos, M. A. Webster, Adaptation to interocular differences in blur. *J. Vis.* **13**, 19 (2013).
28. B. N. S. Vlaskamp, G. Yoon, M. S. Banks, Human stereopsis is not limited by the optics of the well-focused eye. *J. Neurosci.* **31**, 9814–9818 (2011).
29. R. Sabesan, G. Yoon, Visual performance after correcting higher order aberrations in keratoconic eyes. *J. Vis.* **9**, 6.1–10 (2009).
30. P. K. Ahnelt, The photoreceptor mosaic. *Eye (Lond.)* **12**, 531–540 (1998).
31. J. B. Jonas, U. Schneider, G. O. Naumann, Count and density of human retinal photoreceptors. *Graefes Arch. Clin. Exp. Ophthalmol.* **230**, 505–510 (1992).
32. D. Kane, P. Guan, M. S. Banks, The limits of human stereopsis in space and time. *J. Neurosci.* **34**, 1397–1408 (2014).
33. C. W. Tyler, Depth perception in disparity gratings. *Nature* **251**, 140–142 (1974).
34. J. M. Bosten *et al.*, A population study of binocular function. *Vision Res.* **110**, 34–50 (2015).
35. D. H. Peterzell, I. Serrano-Pedraza, M. Widdall, J. C. A. Read, Thresholds for sine-wave corrugations defined by binocular disparity in random dot stereograms: Factor analysis of individual differences reveals two stereoscopic mechanisms tuned for spatial frequency. *Vision Res.* **141**, 127–135 (2017).
36. G. Westheimer, S. P. McKee, Stereogram design for testing local stereopsis. *Invest. Ophthalmol. Vis. Sci.* **19**, 802–809 (1980).
37. R. Sabesan, A. Barbot, G. Yoon, Enhanced neural function in highly aberrated eyes following perceptual learning with adaptive optics. *Vision Res.* **132**, 78–84 (2017).
38. E. A. Rossi, P. Weiser, J. Tarrant, A. Roorda, Visual performance in emmetropia and low myopia after correction of high-order aberrations. *J. Vis.* **7**, 14 (2007).
39. C. Schwarz *et al.*, Binocular visual acuity for the correction of spherical aberration in polychromatic and monochromatic light. *J. Vis.* **14**, 8 (2014).
40. F. W. Campbell, D. G. Green, Optical and retinal factors affecting visual resolution. *J. Physiol.* **181**, 576–593 (1965).
41. S. Li *et al.*, Effects of monochromatic aberration on visual acuity using adaptive optics. *Optom. Vis. Sci.* **86**, 868–874 (2009).
42. K. M. Rocha, L. Vabre, N. Chateau, R. R. Krueger, Enhanced visual acuity and image perception following correction of highly aberrated eyes using an adaptive optics visual simulator. *J. Refract. Surg.* **26**, 52–56 (2010).
43. R. Sabesan, L. Zheleznyak, G. Yoon, Binocular visual performance and summation after correcting higher order aberrations. *Biomed. Opt. Express* **3**, 3176–3189 (2012).
44. S. P. McKee, The spatial requirements for fine stereoacuity. *Vision Res.* **23**, 191–198 (1983).
45. S. B. Stevenson, L. K. Cormack, C. M. Schor, Hyperacuity, superresolution and gap resolution in human stereopsis. *Vision Res.* **29**, 1597–1605 (1989).
46. G. Westheimer, Editorial: Visual acuity and hyperacuity. *Invest. Ophthalmol.* **14**, 570–572 (1975).
47. G. Westheimer, Cooperative neural processes involved in stereoscopic acuity. *Exp. Brain Res.* **36**, 585–597 (1979).
48. J. Otero-Millan, S. L. Macknik, S. Martinez-Conde, Fixational eye movements and binocular vision. *Front. Integr. Nuerosci.* **8**, 52 (2014).
49. P. Mowforth, J. E. Mayhew, J. P. Frisby, Vergence eye movements made in response to spatial-frequency-filtered random-dot stereograms. *Perception* **10**, 299–304 (1981).

50. M. T. Ukwade, H. E. Bedell, R. S. Harwerth, Stereopsis is perturbed by vergence error. *Vision Res.* **43**, 181–193 (2003).
51. R. S. Harwerth, E. L. Smith III, J. Siderov, Behavioral studies of local stereopsis and disparity vergence in monkeys. *Vision Res.* **35**, 1755–1770 (1995).
52. N. Qian, S. Mikaelian, Relationship between phase and energy methods for disparity computation. *Neural Comput.* **12**, 279–292 (2000).
53. R. Blake, H. Wilson, Binocular vision. *Vision Res.* **51**, 754–770 (2011).
54. D. J. Fleet, H. Wagner, D. J. Heeger, Neural encoding of binocular disparity: Energy models, position shifts and phase shifts. *Vision Res.* **36**, 1839–1857 (1996).
55. J. S. Lappin, What is binocular disparity? *Front. Psychol.* **5**, 870 (2014).
56. I. Ohzawa, G. C. DeAngelis, R. D. Freeman, Stereoscopic depth discrimination in the visual cortex: Neurons ideally suited as disparity detectors. *Science* **249**, 1037–1041 (1990).
57. D. Y. Tsao, B. R. Conway, M. S. Livingstone, Receptive fields of disparity-tuned simple cells in macaque V1. *Neuron* **38**, 103–114 (2003).
58. J. S. Lappin, W. D. Craft, Definition and detection of binocular disparity. *Vision Res.* **37**, 2953–2974 (1997).
59. J. C. A. Read, B. G. Cumming, Sensors for impossible stimuli may solve the stereo correspondence problem. *Nat. Neurosci.* **10**, 1322–1328 (2007).
60. A. Barbot *et al*., Neural adaptation to optical aberrations through phase compensation. *J. Vis.* **20**, 1130 (2020).
61. A. Barbot *et al*., Functional reorganization of sensory processing following long-term adaptation to optical defects. *eLife* **10**, e58734 (2021).
62. A. K. C. Lam, A. S. Chau, W. Y. Lam, G. Y. Leung, B. S. Man, Effect of naturally occurring visual acuity differences between two eyes in stereoacuity. *Ophthalmic Physiol. Opt.* **16**, 189–195 (1996).
63. M. A. Webster, M. A. Georgeson, S. M. Webster, Neural adjustments to image blur. *Nat. Neurosci.* **5**, 839–840 (2002).
64. N. W. Daw, Critical periods and amblyopia. *Arch. Ophthalmol.* **116**, 502–505 (1998).
65. M. S. Banks, R. N. Aslin, R. D. Letson, Sensitive period for the development of human binocular vision. *Science* **190**, 675–677 (1975).
66. B. Bridgeman, Restoring adult stereopsis: A vision researcher's personal experience. *Optom. Vis. Sci.* **91**, e135-9 (2014).
67. J. Ding, D. M. Levi, Recovery of stereopsis through perceptual learning in human adults with abnormal binocular vision. *Proc. Natl. Acad. Sci. U.S.A.* **108**, E733–E741 (2011).
68. I. Vedamurthy *et al*., A dichoptic custom-made action video game as a treatment for adult amblyopia. *Vision Res.* **114**, 173–187 (2015).
69. H. V. Athaide, M. Campos, C. Costa, Study of ocular aberrations with age. *Arq. Bras. Oftalmol.* **72**, 617–621 (2009).
70. S. Amano *et al*., Age-related changes in corneal and ocular higher-order wavefront aberrations. *Am. J. Ophthalmol.* **137**, 988–992 (2004).
71. J. D. Marsack *et al*., Wavefront-guided scleral lens correction in keratoconus. *Optom. Vis. Sci.* **91**, 1221–1230 (2014).
72. R. Sabesan *et al*., Wavefront-guided scleral lens prosthetic device for keratoconus. *Optom. Vis. Sci.* **90**, 314–323 (2013).
73. J. E. Lovie-Kitchin, Validity and reliability of visual acuity measurements. *Ophthalmic Physiol. Opt.* **8**, 363–370 (1988).
74. A. B. Watson, QUEST+: A general multidimensional Bayesian adaptive psychometric method. *J. Vis.* **17**, 10 (2017).
75. M. S. Banks, S. Gepshtein, M. S. Landy, Why is spatial stereoresolution so low? *J. Neurosci.* **24**, 2077–2089 (2004).
76. P. Burt, B. Julesz, A disparity gradient limit for binocular fusion. *Science* **208**, 615–617 (1980).
77. F. A. Wichmann, N. J. Hill, The psychometric function: I. Fitting, sampling, and goodness of fit. *Percept. Psychophys.* **63**, 1293–1313 (2001).
78. L. Zheleznyak, M. J. Kim, S. MacRae, G. Yoon, Impact of corneal aberrations on through-focus image quality of presbyopia-correcting intraocular lenses using an adaptive optics bench system. *J. Cataract Refract. Surg.* **38**, 1724–1733 (2012).