

Suprathreshold Contrast Perception Is Altered by Long-term Adaptation to Habitual Optical Blur

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PURPOSE. To investigate whether visual experience with habitual blur alters the neural processing of suprathreshold contrast in emmetropic and highly aberrated eyes.

METHODS. A large stroke adaptive optics system was used to correct ocular aberrations. Contrast constancy was assessed psychophysically in emmetropic and keratoconic eyes using a contrast matching paradigm. Participants adjusted the contrasts of gratings at various spatial frequencies to match the contrast perception of a reference grating at 4 c/deg. Matching was done both with fully corrected and uncorrected ocular aberrations. Optical correction allowed keratoconus patients to perceive high spatial frequencies that they have not experienced for some time.

RESULTS. Emmetropic observers exhibited contrast constancy both with their native aberrations and when their aberrations were corrected. Keratoconus patients exhibited contrast constancy with their uncorrected, native optics but they did not exhibit constancy during adaptive optics correction. Instead, they exhibited striking underconstancy: they required more contrast at high spatial frequencies than the contrast of the 4-c/deg stimulus to make them seem to have the same contrast.

CONCLUSIONS. The presence of contrast constancy in emmetropes and keratoconus patients viewing with their native optics suggests that they have learned to amplify neural signals to offset the effects of habitual optical aberrations. The fact that underconstancy was observed in keratoconus patients when their optics were corrected suggests that they were unable to learn the appropriate neural amplification because they did not have experience with fine spatial detail. These results show that even adults can learn neural amplification to counteract the effects of their own optical aberrations.

Keywords: adaptation, contrast constancy, ocular optical aberrations, adaptive optics, keratoconus

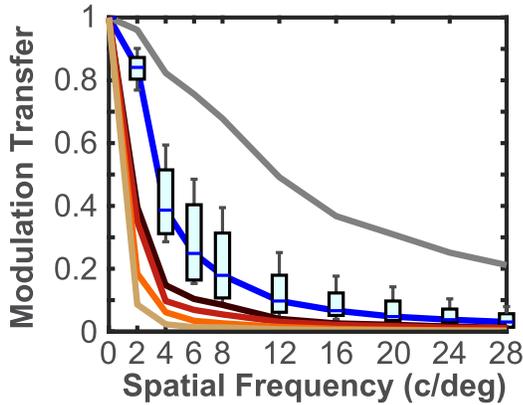
The optics of the human eye are imperfect. Like any optical device, wavefronts become aberrated in passing through the eye's light-transmitting structures. These aberrations cause significant blur in the retinal image and, therefore, limit the ability to see fine spatial detail. Advances in wavefront technology have made it possible to measure these aberrations accurately and to correct them so that observers can be presented retinal images that are sharper than they have ever experienced.

The blur caused by wavefront aberrations is quantified by the optical transfer function, which describes how different spatial frequencies are transmitted through the eye's optics. The modulation transfer function (MTF) (Fig. 1A) is derived from the optical transfer function; it describes the decrease in contrast that occurs frequency by frequency. As Figure 1A shows, the contrast of higher spatial frequencies is attenuated more than that of lower frequencies, and this phenomenon results in a loss of spatial detail. A person's

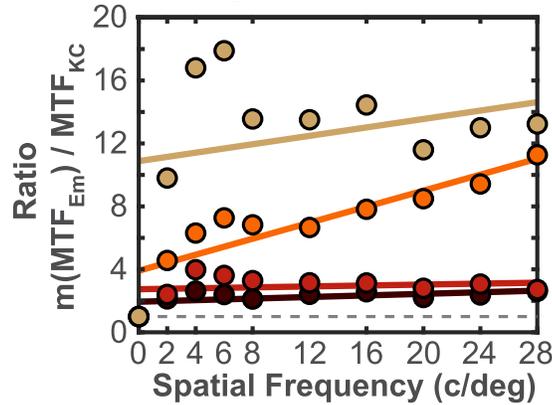
ability to perceive contrast at various frequencies is given by the contrast sensitivity function (CSF), which describes the amount of contrast required to detect a sinewave grating as a function of its spatial frequency. The shape of the CSF is determined in large part by the high-frequency attenuation caused by the eye's aberrations.¹⁻⁶

The CSF quantifies vision at threshold, but does not predict the appearance of high-contrast objects. The fact that the CSF is so widely used in clinical measures of vision is ironic, because the great majority of our visual experience is above the threshold. The distinction between contrast threshold and contrast appearance is illustrated by the phenomenon of contrast constancy. This phenomenon is observed when observers are asked to adjust the contrast of one spatial frequency to match the perceived contrast of another. When the contrasts are sufficiently greater than the threshold, observers report that the perceived contrasts are the same when the physical contrasts are

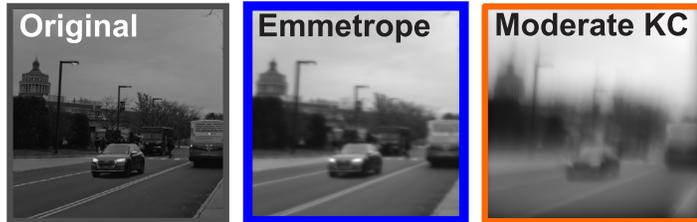
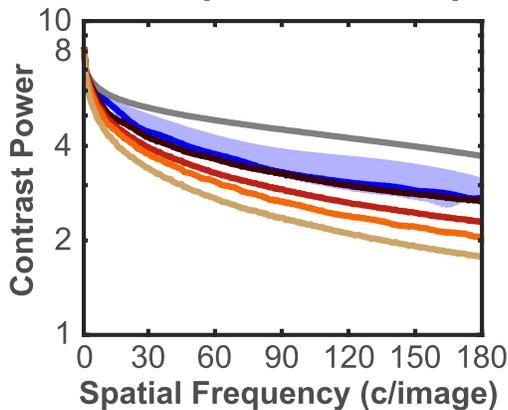
A Native Optics MTF



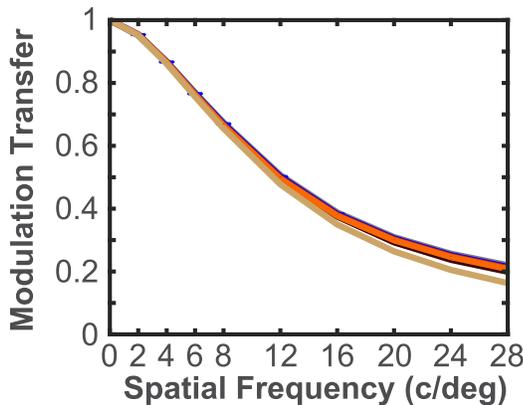
B Optical Degradation in Keratoconus



C Native Optics Power Spectra



D Corrected Optics MTF



E Corrected Optics Power Spectra

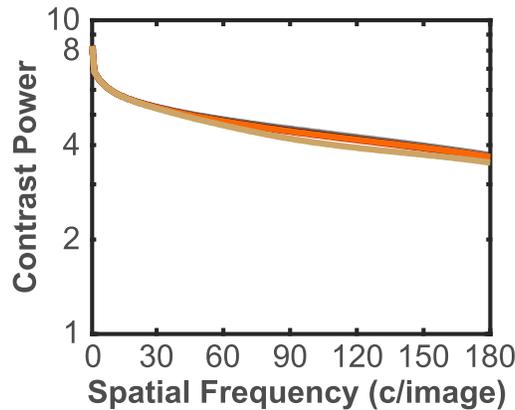


FIGURE 1. Retinal-image quality. (A) MTFs with native optical aberrations. The MTF of an eye with a 6-mm pupil and only limited by diffraction is represented by the *black curve*. The blue curve indicates the MTF (averaged across orientation) for the native optics of our four emmetropic participants. Boxes indicate the 25th and 75th percentiles. Error bars are the maximum and minimum values. The other curves are the MTFs for each keratoconus patient (Table); different colors represent different patients (see legend). (B) Optical degradation. We quantified optical degradation in each keratoconus patient by computing the ratio of the median emmetropic MTFs divided by the MTF of each keratoconus patient. Values greater than 1 indicate poorer quality in the keratoconus patient than in the median emmetrope. Best fits to those ratios are given by: $0.025sf + 1.94$ (mild keratoconus), $0.25sf + 3.91$ and $0.015sf + 2.74$ (moderate), and $0.13sf + 10.88$ (severe), where sf represents spatial frequency. (C) *Left*: Corresponding power spectra. One hundred randomly chosen images from the McGill image database²⁵ were convolved with the point spread functions (PSFs) of the participants to simulate their retinal images with native optics. The mean radially averaged power from the 100 images is plotted here. The *blue shaded area* represents the range across the emmetropic eyes. Other colors are the keratoconus patients (see legend). *Right*: Polychromatic simulations of the retinal images for a 6-mm pupil. (D) Radially averaged MTFs during adaptive optics correction. The improvement in the MTF during correction is given in Supplementary Figure S1. (E) Corresponding power spectra during adaptive optics correction, computed as in (C), except now using the PSFs during correction.

the same.⁷⁻¹³ This means that they report equal perceived contrast even when the retinal image contrasts are quite different. Contrast constancy—like size, shape, brightness, and color constancy—is a perceptual invariant that helps the viewer to experience the physical world less encumbered by variations in the retinal image.¹⁴ In particular, it helps one to perceive the contrast properties of an object as invariant, even when the object is viewed at different distances.⁷ For contrast constancy to occur, the neural representation of different spatial frequencies must somehow compensate for the frequency-dependent attenuation of contrast owing to the eye's optics (Fig. 1A). Specifically, the neural visual system must in effect amplify low retinal contrast at high spatial frequencies.⁸ For constancy to be accurate, the amplification must be the inverse of the attenuation owing to the optics. Presumably, this compensation function is learned through experience with one's own optics.

Keratoconus patients have unusually aberrated corneas, which causes an even greater attenuation of high frequencies (as shown in Fig. 1B) and spatial detail (Fig. 1C) than occurs in people with normal optics. Not surprisingly, people with keratoconus have poor visual acuity and even poorer contrast sensitivity.¹⁵⁻¹⁷ Interestingly, these people report that the world appears higher in contrast than expected from their severely attenuated retinal images. This finding suggests that keratoconus patients may also have developed an ability to compensate for contrast attenuation owing to the optics.¹⁸⁻²²

Here we use adaptive optics technology to investigate the appearance of suprathreshold contrast in observers with normal optics and in those with keratoconus. We do so when the observers view stimuli with their native optics and also when they view stimuli when their optics have been fully corrected, allowing them to see contrasts they have not experienced in a while (Fig. 1D and E; Supplementary Fig. S1). Our hypothesis is that the visual system learns from daily experience the frequency-dependent neural compensation required to offset the optical attenuation associated with one's native optics, and that this compensation enables contrast constancy. But we also hypothesize that this learning requires visible experience, which implies that keratoconus patients may not exhibit constancy when presented with the high spatial frequencies they have not experienced in some time.

METHODS

Participants

Four emmetropic individuals and four keratoconus patients participated. Keratometry readings from corneal topography maps were used to classify disease severity in the keratoconus patients according to the metric in the Collab-

orative Longitudinal Evaluation of Keratoconus (CLEK) study.²⁴ Of the four, one had mild, two had moderate, and one had severe disease. Corrections for lower order aberrations—spherical and cylindrical errors—were made using a phoropter and Badal system. With those corrections in place, the emmetropes' root mean square wavefront error over a 6-mm pupil was 0.16 to 0.55 μm with a median of 0.40 μm. The keratoconus patients' root mean square error was significantly higher and more variable, spanning 1.52 to 4.98 μm, with a median of 2.09 μm. The emmetropic and keratoconus errors were significantly different (one-tailed Wilcoxon rank-sum test: $Z = 26$; $P = 0.01$; details in the Table). Testing was done monocularly. Participants were treated with 1% tropicamide ophthalmic solution to paralyze accommodation and dilate the pupil during testing. The University of Rochester Institutional Review Board approved the protocol. Participants signed an informed consent form before beginning testing. All procedures followed the tenets of the Declaration of Helsinki.

Adaptive Optics

The adaptive optics system we used has been described in detail elsewhere.¹⁸ It consists of a custom Shack–Hartmann wavefront sensor and a large stroke deformable mirror (Imagine Eyes: Mirao-52, Orsay, France) suited for correcting large amounts of higher order aberrations such as those in keratoconus. Inexperienced participants were given practice sessions until they were familiar with the apparatus and procedure. All participants were carefully positioned with an adjustable bite bar at the beginning of each session. The stimuli were presented on a luminance-calibrated cathode-ray tube (MultiSync FP950; NEC, Irving, TX) that was optically conjugate to the retina. The circular visual field was 2° in diameter. Aberrations were corrected over a 6.5-mm pupil using the adaptive optics system while the participant viewed the stimuli through a 6-mm artificial pupil that was conjugate to the natural pupil. Participants blinked at their discretion. They were asked to monitor the retinal image quality continuously using the edges of the screen and to stop data collection if the quality degraded or became unstable.

Definitions of Contrast

It is important for the purposes of this article to distinguish three types of contrast. For all three we use the standard definition for contrast

$$c = \frac{L_{max} - L_{min}}{L_{max} + L_{min}},$$

where L_{max} is the highest luminance of the grating stimulus and L_{min} is the lowest. Space average luminance

TABLE. Participant Details

Participant	Age (Years)	Sex	Condition	Higher-Order Root Mean Square Wavefront Error (μm)
H1	25	Male	Emmetropic	0.31
H2	26	Male	Emmetropic	0.49
H3	27	Male	Emmetropic	0.55
H4	25	Male	Emmetropic	0.16
K1	39	Male	Mild keratoconus	1.52
K2	27	Male	Moderate keratoconus	1.72
K3	57	Female	Moderate keratoconus	2.47
K4	48	Male	Severe keratoconus	4.98

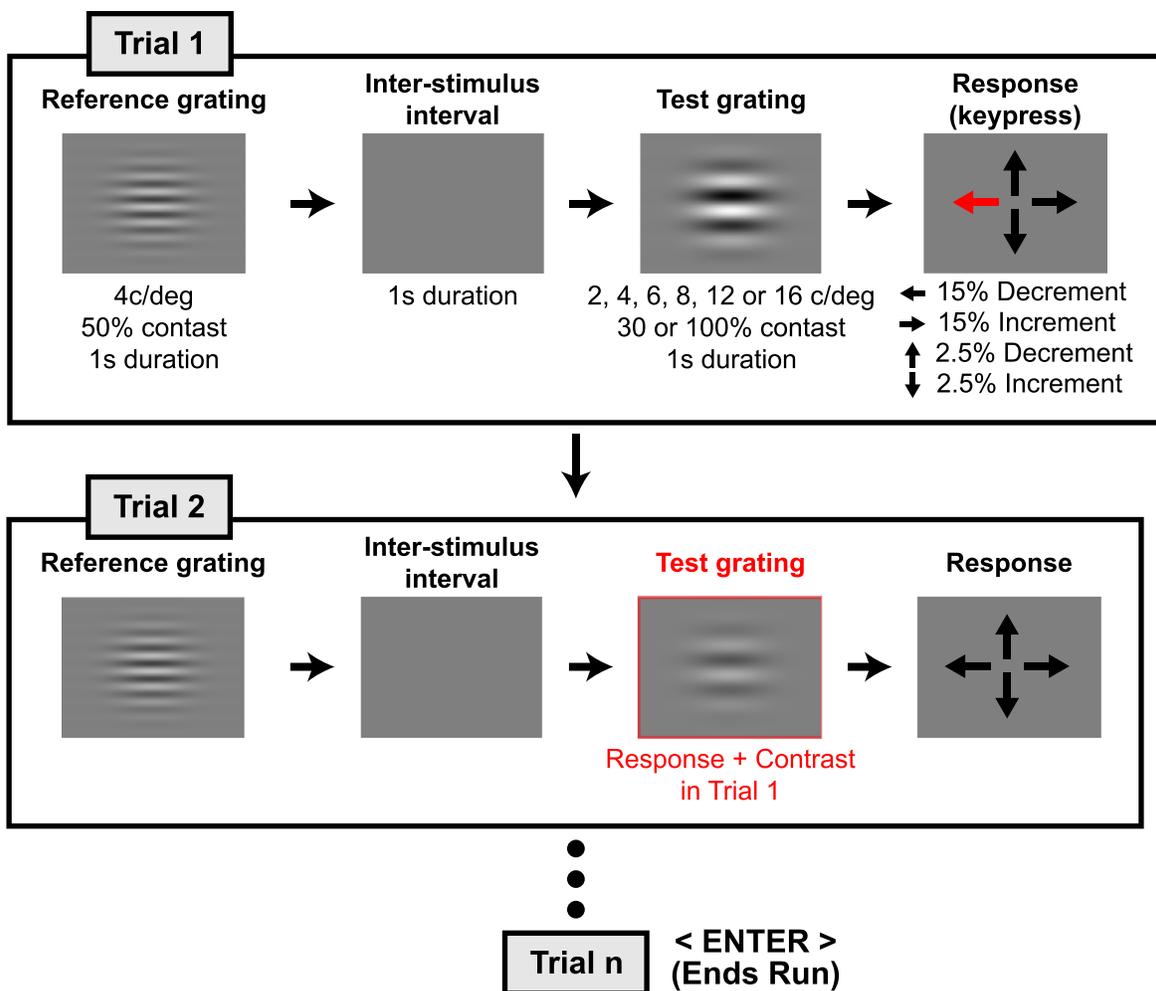


FIGURE 2. Contrast matching procedure. The upper and lower rows represent two consecutive trials. Each trial had three 1-s intervals: the reference grating, a blank interval, and the test grating. The reference grating was always 4 c/deg and 50% contrast. Test grating frequencies were 2 to 16 c/deg. After observing the reference and testing stimuli, the participant indicated with a keypress whether the test stimulus should be increased or decreased in contrast to make it have the same perceived contrast as the reference. They could request a large (15%) or small (2.5%) change. The next trial began immediately after the response was made. The process repeated until the observer indicated that the reference and test gratings had the same perceived contrast.

was always 10 cd/m². Displayed contrast is the contrast of the grating stimulus presented on the display screen. Retinal contrast is the contrast of the stimulus on the retina. Retinal contrast was always lower than displayed contrast owing to the eye’s aberrations (correctable by adaptive optics) and diffraction (not correctable by adaptive optics). Perceived contrast is the participant’s subjective experience of the contrast of the grating stimulus.

Procedure

Suprathreshold contrast perception was measured in the emmetropic and keratoconus eyes with and without adaptive optics correction. When measured with their native optics (i.e., no correction for higher order aberrations), participants viewed stimuli with the appropriate spherical and cylindrical refractive error correction. Keratoconus causes significant higher order aberrations, in particular, vertical coma, which primarily affects resolution

along the vertical meridian of the retinal image. Hence, we used horizontal grating stimuli because they coincided with the blurriest meridian in the keratoconus eyes.

Participants adjusted the displayed contrast of a test grating to match the perceived contrast of a 4-c/deg reference grating with a displayed contrast of 50%. This adjustment was done using a hybrid method that combines a four-alternative forced-choice procedure and a method of adjustment (Fig. 2). Trials consisted of a 1-second presentation of the reference grating, followed by a 1s blank interval with the same average luminance, followed by a 1-second presentation of the test grating. The displayed contrast of the test grating was initially 30% or 100%. After the test grating was extinguished, the observer made one of four responses: to decrease the contrast of the test grating by 15% or 2.5% or to increase it by 15% or 2.5%. The test grating’s contrast was then adjusted accordingly for the next trial. Adjustments that would have brought the contrast below 0% or above 100% were clamped at those values. Trials continued until

the observer terminated the run because the reference and test contrasts appeared to be the same. The matched contrast on the last trial before termination was recorded.

Test gratings were 2, 4, 6, 8, 12, or 16 c/deg; grating phases were randomized across trials. Adjustments from at least four runs per test spatial frequency were averaged to obtain the point of subjective equality; that is, the displayed contrast at which the test grating appears to be the same as the reference grating.

RESULTS

Perceived Contrast With Native Optics

We first examined suprathreshold contrast perception in the emmetropes when they were viewing with their native optics. Figure 3A shows the results. The panels plot the displayed contrast of the test grating as a function of its spatial frequency for each emmetrope. The upper panel shows what one predicts if observers reported equal perceived contrast when the retinal contrasts of the reference and test gratings were the same. Because optical attenuation is greater at high spatial frequencies than at 4 c/deg, observers would have to set displayed contrast at 6 and 8 c/deg to more than 50% to match the retinal contrast of 4 c/deg at 50% displayed contrast. They would also have to set displayed contrast at 2 c/deg to less than 50% because modulation transfer is greater at 2 than at 4 c/deg. The lower panels show the actual data. As can be seen, emmetropic observers reported equal perceived contrast when the displayed contrasts, not the retinal contrasts, were the same. The differences between the displayed contrast of the reference grating and the contrast setting for the test gratings were not statistically significant (Wilcoxon rank-sum test, $Z = 272$; $P = 0.75$). Thus, they exhibited contrast constancy when viewing with their native, aberrated optics. This is, of course, what one expects from previous work.⁷⁻¹³ We did not make measurements for test frequencies of greater than 8 c/deg because the observers had difficulty seeing higher frequencies clearly with their dilated pupils.

We next examined contrast matching in the keratoconus patients when they viewed with their native, aberrated optics. Figure 3B shows the results. Again, the upper panel plots what one would predict if the perceived contrasts were the same when the retinal contrasts of the test and reference gratings were equal. The lower panels plot the results. As with the emmetropic observers, the patients reported equal perceived contrast when the displayed contrasts of the reference and test were the same. The differences between those contrasts were not statistically significant (Wilcoxon rank-sum test, $Z = 174$; $P = 0.15$). Thus, the keratoconus patients also exhibited contrast constancy at least for the test frequencies we presented. We did not present higher frequencies because the patients could not see such fine patterns owing to their highly aberrated optics. In fact, the 8 c/deg gratings were not even visible to three of the four patients; 6 c/deg was also invisible to one patient.

It is remarkable that, just like emmetropic observers, the keratoconus patients exhibited contrast constancy even though the retinal contrasts they experienced were much lower than the ones experienced by the emmetropes. This finding is consistent with personal feedback from the keratoconus patients that they perceive higher contrast than expected from simulations of their retinal images.

Perceived Contrast With Corrected Optics

We next examined contrast matching in emmetropic and keratoconus observers when their aberrations were corrected with adaptive optics. Because the optics were fully corrected, retinal image quality was the same across observers, so any differences in matching had to be caused by differences in neural processing.

Figure 4 shows the results with optical correction in the same format as Figure 3. Figure 4A shows the results for the emmetropes and Figure 4B the results for the keratoconus patients. In both cases, the upper panels plot the predicted results if observers equated the retinal contrasts of the test and reference gratings, and the lower panels show the actual data. We note that the adaptive optics correction increased the retinal contrast associated with a given displayed contrast for both the reference grating (4 c/deg) and the test gratings (various spatial frequencies); one can see this by comparing the native MTFs in Figure 1A to the corrected MTFs in Figure 1D. Indeed, the adaptive optics correction made some higher frequencies (12 and 16 c/deg) much more visible to emmetropes than before. Of course, the correction had an even greater effect on the keratoconus patients (Fig. 1 and Supplementary Fig. S1): it made previously invisible gratings (8–16 c/deg) now visible.

The upper panels of Figure 4A show predictions for the emmetropes if they matched retinal contrasts. The lower panels show the data and make clear that these observers matched according to displayed contrast, not retinal contrast. That is, they still exhibited contrast constancy despite the correction of their optical aberrations. This is an interesting and somewhat puzzling finding that we explore further in the Discussion.

The upper panels of Figure 4B show the predictions for the keratoconus patients if they perceived equal contrast when the retinal contrasts were the same. The lower panels show the contrast-matching results. The keratoconus patients clearly did not exhibit contrast constancy when their aberrated optics were corrected, Kruskal–Wallis test, $H(6) = 12.36$, $P = 0.05$. Instead they perceived equal contrast when the retinal contrasts were the same, which is indicated by the similarity between the upper and lower panels. The keratoconus patients exhibited underconstancy at spatial frequencies of greater than 8 c/deg because they had to set the displayed contrast to values greater than the 50% displayed contrast of the 4 c/deg reference grating. Thus, the keratoconus patients exhibited strikingly different behavior than the emmetropes with corrected optics.

It is interesting to note that the degree to which the keratoconus patients exhibited contrast constancy is correlated with the severity of their disease. Specifically, the patient with mild disease (K1) made settings that were approximately contrast constant from 2 to 16 c/deg while the patients with moderate or severe disease did not make such settings.

It is also interesting to note that in previous reports the correction of an optical aberration produced over- rather than underconstancy. For example, Georgeson and Sullivan (1975)⁸ asked an uncorrected astigmat to match the perceived contrasts of gratings aligned with his sharp and blurred meridians. They observed contrast constancy, which means that the subject had compensated for the astigmatic blur. When they corrected the astigmatism, the subject experienced greater contrast in the previously blurred meridian and, therefore, decreased its contrast to match that of the

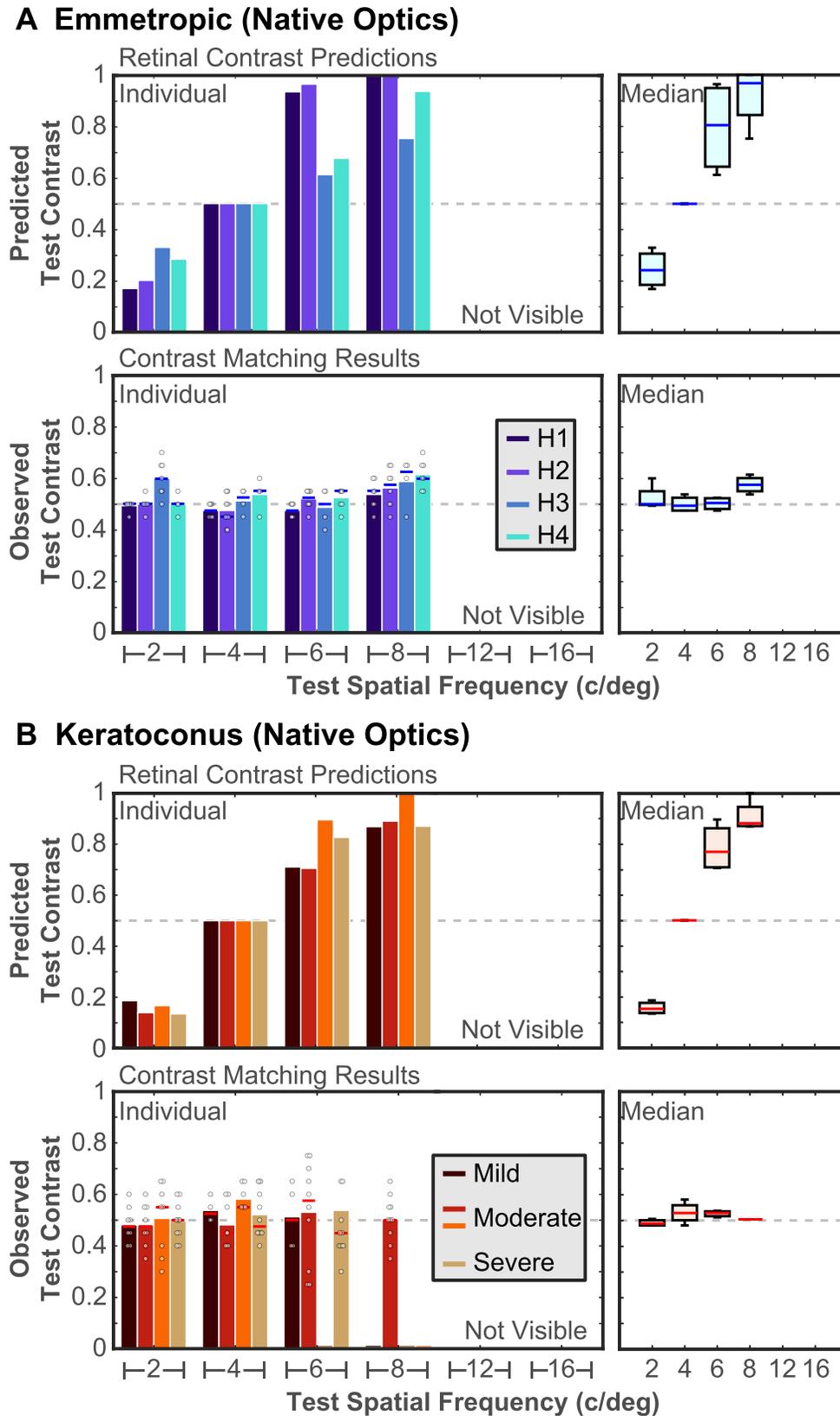


FIGURE 3. Contrast matching in emmetropic and keratoconus observers when viewing with native optics. **(A)** For the emmetropes. **(B)** For the keratoconus patients. **(A) Top left panel:** Displayed contrast for the test grating required to produce the same retinal contrast as the reference grating plotted as a function of test frequency for each observer. Individual observers are represented by different colors. The predictions are calculated by the formula $(0.5 \times MTF(4))/MTF(s_{f_{test}})$, where 0.5 represents the displayed contrast (indicated by the horizontal dashed line) and $MTF(4)$ the modulation transfer of the 4 c/deg reference grating; $MTF(s_{f_{test}})$ is the modulation transfer at each

test frequency. *Bottom left panel:* Contrast matching data for the emmetropes. The displayed contrast of the test grating that appeared to have the same perceived contrast as the reference grating is plotted as a function of test spatial frequency. Different color bars represent the average contrast settings for different observers. Medians are the *blue lines*. *Small circles* represent settings for each run. The gray horizontal *dashed line* is 50% contrast, the expected setting if contrast constancy occurred. *Right panels:* Corresponding summary statistics. Lines within each box are the median settings across observers. The tops and bottoms of the boxes are the 25th and 75th percentiles. Error bars are the maximum and minimum settings. **(B)** The same plots as in **(A)**, but for the keratoconus patients. The displayed contrast theoretically needed for a retinal match at 8 c/deg exceeded 1 in the emmetropes H1 and H2, as well as the moderate keratoconus patient, K3. We clamped those values to 1.

sharp meridian. In this case, optical correction of a long-standing aberration produced overconstancy. Likewise, Fine et al.²⁵ also reported contrast overconstancy after removing congenital cataracts in an adult. In the Discussion, we examine the issue of why optical correction in our study produced underconstancy while correction in previous studies produced the opposite: overconstancy.

Neural Amplification

To achieve contrast constancy across a range of spatial frequencies, the visual system has to, in effect, undo the frequency-dependent attenuation owing to the eye's optics. One can think of this in terms of neural transducer functions that convert an input signal of one strength to an output signal of another. Our data cannot inform us about the shape of such a transducer at individual spatial frequencies, but they can inform us about the relative gains across spatial frequencies. We quantified this differential gain across frequencies with what we call the neural amplification factor.

The retinal contrast for a given spatial frequency and displayed contrast is the product of the displayed contrast and the modulation transfer at that frequency:

$$C_{retinal}(sf) = C_{displayed}(sf) \times MTF(sf), \quad (1)$$

where $C_{retinal}$ and $C_{displayed}$ are the retinal and displayed contrasts at spatial frequency sf and $MTF(sf)$ is the modulation transfer at that frequency. In our case, the reference grating was 4 c/deg with a contrast of 0.5, so the retinal contrast of the reference grating is:

$$C_{retinal}(4) = 0.5 \times MTF(4). \quad (2)$$

Similarly, the retinal contrast of the test grating is:

$$C_{retinal}(sf_{test}) = C_{displayed}(sf_{test}) \times MTF(sf_{test}), \quad (3)$$

Where the sf_{test} is 2, 4, 6, 8, 12, or 16 c/deg.

In our contrast-matching experiment, the observer sets the displayed contrast of the test grating $C_{displayed}(sf_{test})$ to match the perceived contrast of the reference grating. We took the value of $C_{displayed}(sf_{test})$ to be the average setting of all runs per spatial frequency (height of the colored bars in the lower panels of Figs. 3 and 4).

The neural amplification factor is the ratio of the two retinal contrasts from Equations 2 and 3 that produce the same perceived contrast:

$$Neural\ amplification\ factor = \frac{C_{retinal}(4)}{C_{retinal}(sf_{test})}. \quad (5)$$

If observers equated the retinal contrasts, Equations 2 and 3 will have the same value:

$$C_{retinal}(sf_{test}) = C_{retinal}(4). \quad (6)$$

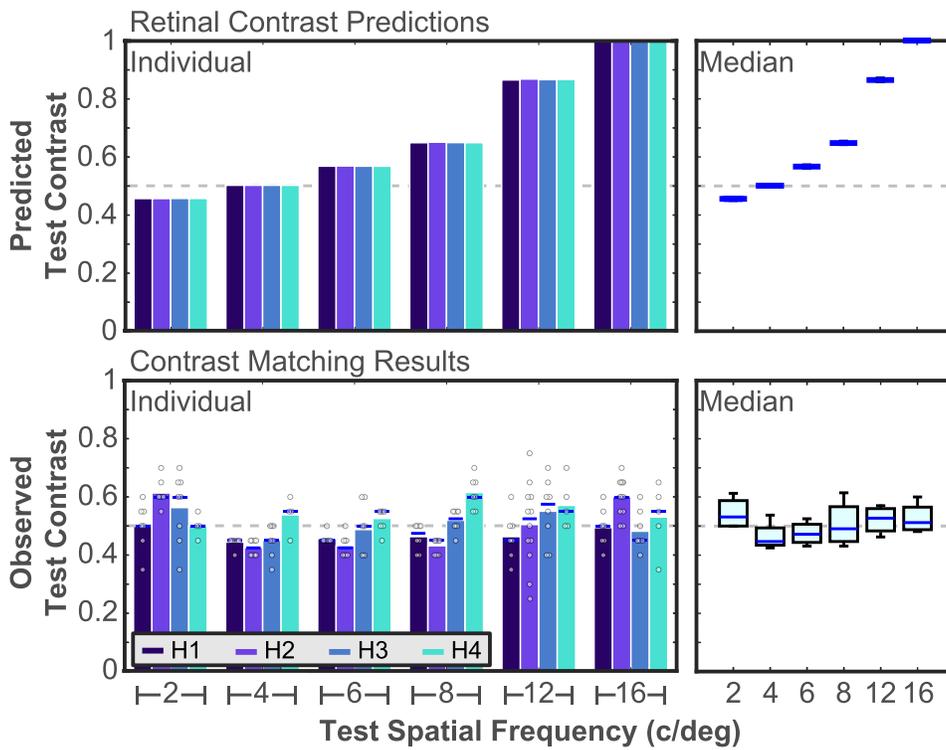
Rearranging:

$$\frac{C_{retinal}(4)}{C_{retinal}(sf_{test})} = 1. \quad (7)$$

The neural amplification factor will be 1 when observers match retinal contrasts. If the retinal contrasts are different, observers could only perceive them as the same if the contrast of the test grating were neurally modified relative to the transduction of the reference grating. The neural amplification factor would be greater than 1 when the retinal contrast of the test stimulus is lower than that of the reference (i.e., the test stimulus has to be relatively amplified). This is needed to achieve contrast constancy at 6 to 16 c/deg compared with 4 c/deg. Likewise, when the retinal contrast of the test is greater than that of the reference, the test should have less amplification than the reference; the amplification factor would, therefore, be less than 1. Thus, the neural amplification factor at matching represents the relative neural gains required to transform contrasts at the retina into equal perceived contrasts.

We calculated neural amplification factors from the matches observers made in our experiment (lower panels of Figs. 3 and 4). The amplification factors are plotted in Figure 5. The factors expected for perfect constancy are provided in Supplementary Figure S2. The empirical amplification factors were very similar to the theoretically perfect ones for the emmetropes with native and corrected optics and the keratoconus patients with native optics. The empirical factors make clear that the emmetropes, whether viewing with native or corrected optics, neurally amplified retinal contrasts at 6 to 16 c/deg to make the displayed contrasts appear equal (Figs. 5A and C). Said another way, they had to amplify high-frequency signals relative to midfrequency signals to achieve contrast constancy. The empirical factors also make clear that the keratoconus patients viewing with native optics neurally amplified at 6 to 8 c/deg to create equal perceived contrast with 4 c/deg (Fig. 5B). And this too enabled contrast constancy. For the keratoconus patients to achieve constancy is, as stated elsewhere in this article, remarkable because the retinal contrasts in their eyes were much lower than in individuals with normal optics. It is further important to note that when their optics were corrected the patients did not apply such amplification at higher frequencies (Fig. 5D and Supplementary Fig. S2B), so they did not exhibit contrast constancy. Rather they perceived equal contrast when the contrasts in the retinal image were the same.

A Emmetropic (Corrected Optics)



B Keratoconus (Corrected Optics)

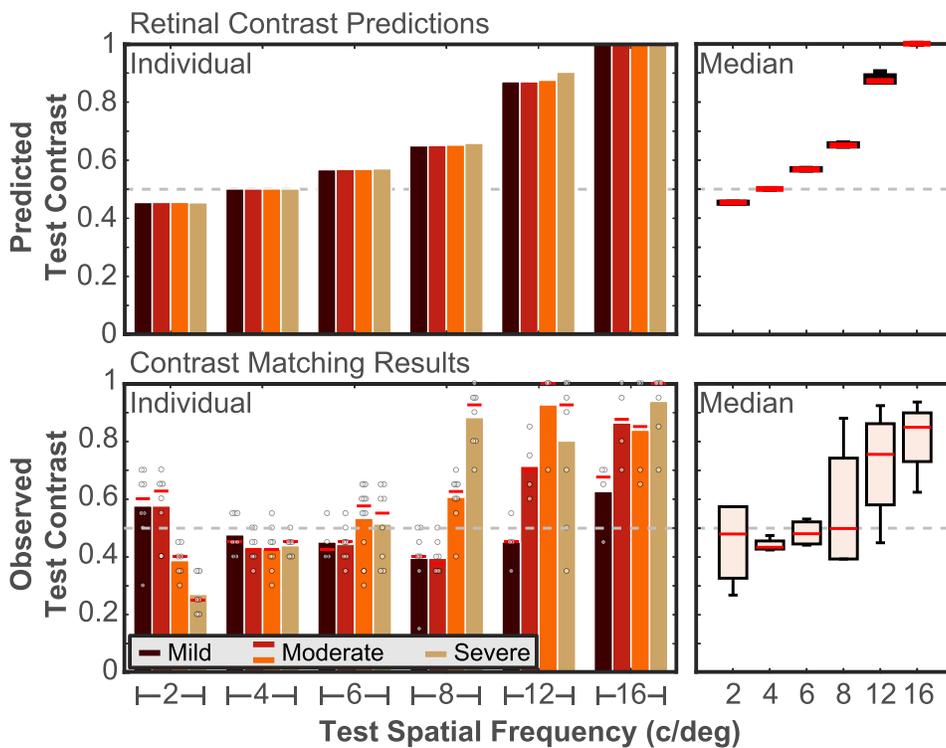


FIGURE 4. Contrast matching in emmetropic and keratoconus observers with adaptive optics correction. **(A)** For emmetropes. **(B)** For keratoconus patients. **(A) Top left panel:** Displayed contrast for the test grating required to produce the same retinal contrast as the reference grating plotted as a function of test frequency for each observer. The predictions were calculated with the same formula in Figure 3. Different colors represent different observers. **Bottom left panel:** Contrast matching data for the emmetropes. The displayed contrast of the test that had the same perceived contrast as the reference is plotted as a function of test frequency. Different colors represent average values for

different observers. Small circles are settings for each run, and blue lines are the medians. *Right panels:* Corresponding summary data. Lines within each box are the median settings across observers. Tops and bottoms indicate the 25th and 75th percentiles. Error bars are maximum and minimum settings. **(B)** The same plots as in **(A)**, but for the keratoconus patients. All observers needed theoretical displayed contrasts above 1 to make retinal matches at 16 c/deg. These values were clamped to 1.

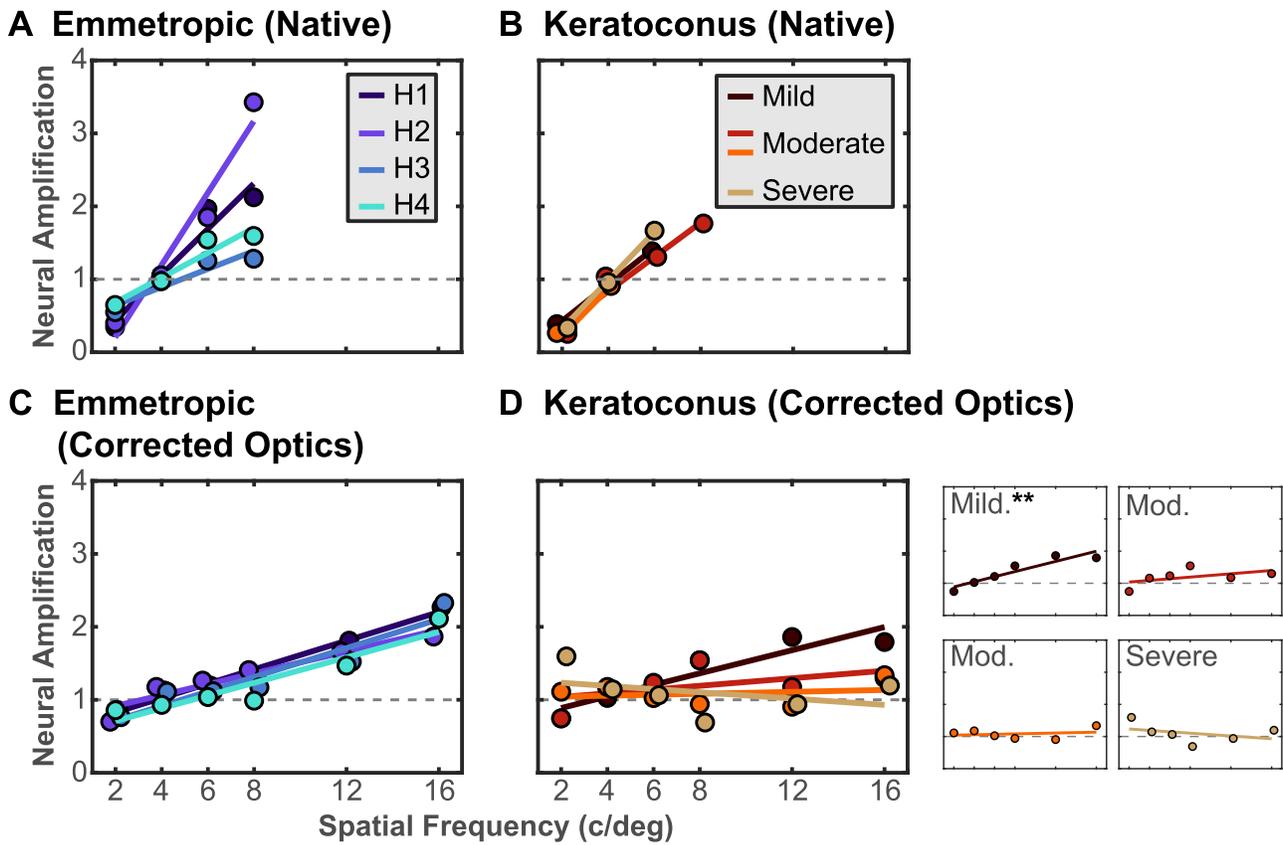


FIGURE 5. Neural amplification. The neural amplification factor is the ratio of the retinal contrast of the reference grating divided by the retinal contrast of the matching test grating at each spatial frequency. A factor of 1 means that observers reported equal perceived contrast when the retinal contrasts were equal to one another. Factors greater than 1 mean that the retinal contrast of the test grating was amplified relative to the reference grating. Factors less than 1 mean that the reference grating was amplified more than the test. **(A, B)** Neural amplification in the emmetropic participants **(A)** and keratoconus patients **(B)** with their native optics. These factors were calculated from matching data in the lower panels of **Figures 3A** and **B**. Individuals are indicated by different colors. **(C, D)** Neural amplification in the emmetropic **(C)** and keratoconus patients **(D)** with corrected optics. In this case, the matching data are from the lower panels of **Figures 4A** and **B**. The small panels to the right in **(D)** show the neural amplification factors separately for each keratoconus patient in order of disease severity. Only the patient with the mildest disease had amplification factors that were positively correlated with spatial frequency (**Pearson's $r = 0.93$; $P < 0.01$) like the emmetropes. The other patients did not amplify the high spatial frequencies (Pearson's $r = 0.52$; 0.21 , and -0.38 ; $P = 0.30$, 0.68 , and 0.46 , respectively).

We reiterate that the adaptive optics correction of the emmetropes and keratoconus patients made their retinal image contrasts very similar. So, the fact that they behaved so differently under the corrected condition means that the neural processing of contrast is very different in these two populations.

DISCUSSION

A key question in perceptual science is how invariant perceptions are achieved from varying inputs: that is, how do we identify and locate common objects reliably despite variations in their distance, orientation, slant, illumination,

and other factors that confound the retinal image? Contrast constancy is a clear example of a useful invariant, and here is why. If a common object like a face is viewed at close distance, lower spatial frequencies represent the structural features required for identification. The MTF has values close to 1 at those frequencies, so the contrasts of those features are represented faithfully in the retinal image. However, when the distance to the object increases, the frequencies associated with those same features increase and encroach upon the high-frequency falloff of the MTF. This means that their relative retinal image contrasts will change, perhaps dramatically, making the same object now more difficult to recognize. The phenomenon of contrast constancy demonstrates that the visual system compensates for the differences

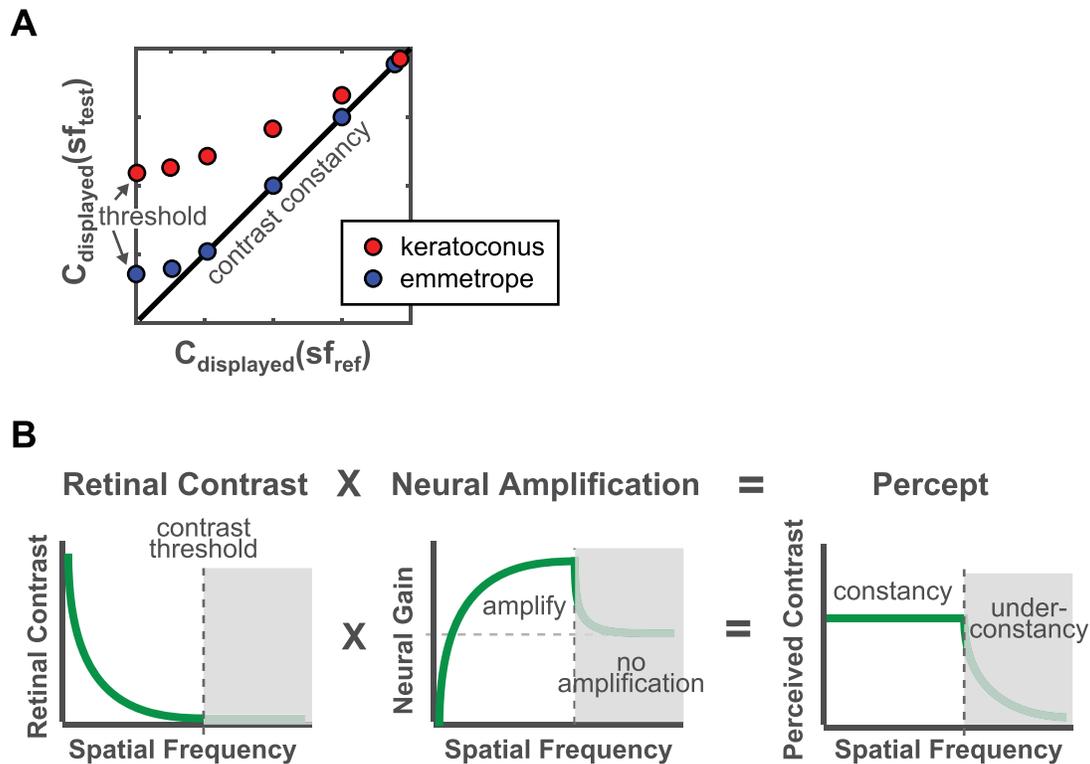


FIGURE 6. Schematic diagram modeling constancy. **(A)** Contrast threshold and contrast constancy. The displayed contrasts of test gratings that have the same perceived contrast as the reference grating is plotted against the displayed contrast of the reference grating. Here the spatial frequency of the test grating is greater than the frequency of the reference. The *black diagonal line* represents contrast constancy, where observers perceive the displayed contrasts of the reference and test as equal. The *left end* of the abscissa represents contrast threshold for the reference grating. The *red and blue circles* on the ordinate represent thresholds for the test grating. *Blue* is for an emmetrope with normal optics and *red* for a keratoconus patient with highly aberrated optics. Threshold is much higher for the patient. The transition from threshold to constancy is represented by the other data points. The displayed contrast of the reference must be greater for the keratoconus patient than for the emmetrope before contrast constancy is observed. **(B)** Spatial frequency-dependent amplification. The neural amplification function is modeled as a nonlinear transducer function. Constancy is achieved when the amplification is sufficient to compensate for contrast attenuation owing to the MTF. This occurs for frequencies that are visible. No amplification occurs for frequencies that are not visible. When the previous invisible frequencies become visible, the transducer does not compensate for attenuation owing to the optics and observers begin to match according to retinal contrast instead (*grey box*).

in relative retinal image contrasts. Contrast constancy enables the perceived contrasts of the same object features to remain the same despite changes in object distance.

We examined suprathreshold contrast perception in people with normal optics (emmetropes) and in those with highly aberrated optics (keratoconus patients). We first discuss the results with the patients.

We found, rather remarkably, that keratoconus patients, when viewing with their native highly aberrated optics, exhibit contrast constancy over the relatively small range of spatial frequencies they can normally see. Keratoconus usually begins in early adulthood and progresses over time.²⁶ Therefore, these patients must have learned the neural amplification needed to offset the severe optical degradation they experienced as the disease progressed. The fact that they must have learned it during adulthood implies that this form of perceptual learning persists well beyond childhood. Very interestingly, the keratoconus patients behaved quite differently when their optical aberrations were corrected with adaptive optics. They were now able to perceive higher spatial frequencies for the first time in perhaps years. When asked to match the

perceived contrast of those newly experienced frequencies, they reported equal contrasts when the retinal contrasts were the same. This is a clear failure of contrast constancy. They instead exhibited underconstancy. This behavior is sensible. The patients were unable to learn the needed compensation for high spatial frequencies because they had not experienced those frequencies in quite some time. So, they defaulted to applying no relative amplification, which led them to report that equal retinal contrasts are perceptually equal. The important implication of this finding is that fine detail content must be experienced to enable learning of the appropriate neural amplification.

We also note that the contrast thresholds of these patients could have affected their contrast-matching behavior. Previous work has shown that keratoconus patients have higher contrast thresholds (i.e., lower contrast sensitivity) than emmetropic observers at mid to high spatial frequencies, even when their optical aberrations are corrected.^{20–22,27} The difference in contrast threshold is due to greater internal noise.^{20,21} Higher thresholds should affect contrast matching and [Figure 6A](#) explains why. The abscissa is the displayed contrast of a reference grating at 4 c/deg. The ordinate is

the displayed contrast of a high-frequency test grating that appears to have the same contrast as the reference grating. If a person exhibited contrast constancy, the data would lie along the black diagonal line. As one considers lower and lower contrasts of the reference grating, there will be some contrast that is just at threshold. That contrast is represented by the left end of the abscissa. The contrast threshold of the test stimulus is higher in keratoconus patients (red circle on the ordinate) than in emmetropes (blue circle). We know from previous theoretical and empirical work that neural amplification of a retinal response should not occur if the response is mostly due to noise.^{28–30} Such amplification would adversely affect the signal-to-noise ratio in subsequent neural processing.³¹ Instead, one should only amplify once there is evidence that the response is a reliable signal, thereby maintaining an adequate signal-to-noise ratio. In the figure, we see that the visual system transitions from no amplification at threshold to full amplification across a range of contrasts, which helps to maintain a reasonable signal-to-noise ratio (also see Fig. 3 in Georgeson and Sullivan, 1975⁸). This transition is more difficult to achieve with higher thresholds (more points between the red and black lines than between the blue and black lines). We conclude that part of the reason keratoconus patients failed to achieve contrast constancy at high spatial frequencies when their optics were corrected is because of their elevated contrast thresholds at those frequencies.

As stated elsewhere in this article, contrast constancy requires neural amplification to vary as a function of spatial frequency. Figure 6B illustrates this schematically. The left panel shows the decrease in retinal contrast as a function of frequency owing to the habitual optics. The gray zone represents the range of spatial frequencies that are not visible, being below or at the noise floor owing to optical attenuation, low neural sensitivity, or both. The middle panel shows the amplification required for each frequency to compensate for the optical attenuation. Amplification does not occur for spatial frequencies in the gray zone because the contrast signal is not strong enough in that range. The right panel shows the perceptual result: contrast constancy for visible frequencies and underconstancy for routinely invisible frequencies.

It would be intriguing to investigate if keratoconus patients could learn a new set of neural amplifications if they were given a permanent correction for their aberrated optics. One can do this with scleral contact lenses. We intend to fit to these patients with such lenses to enable long-term optical correction. We will then track their contrast-matching behavior to see if they can learn a new set of neural amplifications and thereby achieve contrast constancy with corrected optics. It would be particularly interesting to see what happens, after they have achieved constancy with their contact lenses in place, if we then gave them an adaptive optics correction to yield even better image quality than the lenses provide. They presumably would have had the experience to kickstart neural amplification at high spatial frequencies but not quite as good as the emmetropes. The adaptive optics correction would provide much better retinal contrasts, so we predict overconstancy during adaptive optics correction (Georgeson and Sullivan⁸ and Fine et al.²⁵).

We also examined suprathreshold contrast perception in emmetropes who have normal optical aberrations. We found that they exhibited contrast constancy when viewing stimuli with their native optics. This finding is, of course, a confirmation of previous observations.^{7–13} We then applied

adaptive optics to fully correct their optical aberrations. This changed their MTFs and therefore changed the mapping between contrasts in the world and contrasts in the retinal image. Despite the change, they again exhibited contrast constancy. To do so, they had to apply a different neural amplification factor than they did when their optics were not corrected (Fig. 5 and Supplementary Results). It is somewhat surprising that they could do this because it is not clear how they would have known to apply a different amplification factor when the optical correction was in place compared to when the correction was not in place. And how would they have known which amplification factor to apply even if they figured out that the adaptive optics correction was in place? These are difficult questions because the stimuli were sinewave gratings and with such single-frequency stimuli one cannot distinguish a change in retinal contrast versus a change in displayed contrast. We speculate that the emmetropic observers' visual system might have figured out the optical condition from viewing the spectrum of the fixation point at the outset of the experiment and from the edges of the display window, both of which have broadband spectra. They have previously experienced MTFs similar to the ones in the adaptive optics correction when they viewed the environment with constricted pupils (aberrations have much less effect on the retinal image when the pupil is constricted compared to when it is dilated).^{32–35} Given that the emmetropes have good optics to begin with, it is unsurprising that they may have had sufficient everyday experience under bright daylight to learn the mapping between contrast in the world and contrast in near-perfect retinal images. If this hypothesis is correct, it suggests that the visual system is able to learn and apply the appropriate neural amplifications in more than one viewing condition.

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