Neural compensation for the eye's optical aberrations

Pablo Artal	Laboratorio de Optica, Departamento de Física, Universidad de Murcia, Campus de Espinardo, Murcia, Spain	
Li Chen	Center for Visual Science, University of Rochester, Rochester, NY, USA	
Enrique J. Fernández	Laboratorio de Optica, Departamento de Física, Universidad de Murcia, Campus de Espinardo, Murcia, Spain	
Ben Singer	Center for Visual Science, University of Rochester, Rochester, NY, USA	
Silvestre Manzanera	Laboratorio de Optica, Departamento de Física, Universidad de Murcia, Campus de Espinardo, Murcia, Spain	
David R. Williams	Center for Visual Science, University of Rochester, Rochester, NY, USA	

A fundamental problem facing sensory systems is to recover useful information about the external world from signals that are corrupted by the sensory process itself. Retinal images in the human eye are affected by optical aberrations that cannot be corrected with ordinary spectacles or contact lenses, and the specific pattern of these aberrations is different in every eye. Though these aberrations always blur the retinal image, our subjective impression is that the visual world is sharp and clear, suggesting that the brain might compensate for their subjective influence. The recent introduction of adaptive optics to control the eye's aberrations now makes it possible to directly test this idea. If the brain compensates for the eye's aberrations, vision should be clearest with the eye's own aberrations rather than with unfamiliar ones. We asked subjects to view a stimulus through an adaptive optics system that either recreated their own aberrations or a rotated version of them. For all five subjects tested, the stimulus seen with the subject's own aberrations was always sharper than when seen through the rotated version. This supports the hypothesis that the neural visual system is adapted to the eye's aberrations, thereby removing somehow the effects of blur generated by the sensory apparatus from visual experience. This result could have important implications for methods to correct higher order aberrations with customized refractive surgery because some benefits of optimizing the correction optically might be undone by the nervous system's compensation for the old aberrations.

Keywords: neural adaptation, optical aberrations, eye, adaptive optics

Introduction

The human eye is affected by aberrations that degrade the retinal image and ultimately limit spatial vision (Liang & Williams, 1997; Artal, Guirao, Berrio, & Williams, 2001; Hofer, Artal, Singer, Aragón, & Williams, 2001a). The lower order aberrations, defocus and astigmatism, are corrected routinely with spectacles, contact lenses, intraocular lenses, and refractive surgery. The higher order aberrations, beyond defocus and astigmatism, have been known to exist in the eye for more than 150 years (Helmholtz, 1881). However, it has only recently been possible to correct these aberrations in the living eye. Adaptive optics (AO), a technique developed in astronomy to remove the effect of atmospheric turbulence from telescope images (Hubbin & Noethe, 1993), can also be used to correct the eye's higher order aberrations (Liang, Williams, & Miller,

1997; Vargas-Martín, Prieto, & Artal, 1998; Fernández, Iglesias, & Artal, 2001; Hofer et al., 2001a). One application of this technology in the eye is to obtain highresolution images of the retina to resolve individual photoreceptors in vivo (Liang et al., 1997) and to identify the photopigment in each cell (Roorda & Williams, 1999). Another important application of AO is to produce controlled wave-aberration patterns in the eve, enabling new experiments to better understand the impact of the ocular optics on vision. In particular, it is possible to address the intriguing question of whether the visual system is adapted to the particular pattern of optical aberrations of its own eve. To test this idea, subjects viewed visual stimuli with aberrations controlled with adaptive optics. The AO apparatus corrected the eve's wave aberration and replaced it with the same wave aberration or with a rotated copy of it.

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Methods

The wavefront aberration (WA) is a function that characterizes the image-forming properties of any optical system. It is defined as the optical deviation of the wavefront along a certain ray from the perfect spherical wavefront. The WA is related to the image of a point source produced by the system, the point-spread function (PSF), through an integral equation (Born & Wolf, 1985). AO permits the manipulation of the eye's WA by introducing different optical paths over the pupil area.

An AO system consists of a wavefront sensor to measure the WA in real time and a correcting device, typically a deformable mirror, to modify the WA. Figure 1 shows a schematic diagram of the AO system at the University of Rochester used in this study. A Hartmann-Shack wavefront sensor (Liang, Grimm, Goelz, & Bille, 1994; Liang & Williams, 1997; Prieto, Vargas-Martín, Goelz, & Artal, 2000) measures the eye's WA at 30 Hz. A narrow infrared beam (810 nm, with a spectral spread of 20 nm) produced by a super-luminescent diode (SLD) is projected into the subject's retina acting as a beacon source. The irradiance on the cornea was approximately 5 μ W, which is about 30



Figure 1. Schematic diagram of the adaptive optics system used in the blur matching experiment. The red path represents the infrared light used for measuring the wavefront aberration and driving the deformable mirror, whereas the green path is the light used for the visual experiments. From beam splitter (BS) after the eye to the cold mirror, both lights are together, although not represented for clarity. See the text for additional details. CCD, charged-coupled device camera; DLP, digital light-processing; H-S, Hartmann-Shack; SLD, super-luminescent source. The picture in the lower right corner represents the visual stimulus used in the experiment without preferred orientation (see the text for additional details).

times smaller than the maximum permissible exposure for continuous viewing according to the safety standards (ANSI Z136.1, 1993). In the second pass, after the light is reflected from the retina and passes through the complete system, an array of 177 lenslets produces an image of spots on a charged-coupled device (CCD) camera. The locations of the spots in this image provide the local slopes of the ocular WA. The aberrations were measured for a 6-mm pupil up to 10th radial order, corresponding to an expansion of 63 Zernike modes (Noll, 1976).

A 97-channel deformable mirror (Xinetics), with an aluminized glass faceplate and lead magnesium niobate (PMN) actuators, was used as the wavefront-correcting device. It is placed in the system optically conjugated both with the subject's pupil plane and the wavefront sensor, by using appropriate lenses and two off-axis parabolic mirrors. The AO system worked in closed-loop, with the deformable mirror driven by the measured aberration data. Typical aberrations were nearly eliminated after 5-10 iterations, thus a correction of the eye's aberrations was completed automatically in 0.17-0.33 s.

In this experiment, besides removing the higher order aberrations in the eye on each trial, the deformable mirror also acted as an aberration generator to blur the subject's vision either with the subject's own aberrations or a rotated version of the aberrations. After the currently present aberrations were corrected, eight different aberration patterns were produced in each case: an average normal aberration pattern and seven similar versions rotated by 45-deg intervals. Figure 2 shows an example of the actual eight aberration patterns and the associated PSFs for one of the subjects. The desired aberrations were kept stable by the AO system working in closed-loop while subjects performed the matching experiment.

We relied on the wavefront sensor to indicate how well we succeeded in creating the same PSF at all orientations. The wavefront sensor can measure the combined wave aberration of the eye and the optical system through which the subject views the stimulus, with the exception of a beam-splitter, a mirror, and a lens. These uncommon path elements are diffraction-limited and have negligible impact on the wave aberration. We computed the Strehl ratio of the PSF generated at each orientation for every subject. These values were independent of the orientation. Specifically, there is no tendency for the image quality, assessed with these objective measures, to be any better in the zeroorientation condition.

Subjects viewed a binary noise stimulus, produced by a digital light-processing (DLP) video projector (Packer et al., 2001), through the AO system. The stimulus was viewed in 550-nm monochromatic light (shown schematically as the green light path in Figure 1). The stimulus, also shown in Figure 1, contains sharp edges at all orientations and subtended 1 deg of visual angle. The binary noise stimulus was produced from a uniform distribution filtered by taking the FFT of the noise, applying an annular filter via point-by-point multiplication, and then inverting back into the spa-

(a) rotated aberrations



(b) rotated PSFs



Figure 2. Example of the wavefront aberration (a) and the associated point-spread functions (PSFs) (b) for the normal (0) and the seven orientations for one of the subjects. The numbers represented the rotated angle.

tial domain. To get black-and-white spots rather than gray levels, the intensities were thresholded. Because the bandpass annular filter is circularly symmetric, it will eliminate all lower spatial frequencies and higher ones, which make energy at all orientations get through. A Gaussian function smoothed the edge of the field. On each trial, the computer randomly generated a different stimulus pattern.

The subject viewed the stimulus for 500 ms immediately after the deformable mirror generated the subject's own aberrations or the rotated version. At other times, the subject viewed a uniform field.

The matching experiment was performed on the right eyes of five subjects. During the measurement, the subject's head was stabilized with a bite bar, and the subject's pupil was dilated and accommodation paralyzed with cyclopentholate hydrochloride (2.5%). The experiment was performed for a 6-mm diameter artificial pupil. Figure 3 shows schematically the rationale of the matching experiment.



Figure 3. Schematic representation of the blur matching experiment. (a). The stimulus was seen alternatively for 500 msec with the normal and the rotated wavefront aberration. The yellow part represents the time where the desired aberration is produced. The next green part represents the 500 ms while the stimulus is presented to the subject with the appropriate aberrations. In each trial, the stimulus is seen with the normal and one (randomly selected) rotated version of the eye's aberrations. (b). The subject's task is to adjust the amount of the aberrations by choosing a factor (F) in the rotated case to match the subjective blur of the stimulus to that seen when the wave aberration was in the normal orientation. Additional pairs of presented until a factor F value is obtained for each orientation.

Subjects were asked to view the stimulus through the AO system with their own aberrations or with a rotated version of their aberrations. The stimulus was seen alternatively for 500 msec with both the normal and the rotated PSF (Figure 3a). The yellow part in Figure 3 represents the time when the desired aberration is produced. The eye's optics remain stable during the next 500 ms when the stimulus is presented to the subject. The subject's task was to adjust the magnitude (the root mean square [RMS]) of the aberrations by multiplying it by a factor (F) in the rotated case to match the subjective blur of the stimulus to that seen when the wave aberration was in the normal orientation (Figure 3b). Subjects were unaware of when the stimulus was seen through the normal or rotated aberrations. In the matching process, one of the seven different

rotated versions of the aberrations was randomly selected. Subjects were asked to match the blur with all eight orientations, including the normal orientation, in random order. Subjects could not tell which orientation was presented on a given trial. Because the subjects matched the blur in the normal orientation with an amplitude that was a physical match to that of normal wave aberration, there is no possibility that increased blur for other orientations.

If the rotated (uncommon) aberrations degraded the subjective image quality, a factor F smaller than 1 was required, as further illustrated in Figure 4 with a blurred stimulus. If the rotated wave aberration is less damaging for vision, a factor F greater than 1 should have been required. The complete process of matching took several minutes and was repeated up to 5 times to obtain robust estimates of the adjustment factor for each rotated aberration pattern.

Results

Figure 5 shows the values of the matching (or adjustment) factor F for the normal aberrations (0-deg angle) and the other seven rotations in four of the subjects that participated in the experiment. The error bars indicate the SD for each and provide a direct indication of the statistical significance of the decline in the matching for all orientations.

Figure 6 shows the average values of the matching (or adjustment) factor F (with the error bars indicating the individual variability) for the normal aberrations (0-deg angle) and the other seven rotations. In all subjects tested, the



Figure 4. Additional schematic example of the blur matching experiment.

RMS wavefront error of the rotated wave aberration required to match the blur with the normal wave aberration was found to be on average 20-40% less than in the normaloriented aberration case. That is to say, the matching factor F was between 0.6 and 0.8, indicating that the subjective blur for the stimulus increased significantly when the PSF was rotated.

Even though the matching factor was slightly higher for the rotation of 180 deg than for the other rotations, it too was significantly below a value of 1. A 180-deg rotation of the aberrations produces a retinal image with an identical modulation transfer function (that is to say with the same



Figure 5. Blur matching values (*F*) in four of the subjects as a function of the orientation of the aberrations (in degrees). Error bars represent *SD* of responses. The red line shows value 1 that indicates no adaptation effect. Letters are subjects' initials.



Figure 6. (a). Average blur matching value (*F*) for the five subjects as a function of the orientation of the aberrations (in degrees). Error bars represent *SD* of responses across subjects. The red line shows value 1 that indicates no adaptation effect. (b). The same data in a polar representation.

reduction in contrast for every sine-wave grating), although with a different phase transfer function, as compared with the normal orientation PSF. The fact that the subjective blur also increases in this case shows that the adaptation process is phase sensitive. This implies that the process is not simply a matter of adjusting the contrast of different portions of the spatial frequency spectrum.

If the neural system is adapted to the specific shape of the aberrations, the relative blur and then the matching factor should be lower for those orientations that are most different from the normal aberrations. To verify this assumption, we computed a parameter, the maximum of the cross-correlation function, which provided information on the difference between the original and rotated PSF. Figure 7 shows the comparison of the matching factor and the asymmetry parameter in four of the subjects. This parameter resulted in a good qualitative agreement with the values of the blur matching factor for each orientation.

It is also interesting to show the effect of the matching factor as the adjustment took place on the PSFs. As an example, Figure 8 shows the wavefront and the PSFs in one subject (MC) for the normal case (0) and for the 45-deg rotations with matching value 1 and 0.75. This last value actually corresponds to the matching value for that subject and condition. The PSFs on the left (yellow label) and on the right (blue label), although having a different extension, provide the same subjective blur.



Figure 7. Blur matching value (*F*) (black circles and lines) and asymmetry parameter (*M*) (red circles and lines) for every orientation in four of the tested subjects.



Figure 8. Example of the wavefront aberration (top panels) and the associated point-spread functions (PSFs) in one of the subjects for the normal (0) and the 45-deg rotation with two values of the matching factors: 1 (pink label) and 0.75, corresponding to the actual matching value for that subject and orientation (blue label). The PSF subtends 40 arcmin.

Discussion

The results of this experiment support the hypothesis that the neural visual system is adapted to the eye's particular aberrations, so that edges appear sharp despite the modest blur in the normal retinal image. Although as far as we know this is the first time that strong evidence for adaptation to higher order monochromatic aberrations has been reported, adaptability in the visual system is indeed ubiquitous (Held, 1980). The phenomenon reported here may be the monochromatic equivalent of chromatic fringe adaptation that renders less visible the effects of chromatic aberration in the eye, an effect that is closely associated with the McCollough effect (McCollough, 1965). Moreover, the neural visual system adapts to prismatic distortions, contrast or blur (Webster, Georgeson, & Webster, 2002). Adaptation to blurred images can also improve letter acuity (Mon-Williams et al., 1998).

A practical example is the adaptation to the optical distortions present in power progressive lenses widely used to correct presbyopia. Although these lenses suffer for a large amount of aberrations (Villegas & Artal, 2003), mainly astigmatism, most subjects adapt and wear those lenses comfortably.

Moreover, in the clinical practice, astigmatism is routinely under-corrected because patients usually do not tolerate a full correction. This is probably another example of the neural visual system not being adapted to the correction that provides the best optical quality objectively.

We have not yet measured the rate at which the visual system can adapt to changes in its monochromatic aberrations. If the adaptation to chromatic aberrations is a valid guide, then the process could be expected to take short periods of time, even a few minutes. However, adaptation processes in the visual system occur at many different rates, and only direct measurements will settle this issue. With the AO system, we tried to reverse or induce this adaptation by exposing subjects to a modified aberration pattern. With exposures of several (up to five) minutes, we were not able to see any significant change in the blur matching results. This suggests that a long time scale is probably involved; we do not know yet if it is in the range of days, weeks, or months.

Aberrations in the eye are dynamic by nature (Hofer et al., 2001b). They change with pupil diameter and accommodation during normal viewing (Artal, Fernández, & Manzanera, 2002). This creates an apparent paradox: If the retinal PSF is not stable over time, how can sluggish neural adaptation maintain a clear perceptual world? A possible explanation is that changes in pupil diameter and defocus (accommodation) preserve most of the shape features characteristics of a particular PSF, allowing the brain a coarse adaptation. In a recent experiment (Artal, Manzanera, & Williams, 2003), we confirmed that some shape features in the PSFs remained stable under most normal conditions.

Another possibility is that the brain can simultaneously accept a number of different PSFs, as long as it has sufficient experience with each. There is some evidence in support of the latter view, and studies have shown that the brain can maintain multiple adaptive states simultaneously, switching rapidly between them as when spectacles are donned and removed (Peterson & Peterson, 1938).

Another important practical aspect is the amount of aberration that the neural system can "compensate." All subjects who participated in the study had normal (small) levels of aberrations. Although it is well known that a large amount of aberrations degrades vision, it is possible that in those eyes, the neural system also is adapted to slightly improve vision. From the results of our blur matching experiment, it is not completely clear what is the nature of the visual improvement produced by the neural adaptation. While the increases of subjective sharpness would surely benefit tasks such as letter recognition (i.e., visual acuity), identifying the effect in other types of visual tests (e.g., contrast sensitivity) would require additional experiments.

Conclusions

We demonstrated that the neural visual system adapts to the particular eye's monochromatic aberrations. In addition to the fundamental nature of our finding, this adaptation phenomenon also may have important implications for vision correction. In particular, in the area of wavefront guided customized refractive surgery or customized contact lenses, this effect will reduce the immediate benefit for the patient of attempts to produce diffraction-limited eyes. If the brain is adapted to a particular aberration pattern, when this is changed by the surgery or contact lens, the neural compensation will remain adjusted to the first aberration pattern for some time. The importance of this will depend on the time required to reverse the previous adaptation.

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Corresponding author: Pablo Artal.

Email: pablo@um.es.

Address: Laboratorio de Optica, Departamento de Física, Universidad de Murcia, Campus de Espinardo, (Edificio C), Murcia, Spain.

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