Single neural code for blur in subjects with different interocular optical blur orientation

Aiswaryah Radhakrishnan
Laboratory of Visual Optics and Biophotonics,
Instituto de Óptica "Daza de Valdés,"
Consejo Superior de Investigaciones Científicas,
Madrid, Spain

Lucie Sawides
Laboratory of Visual Optics and Biophotonics,
Instituto de Óptica "Daza de Valdés,"
Consejo Superior de Investigaciones Científicas,
Madrid, Spain

Carlos Dorronsoro
Laboratory of Visual Optics and Biophotonics,
Instituto de Óptica "Daza de Valdés,"
Consejo Superior de Investigaciones Científicas,
Madrid, Spain

Eli Peli
Schepens Eye Research Institute, Mass Eye and Ear,
Harvard Medical School, Boston, MA, USA

Susana Marcos
Laboratory of Visual Optics and Biophotonics,
Instituto de Óptica "Daza de Valdés,"
Consejo Superior de Investigaciones Científicas,
Madrid, Spain

The ability of the visual system to compensate for differences in blur orientation between eyes is not well understood. We measured the orientation of the internal blur code in both eyes of the same subject monocularly by presenting pairs of images blurred with real ocular point spread functions (PSFs) of similar blur magnitude but varying in orientations. Subjects assigned a level of confidence to their selection of the best perceived image in each pair. Using a classification-images–inspired paradigm and applying a reverse correlation technique, a classification map was obtained from the weighted averages of the PSFs, representing the internal blur code. Positive and negative neural PSFs were obtained from the classification map, representing the neural blur for best and worse perceived blur, respectively. The neural PSF was found to be highly correlated in both eyes, even for eyes with different ocular PSF orientations ($r_{\mathrm{Pos}} = 0.95$; $r_{\mathrm{Neg}} = 0.99$; $p < 0.001$). We found that in subjects with similar and with different ocular PSF orientations between eyes, the orientation of the positive neural PSF was closer to the orientation of the ocular PSF of the eye with the better optical quality (average difference was ~10°), while the orientation of the positive and negative neural PSFs tended to be orthogonal. These results suggest a single internal code for blur with orientation driven by the orientation of the optical blur of the eye with better optical quality.

Introduction

The human visual system is highly robust, constantly compensating for changes in the magnitude of blur in retinal images, thus maintaining a relatively constant perception of the world despite changes in the environment (Elliott, Georgeson, & Webster, 2011; Webster, 2011; Webster, Georgeson, & Webster, 2002; Webster, Mizokami, Svec, & Elliott, 2006) or in the subject's optics (Artal, Benito, & Tabernero, 2006; Artal et al., 2004; Elliott et al., 2011; Mon-Williams,

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Tresilian, Strang, Kochhar, & Wann, 1998; Poulere, Moschandreas, Kontadakis, Pallikaris, & Plainis, 2013; Webster, 2011; Webster et al., 2002). Experiments by Webster and colleagues showed that even brief (i.e., within seconds) exposures to altered blur can result in a measurable change in the neural adaptation states of the visual system (Elliott et al., 2011; Webster, 2011; Webster et al., 2002). Adaptation is measured by shifts in the perceived best focus (PBF; aftereffects) following change in stimulation. Another study (Sawides, de Gracia, Dorronsoro, Webster, & Marcos, 2011b) showed that the PBF under natural adaptation is highly correlated with the magnitude of optical blur at the retina, introduced by the higher order aberrations of the eye. Furthermore, when the subject's aberrations were corrected with adaptive optics, adapting to images blurred by the subject's own higher order aberrations did not produce aftereffects, while adapting to images blurred by scaled versions of his or her own aberrations or to the aberrations of other subjects did produce aftereffects (Sawides, de Gracia, Dorronsoro, Webster, & Marcos, 2011a; Sawides et al., 2012).

Optical blur may be different across orientations, such as that produced by astigmatism. There is strong evidence that exposure to astigmatism produces a selectivity in perceived blur orientation. Strong aftereffects in the perception of isotropic focus occur following short-term adaptation to images blurred with horizontal and vertical astigmatism (Sawides, Marcos, et al., 2010). Adaptation selectivity for the axis of astigmatism has been shown to occur in both real and simulated astigmatic images (Ohlendorf, Tabernero, & Schaeffel, 2011). These effects have also been shown in a clinical context such as correction of astigmatism, as uncorrected astigmats show a preference towards the orientation of their retinal blur, which shifts towards isotropy as early as 2 hrs after wearing the astigmatic correction (Vinas, Sawides, de Gracia, & Marcos, 2012).

Oriented blur also occurs in retinal images as a result of asymmetric higher order aberrations such as comas. Several studies have shown that subjects are tuned to the orientation produced by higher order aberrations. A seminal work by Artal et al. (2004), where images blurred with rotated versions of the subject's (higher order) point spread function (PSF), showed that images blurred by the actual subject's PSF were perceived to have up to 40% better quality than images blurred with the rotated PSFs. Sawides et al. (2012) also showed a stronger bias to the images blurred with the subject's natural PSF, as opposed to a 90° rotated PSF, when compared against 100 images blurred with real PSFs of similar blur magnitude but with different orientation. In a later study, Sawides et al. (Sawides, Dorronsoro, Haun, Peli, & Marcos, 2013) introduced a pattern classification method, inspired by the classification images method (Ahumada, 2002), to retrieve the internal code for blur of subjects, and in particular the orientation of the internal code. With this technique, pairs of images blurred with PSFs with similar blur magnitude but different orientation are presented to the subject, who selects the image of the pair that is perceived to be of better quality and assigns a confidence score. Positive and negative orientation classification maps were obtained from the weighted (by the confidence score) averages of the PSFs blurring the images selected as perceived to be either better or worse. Since these classification maps correspond to the shape of the PSF that is perceived better or worse, respectively, the corresponding positive classification maps were termed the positive neural PSF, and the negative classification map termed the negative neural PSF. Both the shape and orientation of the positive neural PSF were very similar to that of the ocular PSF. These results suggest that not only is the internal code tuned to the overall amount of optical blur, but it is also tuned to a specific blur feature—the orientation of the high-order PSF (Sawides et al., 2013). All these prior studies were performed monocularly, and only the aberrations of the tested eyes were considered.

Even though the ocular aberrations are dynamic (Hofer, Artal, Singer, Aragon, & Williams, 2001), the shape of the PSF tends to remain similar across different pupil diameters and accommodation (Artal, Manzanera, & Williams, 2003), enabling strong neural adaptation. Yet, it is not uncommon to find differences between both eyes of the same person in the pattern or magnitude of higher order aberrations (Marcos & Burns, 2000; Porter, Guirao, Cox, & Williams, 2001). Little is known about the way the visual system copes with adaptation when each eye is separately exposed to different adapting images. A short-term adaptation experiment where right and left eyes were adapted to different images (either blurred, focused, or gray, or astigmatic blur with orthogonal orientation) showed a significant interocular transfer in adaptation in both isotropic and astigmatic blur (Kompaniez, Sawides, Marcos, & Webster, 2013). Also, various other studies suggested that a presence of sharp components influence largely the adaptation state in monocular or binocular viewing (Arnold, Grove, & Wallis, 2007; Radhakrishnan, Dorronsoro, Sawides, & Marcos, 2014).

In our previous study, PBF was measured monocularly in both eyes of subjects with similar or different blur magnitude between eyes. We reported that in subjects with different blur magnitude between eyes, the eye with a better optical quality dominates the perception of blur magnitude, and the differences in the blur between eyes are addressed by the neural system, resulting in a single PBF for both eyes (Radhakrishnan, Dorronsoro, Sawides, Webster, & Marcos, 2015). A question then arises on how the neural system deals with these inputs from eyes with different orientation in the optical blur of each eye. Here we measured the internal code for blur in both eyes of subjects with similar and different PSF orientation between eyes and investigated the differences in the orientation bias of the internal code for blur between eyes.

Methods

The internal code for blur of the subjects was estimated using the pattern classification method described previously (Sawides et al., 2013). Subjects selected the better perceived image from each pair of presented images blurred with equal blur magnitude but different PSF orientations (and then scored their confidence in the selection) for a total of 500 pairs. Measurements were performed monocularly for each eye of the subject, covering the other eye with a patch. From the large number of responses, the neural PSF was estimated for each eye using a reverse correlation technique. The procedures are illustrated in detail in an earlier study by Sawides et al. (2013).

Subjects

Both eyes of 10 subjects (22–41 years old) were measured in this study. The subjects had no clinical astigmatism and their spherical refractive error ranged from +1.00 D to −5.50 D. All subjects had prior experience in performing psychophysical tasks. Two subjects with myopia >4 D performed the experiments wearing their habitual spherical soft contact lenses. Sighting dominance was established in subjects using the Miles test (Roth, Lora, & Heilman, 2002).

Ethics statement

The experiments conformed to the tenets of the Declaration of Helsinki, with protocols approved by the Consejo Superior de Investigaciones Cientificas Ethics Committee. All participants provided written informed consent after the nature and consequences of the study had been explained to them.

Setup

Ocular aberrations were measured and corrected using a custom-developed adaptive optics setup. Ocular aberrations were measured in both eyes of all subjects with a Hartmann Shack wavefront sensor (HASO 32 OEM, Imagine Eyes, France). The spherical refractive error was compensated using a Badal system. All measurements were done undilated, with 5-mm artificial pupils. Psychophysical measurements were done under static closed-loop aberration correction using a membrane deformable mirror (MIRAO 52e, Imagine Eyes, France) correcting residual defocus, astigmatism, and high order aberrations. In the current study an average correction efficiency of 88.7% (in RMS wavefront error) was achieved. Visual stimuli were presented on a CRT monitor through the psychophysical ViSaGe platform (Cambridge Research Systems, UK). A detailed description of the setup, quality of the correction, and psychophysical measurements through manipulated aberrations with this instrument has been described in several previous papers (Gambra, Sawides, Dorronsoro, & Marcos, 2009; Marcos, Sawides, Gambra, & Dorronsoro, 2008; Sawides, Gambra, Pascual, Dorronsoro, & Marcos, 2010).

Test stimuli

A face image (480 pixels square, 256 gray levels) that subtended 1.98° at the retina was used. For each subject, test images were generated by convolving the face image with 100 ocular PSFs (only higher order aberrations; Sawides et al., 2013) that had various orientations but similar blur magnitude, optimized with defocus correction. This set of PSFs had been shown to have isotropic distribution of orientations (Sawides et al., 2013). The PBF from both eyes of the subjects participating in the current study had been measured in a previous study as the amount of Strehl Ratio (SR; defined as the peak [maximum] of the given PSF, relative to diffraction-limited PSF) producing a neutral percept (Radhakrishnan et al., 2015). The blur magnitude of all test images used for each subject (in terms of SR) was matched to that of the subject's better eye optical PSF or to that of the PBF (whichever had a higher SR). In a previous study we found that generally, the PBF blur magnitude (SR) matched the optical blur (SR) of the eye with better optical quality. Except subject S2, all subjects had PBF better than or equal to optical blur magnitude. The PBF blur magnitude was used for all subjects except for subject S2, for whom the better eye optical quality was used to generate the images. All convolutions were performed for a 5-mm pupil diameter. In total, 10 sets of 100 test images were generated, one set for each subject, with the same set being used for both eyes of each subject.

Psychophysical measurement

The psychophysical measurements were done under static adaptive optics correction. A gray field adaptation was provided for 30 s at the beginning of the measurements. The subject was then presented sequentially with a pair of images degraded with two different PSFs with different orientations but similar blur magnitude, interleaved with a gray field. Both the images and the gray field were presented for 500 ms. The task of the subject was to respond which of the two images (first or second) of the pair were perceived as better and to indicate the subject confidence in the response on a 3-level scale. One session consisted of presentation of 50 random pairs taken from the 100 images of PSF patterns, ensuring that each image was presented at least once in a session. Each subject performed 10 such sessions (500 random image pairs per eye). A typical experiment involving measurements on both eyes lasted for approximately 5 hrs. The subject was allowed to rest between sessions, and the adaptive optics correction was remeasured after every session.

Data analysis

Magnitude, contour, and orientation of optical blur

The magnitude of the optical blur was described by the SR (maximum of the PSF, relative to diffraction limited PSF). The PSF was calculated from the monochromatic wavefront (555 nm) aberrations at best focus, using Fourier Optics and assuming a 5-mm pupil. Repeated measurements of the PSF in the tested subjects resulted in an average magnitude variability of 6% SR ($SD = 6\%$) difference of >30% SR between eyes was considered a meaningful difference in optical bur magnitude between eyes (>5 times the variability of the measurement).

The PSF contours and orientation axes were obtained by methods described in a previous publication (figure 3; Sawides et al., 2013). Briefly, the PSFs were centered at the center of mass and then sampled in 72 angular sectors of 5° each. The intensity of the PSF at midangle of each sector was obtained, normalized to the maximum intensity and was plotted in a polar plot generating a contour diagram. The orientation axis of the PSF is given by the main axis of the best-fitting ellipse.

The orientation of the optical blur, estimated as indicated above, was highly reproducible across sessions, and marginally affected by fluctuations of accommodation. Typical fluctuations of accommodation amplitudes (1 D; Charman & Heron, 1988) produced differences in the ocular PSF orientation of 0.24° ± 0.2°. The mean difference in ocular PSF orientation estimation for intersession measurements in our study was 0.66° ± 0.34° (averaged across both eyes of 10 patients). In addition, we previously found (Vinas, Dorronsoro, Cortes, Pascual, & Marcos, 2015) that chromatic defocus only affected slightly the orientation axis. The orientation axis difference between the PSFs estimated for different wavelengths, based on wave aberration data across the visible spectrum (450–750 nm), was 3.02° ± 0.62°. Given that the state of focus of the eye tends to be similar in the middle of the visible spectrum and in polychromatic light (Coe, Bradley, & Thibos, 2014), and the small differences in orientation across wavelengths, the use of a monochromatic PSF (555 nm) in the calculations is a good approximation. Finally, for our subjects the orientation axis difference between the PSF with only high order aberrations and the PSF with the residual low order aberrations (including astigmatism) was 2.72° ± 0.95°, indicating minimal influence of residual astigmatism (subjects were selected on the basis of not having clinical cylindrical error).

Estimation of the neural PSF using a pattern classification-inspired method

Sawides et al. (2013) presented a method to estimate the internal code for blur, inspired by the classification images technique, and based on a reverse correlation (Ahumada, 2002; Eckstein & Ahumada, 2002), described briefly below. Calculation of the classification maps and extracting the contours of the positive and negative weights allowed estimation of shape of the neural PSF.

PSFs corresponding to the images that were subjectively selected as better perceived were given positive scores, and the other image in the pair was given a negative score. The PSF intensities were multiplied by a score derived from the confidence score. A score of 10 was given for a very confident response, a 5 to a less confident response, and 1 for the lowest confidence response to each image of the pair selected as better focus. Thus, a PSF that when applied to an image is consistently selected as better focused and with high confidence will get a score of 100 (score 10 × 10 presentations). Alternatively, scores of −10, −5, and −1 were given to the images not selected as better focused. The noise effect by some random comparisons of two rather similar PSFs was countered by the high number of comparisons being made and by the weighted scoring system. The weighted score assigned to each of the PSFs in any pair was very consistent across sessions. For each subject we calculated the standard deviation in the scoring of a specific PSF pattern across different sessions. Pooled variance was calculated as the average of the standard deviations across subjects, the square root of which provided the repeatability parameter. If the scoring were to be random, a PSF could have a maximum score difference of 20 (from −10 to +10). The repeatability across subjects and between sessions thus measured was 2.3 (15% of the full score range).

All the weighted responses were then summed to obtain a pattern classification map (Ahumada, 2002;

Sawides et al., 2013). The contour of the positive weights of the classification map was termed as positive neural PSF, and the contour of the negative weights of the classification map was termed the negative neural PSF.

Correlation and orientation-difference analysis

The correlation between the energy distribution of the ocular PSFs (absolute intensities, not contours) and the sum weighted average of the PSFs perceived better and worse was calculated. The difference in orientation between any two PSF was calculated by rotating the PSF in 1° steps and calculating the image correlation coefficient at each step. The relative rotation that resulted in maximum correlation coefficient was considered the orientation difference (in degrees) between the PSFs. For two PSFs to have similar orientation, the maximum correlation would be obtained for a rotation close to 0°. A difference of $>20°$ (mean orientation difference between optical and neural PSFs) was considered in Sawides et al. (2013) as a meaningful difference in optical blur orientation between eyes.

In an alternative analysis, the correlation coefficients between the ocular PSF contours and the neural PSF contours was calculated using a circular correlation coefficient (Fisher & Lee, 1983). This analysis provided similar results ($t = 0.7$, $df = 71$, $p = 0.27$).

Results

Ocular aberrations and PSFs

Figure 1 shows the ocular higher order aberration patterns, the corresponding PSFs, and the PSF contour plots in both eyes of the 10 subjects. The RMS for higher order aberration, the SRs, and the orientation axes are shown in the insets. Under the criteria defined above for meaningful differences in blur magnitude and orientation between eyes, subjects S1–S5 had similar PSF orientation, but different blur magnitude between eyes; S6 and S7 had similar PSF orientation and similar blur magnitude in both eyes; S8 and S9 had similar blur magnitude but different PSF orientation; and S10 had both different PSF orientation and different blur magnitude between eyes.

Interocular similarity

Figure 2A shows examples of the positive and negative neural PSF contours in comparison with their respective ocular PSF contours for one representative subject in each group. Figure 2A reveals that the orientation of the positive (green) and negative (red) neural PSFs was strikingly similar between the two eyes, despite similar or different optical blur magnitude and/or ocular PSF orientation (blue). There was strong and significant interocular correlation in the orientations of the positive neural PSF ($r = 0.95$, $p < 0.001$) and negative neural PSF ($r = 0.99$, $p < 0.001$). Furthermore, the neural PSF orientations were not statistically significantly different between eyes ($p = 0.9$ and $p = 0.36$, for positive and negative, respectively). Across all subjects, the average difference in orientation between the positive and the negative neural PSFs was 58° ± 18.73° and was statistically significant ($t = 2.82$, $df = 9$, $p = 0.022$).

The orientation differences between eyes in ocular and neural PSFs for each of those subjects are shown in Figure 2B. As seen, the high interocular difference in orientation of ocular PSF (27.1° ± 30.4°, in blue) was not found for neither the positive neural PSF (3.3° ± 1.95°, in green) nor the negative neural PSFs (1.1° ± 0.32°, in red).

Interocular similarity: Intersubject differences

Figure 3 shows the interocular difference in orientation in subjects with similar and different PSF orientations between eyes (Figure 3A) and in subjects with similar and different blur magnitude between eyes (Figure 3B). Similar to the trend noted in average across subjects, the interocular difference between eyes in the positive and negative neural PSFs (green and red bars) was insignificant, irrespective of the difference in ocular blur magnitude or orientation (blue bars) between eyes. The interocular difference in orientation (Figure 3A) of the positive neural PSFs in subjects with similar (S1–S7) and different (S8–S10) ocular PSF orientations between eyes was 3.7° ± 2.03° and 2.33° ± 1.53°, respectively. The difference was slightly higher (4.3° ± 1.68°), yet insignificant in subjects with different blur magnitude between eyes (Figure 3B). The interocular difference in orientation of the negative neural PSF was close to 1° in all groups of subjects.

Neural PSF versus ocular PSF

Figure 4 shows the average orientation differences between the ocular and neural PSFs. On average the largest differences in orientation occur between the negative neural PSF and the ocular PSF with the better optics (51.8° ± 16.9°). The least difference in orientation was found between the orientation of the positive neural PSF and the PSF of the eye with better optical quality (10.5° ± 3.8°). The positive neural PSF

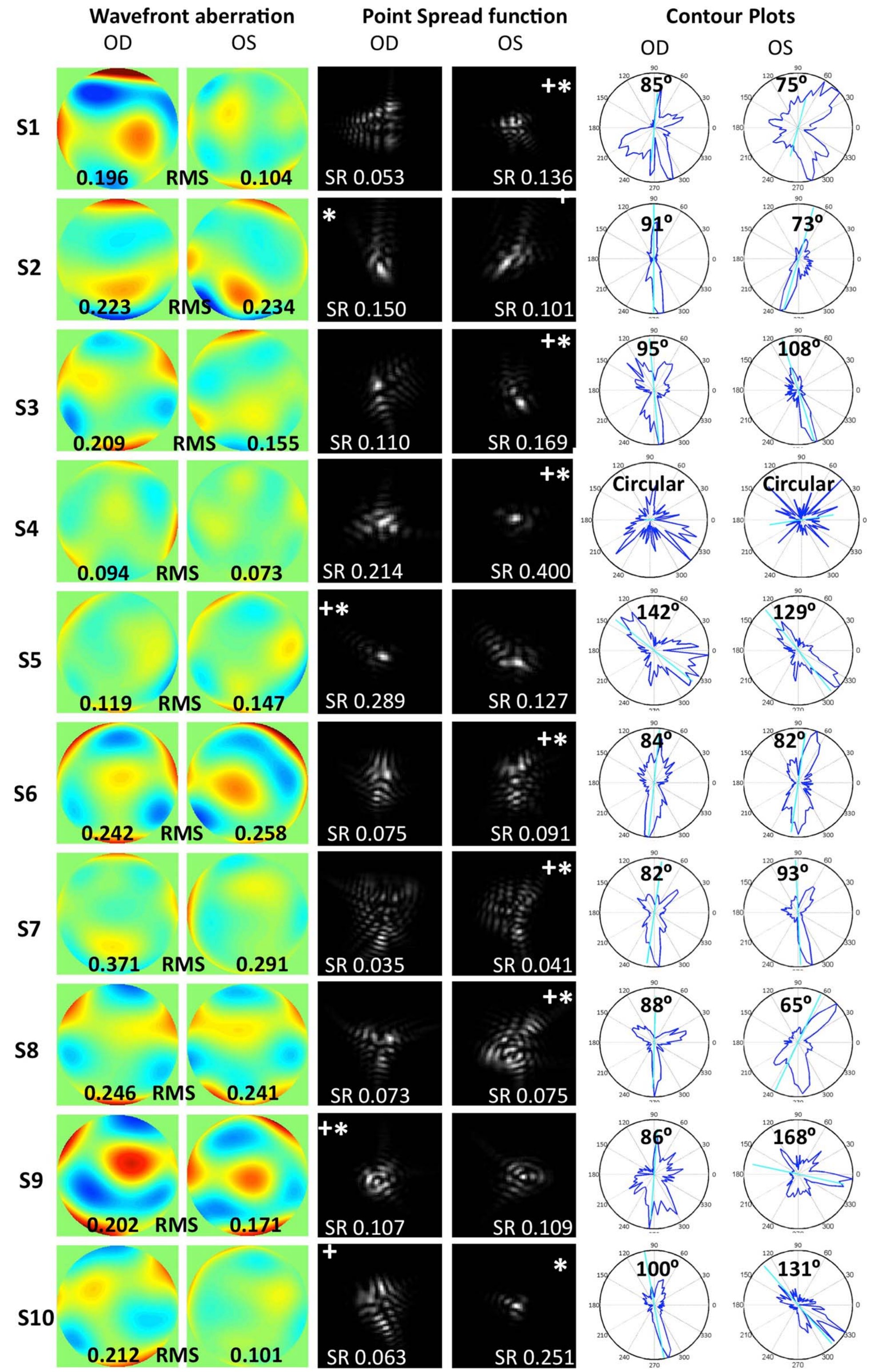

Figure 1. Aberration profile of subjects. Wavefront aberration maps (left), ocular PSFs (middle), and PSF contour plots (right) for both eyes of all subjects. Subjects S1–S7 had similar orientation of ocular PSF between eyes, and subjects S8–S10 had different ocular PSF orientations ($>$20° difference in orientation between eyes). In the PSF panel, $+$ indicates the eye with sighting dominance and * indicates the eye with better optical quality.

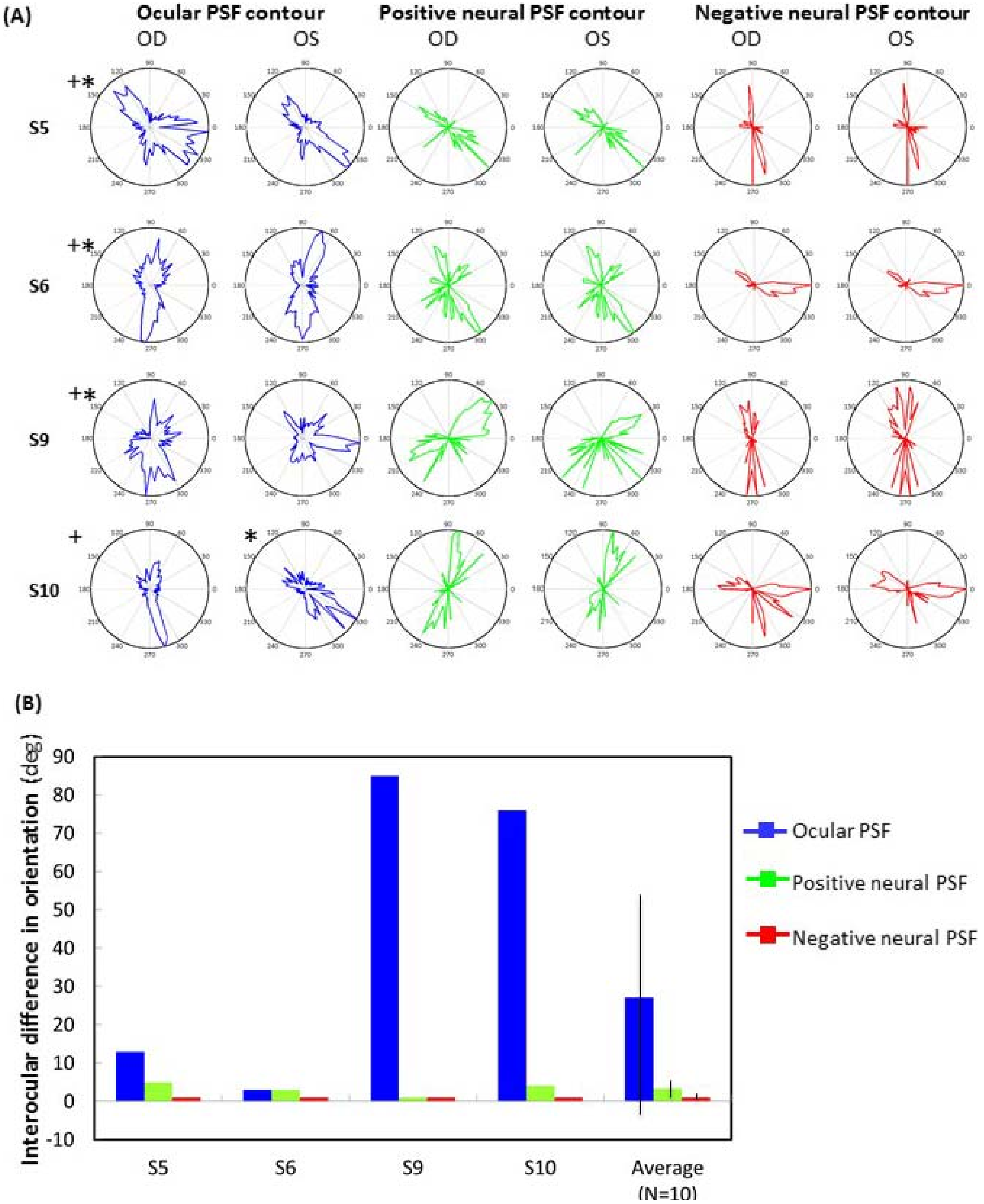

Figure 2. Examples of ocular and neural PSFs in both eyes of one subject in each group (S5, different blur, similar orientation; S6, similar blur, similar orientation; S9, similar blur, different orientation; S10, different blur, different orientation). (A) Ocular PSF contours (blue, left columns), positive neural PSF contour (green, middle columns), and negative neural PSF contour (red, right columns) for both eyes of each subject. (B) Interocular difference in orientation between eyes for ocular PSF (blue), positive neural PSF (green), and negative neural PSF (red) for the corresponding subjects and average across all subjects. In the ocular PSF contour panels, + indicates the eye with sighting dominance and * indicates the eye with better optical quality.

correlated more with the PSF of the eye with better optical quality ($r = 0.60$, $p = 0.002$) than with the worse eye ($r = 0.53$, $p = 0.008$), and the PSFs perceived worse correlated significantly with the PSF of the worse eye PSF ($r = 0.63$, $p = 0.002$) than with the PSF of the better eye ($r = 47$, $p = 0.018$).

Neural PSF: Intersubject differences

Figure 5A shows orientation differences between the ocular PSFs and the positive and the negative neural PSFs, in subjects with similar and different ocular PSF orientations between eyes. In subjects with similar ocular PSF orientation between eyes (S1–S7), as

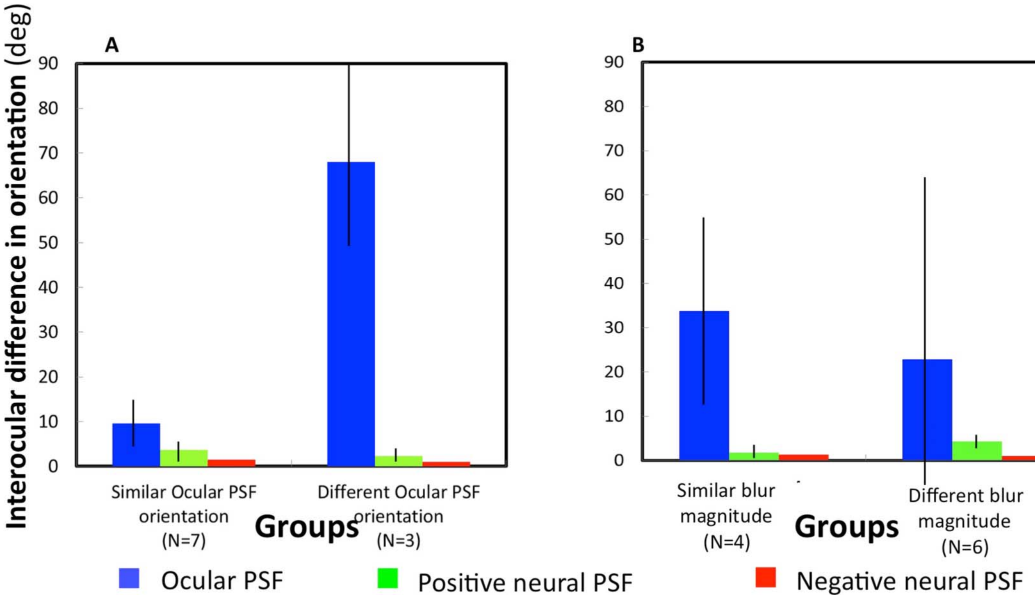

Figure 3. Interocular difference in orientation of the ocular PSF (blue), positive neural PSF (green), and negative neural PSF (red). (A) Subjects with similar ocular PSF orientations (S1–S7) and different ocular PSF orientations (S8–S10). (B) Subjects with similar (S6–S9) and different blur magnitudes (S1–S5, S10). Despite interocular differences in ocular PSF orientation (blue bars), interocular differences between positive and negative neural PSFs orientations were negligible.

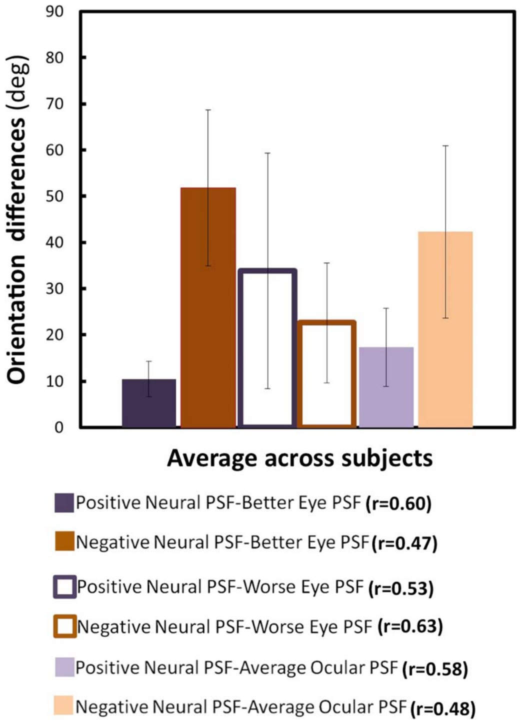

Figure 4. Difference in the orientation between positive and negative neural PSFs and the better eye PSF orientation (filled bars) and the worse eye PSF orientation (open bars). The corresponding correlation is given in parentheses. All correlations are significant ($p < 0.05$).

expected, the positive and negative neural PSF orientations differed similarly from either eye. In subjects with different orientations between eyes, the positive neural PSF differed least from the ocular PSF of eye with better optics (12.6° ± 7.2°), while the negative neural PSF differed the most from the ocular PSF of the eye with better optics (45.7° ± 17.3°).

Figure 5B shows differences between the orientations of the ocular PSFs and the orientation of the positive and the negative neural PSF in eyes with similar and different ocular PSF magnitude. While in both groups of subjects, the orientation difference was least for the positive neural PSF and the ocular PSF of the better eye (14.6° and 13.8°, for subjects with similar and dissimilar blur between eyes, respectively), and the negative PSF differed most from the ocular PSF of the better eye (31.6° ± 13.9° and 58.6° ± 29.6°, for subjects with similar and dissimilar blur between eyes, respectively), the actual differences were larger in subjects with different blur between eyes, indicating the role of blur magnitude in orientation preference.

Discussion

The physical retinal stimulus is blurred by the eye's optical limitations, which are actively compensated for by the neural system, resulting in improved perceptual quality. Some reports show that the perception of stimuli largely depends on the spatial statistics of

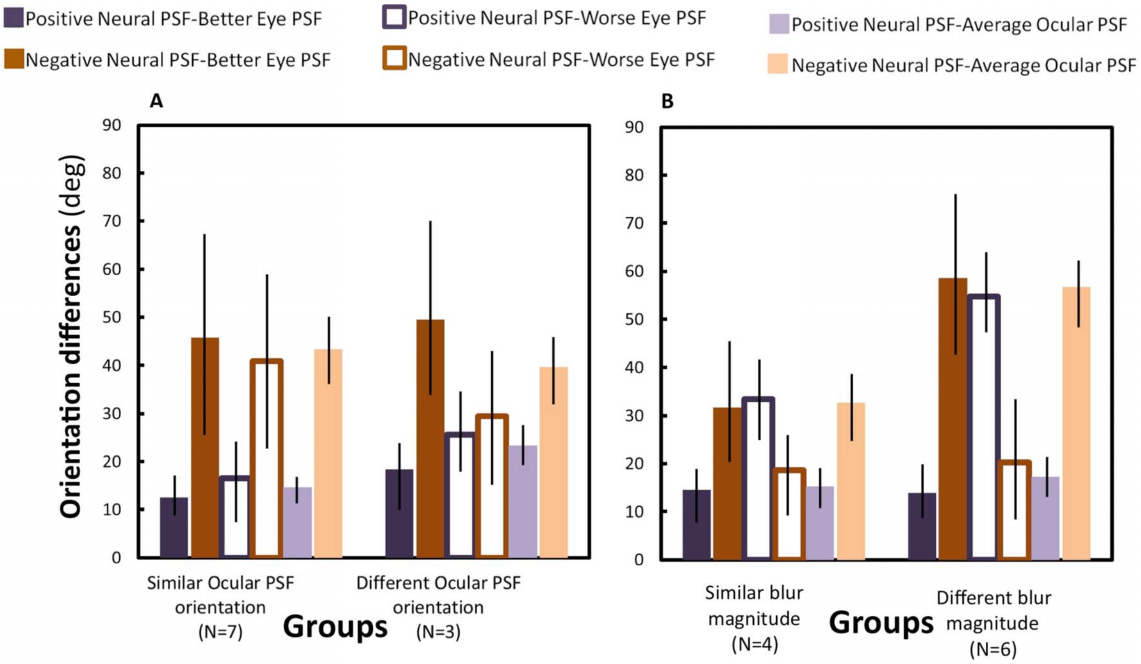

Figure 5. Difference in orientation between ocular and neural PSFs. (A) Subjects with similar (S1–S7) and different (S8–S10) blur orientation. (B) Subjects with similar (S6–S9) and different blur magnitudes (S1–S5, S10). Subject S10 with different blur magnitude and orientation between eyes was included in the group of subjects with different blur between eyes.

natural images (Field, 1987; Field & Brady, 1997). Additionally, the visual system appears to be naturally adapted to the native level of blur and able to rapidly and continuously recalibrate to compensate for intrinsic or environmental changes in blur (Artal et al., 2004; Haun & Peli, 2013; Ohlendorf et al., 2011; Sawides et al., 2012; Sawides et al., 2013; Webster et al., 2002). Our results suggest that the locus of adaptation is cortical.

A recent study reported short-term adaptation to artificially induced interocular differences in blur and demonstrated that the sharper images dominate perception irrespective of which eye was exposed to sharp adaptation (Kompaniez et al., 2013). Interocular differences in refractive error or ocular aberrations are not rare, and therefore the short-term adaptation recreated in the earlier experiment can also occur naturally over long term. We have recently reported that in eyes with different blur magnitude, the eye with a better optical quality dominates adaptation and perception with either eye (Radhakrishnan, Dorronsoro, Sawides, Webster, et al., 2014; Radhakrishnan et al., 2015). In the current study, we further investigated the subjective bias to specific characteristics of high-order blur (i.e., the main orientation of the PSF at the retina) and the relationship between the blur orientation of the perceived best image and the orientation of the PSF, when each eye is natively exposed to optical blur of different orientation. As previously found for the internal code for blur magnitude, there seems to be a single internal code for blur orientation for both eyes, with the preference given to the eye with better optical quality. This calibration appears to operate both at short time scales (Kompaniez et al., 2013) and long time scales (as found in this study, where subjects are chronically exposed to interocular differences in aberrations). The spatial selectivity of both blur magnitude and orientation does not compensate separately for the two eyes, unlike other effects such as the contingent aftereffects for color and orientation known as McCollough effects where the visual system appears to adjust independently for each eye (Webster & Malkoc, 2000). Emmetropization is also shown to be affected by the optical defocus present in either eye (Rabin, Van Sluyters, & Malach, 1981; Smith, Hung, & Arumugam, 2014). Our finding supports the hypothesis that adaptation to spatial blur magnitude and orientation operate at a cortical locus and is controlled by the eye with better image.

Many studies show (Erkelens, 2000; Hoffman & Banks, 2010; Ono & Barbeito, 1982; Ono, Mapp, & Howard, 2002) that people have conscious access to a cyclopean image but not to the monocular images when viewing binocularly. It has been shown that during binocular viewing, the eye with the sharper image has greater influence on the cyclopean percept than the eye with a blurrier image (Hoffman & Banks, 2010). We studied this cyclopean percept by selectively manipulating the blur in the retinal image (after compensating for the ocular aberrations) in each eye of the subjects, monocularly. We show that this sensory dominance persists even when the eyes are stimulated separately, and these PBF matches in magnitude and orientation that of the eye with least optical defects. These results support a single cyclopean locus of neural compensation for the eye's optical defects, adjusting the neural signals carried from either eye, but controlled only by the better eye. This also suggests a close correspondence between subjectively neutral percepts (what looks focused) and neutral states in the neural code (what stimulus neural sensitivity is adapted to). The singleness in the internal code for blur suggests that the visual system adjusts for input from the eye with the less blurry image under binocular viewing conditions, as known from studies of rivalry (Arnold et al., 2007; Kim & Blake, 2007).

This adaptation driven by the optical magnitude and orientation of the eye with the better optical quality appears to be an additional form of ocular dominance. The optimal method to measure ocular dominance is not clear. While methods testing aiming dominance (such as hole-in-the-card) are standard in the clinic, the lack of correspondence with sensory dominance methods (such as binocular rivalry or asymmetry in visual acuity tests) raises questions regarding the practical use of aiming dominance tests in the clinic (Rice, Leske, Smestad, & Holmes, 2008). In our study, sighting dominance and better optical quality matched in most but not all the subjects. However, in eyes with different optical quality, the neural code was driven by the eye with better optical quality, not the sighting dominant eye. There is interest in developing reliable techniques for testing ocular (sensory) dominance suited and reliable in a clinical setting, and some methods based on polarizing glasses (Peli, 2002) or modified balancing techniques (Handa, Shimizu, Uozato, Shoji, & Ishikawa, 2012) have been proposed. Our results suggest that binocular measurement of the ocular aberrations (rapidly done using clinically available wavefront sensors) of the patient can help identifying the sensory dominant eye, at least in eyes free of neural pathology.

Our findings may also have implications for binocular blur perception, and may be related to recent observations of binocular summation. Some aspects of binocular visual performance (binocular summation and maximum disparity) have been shown to decrease with increasing interocular differences in higher order aberrations (Jimenez, Castro, Jimenez, & Hita, 2008; Sabesan, Zheleznyak, & Yoon, 2012). While inducing asymmetric higher order aberrations (like coma) in orthogonal orientations between eyes decreased binocular summation, introducing coma with bilateral mirror symmetry or matched orientation had significantly less impact in reducing binocular summation. The single code for blur imposed by the internal code of blur of one eye may impose limitations on the binocular sensitivity gain in some subjects of our sample who had different PSF orientations between eyes.

Our results have implications for IOL multifocal corrections of presbyopia and outcomes following refractive surgery. While it is true that interocular differences in blur magnitude and orientation could exist (Marcos & Burns, 2000; Porter et al., 2001), it is not uncommon to introduce subtle changes in the pattern of higher order aberrations following refractive surgery. Asymmetries in the PSF could also be introduced by different bilateral decentrations of implanted intra-ocular lenses (IOLs), or through miss-and-match techniques providing different IOL designs or correction alternatives to each eye. Why some subjects easily adapt to these changes while others do not may be explained by the selectivity of the visual system to the native pattern of higher order aberrations. Monovision is an example where much larger differences in magnitude of blur are introduced between eyes. Conventionally, in monovision correction, the dominant eye (sighting dominance usually) is corrected for distance vision, which largely influences the success of the correction (Wright, Guemes, Kapadia, & Wilson, 1999). The selectivity to the sharper image in sensory dominance, as suggested by our results, could be a key in the strategies for clinical treatment, and should be tested prior to providing a patient with a surgical monovision correction for presbyopia. We recently reported that the subjective response to a multifocal pattern depends on the pattern of aberration in the eye (Dorronsoro et al., 2014). It is likely that a better monovision and/or multifocal correction for a patient will be influenced also by prior adaptation to the magnitude and orientation of the native aberrations, which as shown here, is driven by those of the eye with better optical quality, when there are interocular optical differences.

We show that in eyes that have perceptual preference for blur orientation, this is largely influenced by the blur orientation of higher order aberrations in the eye with better optical quality. The current study focused on patients without clinical astigmatism. In the presence of astigmatism, the orientation preference should be largely influenced by the magnitude and orientation of astigmatism (Ohlendorf et al., 2011; Sawides, Marcos, et al., 2010; Vinas et al., 2012). On the other hand, it is not uncommon to leave residual astigmatism in patients when there is no significant visual benefit of its correction (i.e., soft contact lenses or IOLs). In fact correcting all the astigmatism may result in decreased visual performance (Villegas, Alcon, & Artal, 2014), and certain combinations of astigmatism and coma (two aberrations with marked oriented features) may produce better visual quality than coma or astigmatism alone (de Gracia et al., 2010; de Gracia, Dorronsoro, Marin, Hernandez, & Marcos, 2011; Vinas et al., 2013). Interesting subsequent research may involve studying the factors influencing orientation preferences in eyes with residual astigmatism.

Conclusion

In subjects with similar or different PSF orientation between eyes, we found that an identical neural PSF exists for both eyes. In most subjects, the positive neural PSF closely correlated with the PSF of the eye with better optical quality, and the negative neural PSF was oriented on average 58° apart from the positive neural PSF.

Keywords: interocular difference, optical quality, pattern classification, PSF orientation, neural PSF, ocular dominance

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Corresponding author: Aiswaryah Radhakrishnan.
Email: raishu85@gmail.com; aishu@io.cfmac.csic.es.
Address: Visual Optics and Biophotonics Laboratory, Instituto de Optica, CSIC, Madrid, Spain.

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