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Unveiling the foveal blue scotoma through an afterimage

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Abstract

The absence of short-wave-sensitive (S-) cones in the human foveola normally goes unnoticed, but the resulting foveal S-cone, or blue, scotoma can be visualized as the negative afterimage of a short-wavelength adapting field on a larger white background. The afterimage has an annular shape with a lighter inner region that corresponds to Maxwell's spot, and a small bright spot in the center corresponding to the foveal blue scotoma. We have shown that the visibility of the center spot in the afterimage approximately follows the spectral sensitivity curve of the S-cones. We further demonstrate that the central bright spot subtends a retinal area that is coincident with the tritanopic region of the foveola. The macular pigment distribution measured for the same observers also peaks in the central fovea, but has a relatively high density over a broader retinal region than the bright spot in the negative afterimage, and more closely corresponds to the lighter annular region of the afterimage. The results support the hypothesis of an active post-receptoral process for filling-in of chromatic scotomas.

Keywords: Scotoma; Foveal tritanopia; Perceptual filling-in; Stabilized images

1. Introduction

The central human fovea is tritanopic, or "blue blind" (König, 1894; Wald, 1967; Willmer & Wright, 1945). Anatomical studies show that the fovea contains a 20–25 arcmin S-cone free zone with an irregular spacing of S-cones on the foveolar flanks (Curcio et al., 1991). Likewise, psychophysical studies show that the punctate sensitivity map of the S-cone mechanism in the central fovea forms an irregular, 20-arcmin region of low sensitivity surrounded by steep, ragged peaks and valleys (Williams, MacLeod, & Hayhoe, 1981b). At threshold a short-wavelength spot projected to the fovea is colorless (Wald, 1967). Yet under ordinary viewing conditions the perception of blue appears unaffected by the foveal blue scotoma so that a large, extended short-wavelength field appears homogeneous. We propose that the invisibility of the foveal blue scotoma is due to post-receptoral interpolation or neural filling-in processes (Gerrits & Vendrik, 1970; Spillmann & Werner, 1996).

The short-wave sensitivity loss of the central foveola is consistent with the tritanopia reported for approximately the same retinal region, but it also appears in the retinal region in which macular pigment has its highest density for most observers (Hammond, Wooten, & Snodderly, 1997; Werner, Donnelly, & Kliegl, 1987). Magnussen, Spillmann, Stürzel, and Werner (2001) demonstrated that the blue scotoma could be made visible by regeneration of neural border activity between the central fovea and its surrounding regions. They confirmed this by having observers view a flickering, monochromatic, short-wavelength field. Under these conditions the blue scotoma appears as a tiny dark spot in central vision, the visibility of which depends upon the wavelength of the flickering field and the temporal frequency of modulation. In our previous paper (Magnussen et al., 2001), we also compared the foveal dark spot with the area over which Haidinger's brushes could be observed, as this entoptic phenomenon is thought to be due to the dichroic properties of macular pigment

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(Helmholtz, 1867). Although direct measurements of the tritanopic region of the retina and the macular pigment distribution were not obtained, we did find that Haidinger's brushes appeared as a rotating spindle-shaped figure over a region much larger than the foveal dark spot, and that the dark spot faded under conditions in which Haidinger's brushes were clearly visible. This dissociation between the dark spot and the larger region defined by Haidinger's brushes supported the view that the central foveal scotoma is due to the absence of S-cones and that any contribution due to macular pigment absorption is secondary.

In the present paper we provide further evidence for a post-receptoral filling-in process responsible for assigning the uniform color appearance to the central fovea. The experimental idea is that the S-cone scotoma should be visible in the negative afterimage of a short-wavelength adapting field viewed centrally. An afterimage is caused by local bleaching and adaptation of the retinal receptors, and its appearance depends upon the level of neural noise remaining after the bleach, the sensitivity of the adapted receptors and the background upon which the afterimage is projected (Barlow & Sparrock, 1964). When the combined activity of noise and signals from the adapted S-cones falls below the neural activity of the unadapted retina, a negative afterimage is observed on a white background. With a circular, short-wavelength adapting field, two retinal regions are adapted differently: The area of the white background falling outside the adapting field and the foveola containing no S-cone receptors. The resulting negative afterimage observed against a large white background should therefore appear doughnut-shaped, containing a small (~0.25 arcmin) bright spot in the center. Contained within the annular afterimage, there should be two regions, a lighter inner region in which S-cones are relatively less adapted due to the presence of macular pigment and a darker outer region in which the S-cones are relatively more adapted. The short-wave adapting field will also produce a modest amount of bleaching of the middle- and long-wave sensitive cones, but they would not be expected to contribute to any spatial inhomogeneity in the afterimage because they have the same ratio throughout the central retina (Nerger & Cicerone, 1992).

We demonstrate that the afterimage corresponding to the blue scotoma depends upon the wavelength of the adapting field, corresponding approximately to the spectral sensitivity function of the S-cones (Stockman, Sharpe, & Fach, 1999). The absorption of short-wave light by the macular pigment undoubtedly influences the spectral sensitivity of the central foveola, but its retinal distribution corresponds better to the annular region of the afterimage, while the tiny white center has the same spatial dimensions as the tritanopic region of retina. This spatial inhomogeneity of the retina permits an unveiling of the foveal blue scotoma.

2. Experiment 1: Strength of the negative afterimage of the foveal blue scotoma

2.1. Methods

Three normal trichromats (ages 26–36 years) participated in this experiment. Subjects sat in a dark booth and steadied themselves using a combined chin-forehead rest. The right eye was centered relative to the 2 mm exit pupil of a three-channel Maxwellian-view system that was employed for stimulus presentation. A 1000 W Xenon arc lamp powered by an Oriel Universal power supply was used in conjunction with a Jobin–Yvon monochromator (8 nm half-band width) and Schott interference filters (10 nm half-band width). The adapting field channel produced a 5° monochromatic disk whose wavelength was varied randomly from 410–510 nm in 10 nm steps. The background channel provided an 8° white (CIE x, $y = 0.325, 0.366$) disk to make the afterimage visible. To sustain the afterimage (Magnussen & Torjussen, 1974), an electromagnetic shutter provided square-wave flicker of the background with 100% modulation depth and a frequency of 2 Hz.

The adapting stimuli had a retinal illuminance of 79 trolands, as measured with a Spectra Scan 704 photometer, and computed according to the method of Westheimer (1966). This is equal to 1445 scotopic trolands at 470 nm which is in the range of rod saturation (Makous, 2004). The illuminance of the white background against which the afterimage was observed was 100 trolands.

Following 10 min of dark adaptation, an afterimage was induced by asking the subject to fixate the center of the adapting field for 40 s. The adapting channel was then switched to the white background, and the observer viewed the negative afterimage that developed and lasted for approximately 30–60 s. The observers rated the perceived strength or salience of the afterimage using a 10-point scale where a value of 1 meant that the phenomenon was not visible (Magnussen et al., 2001). Practice sessions were provided before formal data collection commenced.

2.2. Results

The most striking demonstration of the foveal blue scotoma was obtained with a 440 or 450 nm monochromatic adapting field. The appearance of the afterimage is illustrated in Fig. 1. It contained three distinct regions: A dark reddish-brownish outer surround with diffuse borders (~5° outer diameter), a somewhat lighter inner surround (~2° diameter), and a tiny hole in the center (~25 arcmin), appearing as a white spot, brighter than the background. Systematic measurements were not made of the color appearance of the annular zones which usually appeared reddish-brown, but varied with

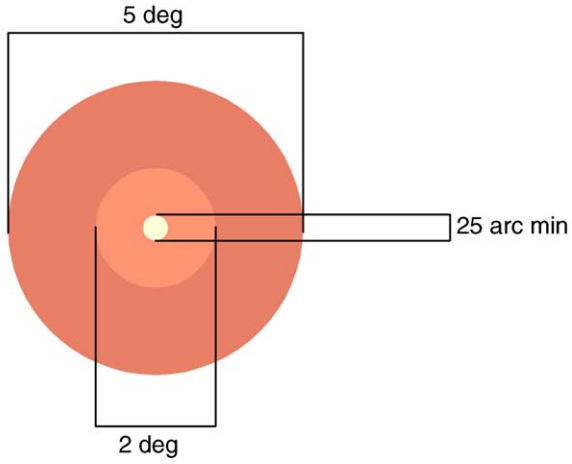

Fig. 1. A schematic representation of the negative afterimage of a circular, monochromatic, short-wavelength (blue, 450 nm), 5° adapting field viewed against an 8° white background. The bright central spot represents the foveal blue scotoma (S-cone free area).

wavelength. Size estimates, indicated in the figure, were made by inserting a reticle in the collimated part of the optical path; the subject projected the afterimage onto the scale and read off the number of divisions subtended by the center spot and the inner surround. The values of the bright center spot correspond well to the size of the dark spot observed with a flickering, monochromatic background (Magnussen et al., 2001). The inner surround (annulus) probably represents Maxwell's spot, reflecting the dense macular pigmentation in the 2° region of central vision (Miles, 1954; Nussbaum, Pruett, & Delori, 1981; Spencer, 1967). The center spot is clearly visible for many seconds, but it gradually weakens and filling-in takes place in the later stages of the fleeting negative afterimage.

Fig. 2 shows the rated salience of the afterimage as a function of the wavelength of the adapting field. The left panel presents results for each observer separately, each data point representing the mean value of five trials. Individual curves show a maximum value between 450 and 470 nm, falling sharply towards shorter and longer wavelengths. Beyond 420 and 510 nm, the bright center spot in the afterimage is not visible for our stimulus conditions. In the right panel, the averaged results for the three observers are plotted in terms of log relative rating values (filled symbols) for comparison with the relative spectral sensitivity function of the S-cones shown by the smooth curve (Stockman et al., 1999). The comparable results for ratings of the foveal dark spot obtained by direct viewing of a flickering monochromatic background are represented by open symbols (taken from Fig. 1, Magnussen et al., 2001). The agreement between the two psychophysical data sets is good, as it is between the psychophysics of the foveal blue scotoma and the sensitivity function of the S-cones. The shift in the rating maxima compared to the peak of the corneally specified S-cone sensitivity function ($\lambda_{max} = 440$ nm) might be due to macular pigment absorption ($\lambda_{max} = 460$ nm).

3. Experiment 2: Duration of the negative afterimage of the foveal blue scotoma

3.1. Methods

The same observers and stimuli as in Experiment 1 were used, however, in this experiment we determined the time required for the bright center spot to fade and become filled in to match the hue and brightness of the surrounding area. The white background was not

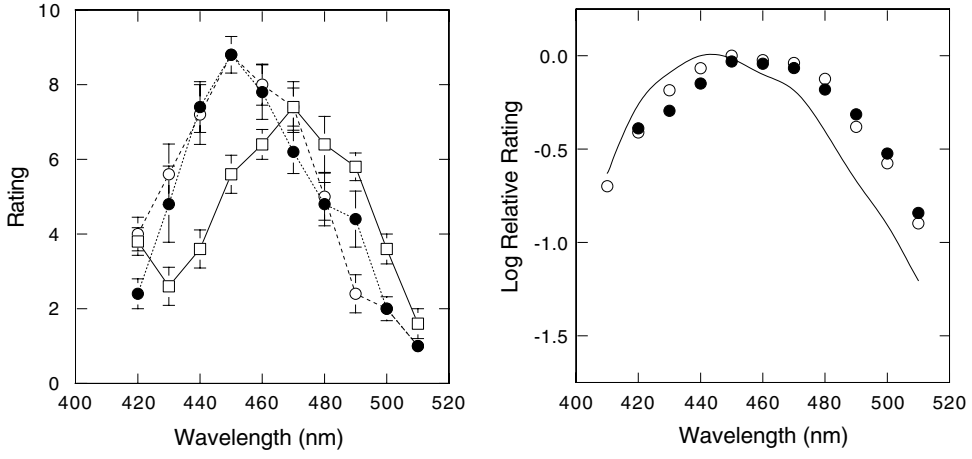

Fig. 2. Rating of the perceived strength or salience of the negative afterimage as a function of the wavelength of the monochromatic adapting fields. Left panel shows results for three individual observers. Error bars denote ±1 standard error of the mean. Right panel (filled symbols) shows the results averaged over observers, plotted in terms of log relative ratings and compared to the log relative spectral sensitivity function of the short-wavelength sensitive cones (smooth curve). Open symbols are data from Magnussen et al. (2001, Fig. 1) representing *rating strength* of the foveal blue scotoma as a function of the wavelength of a temporally modulated field.

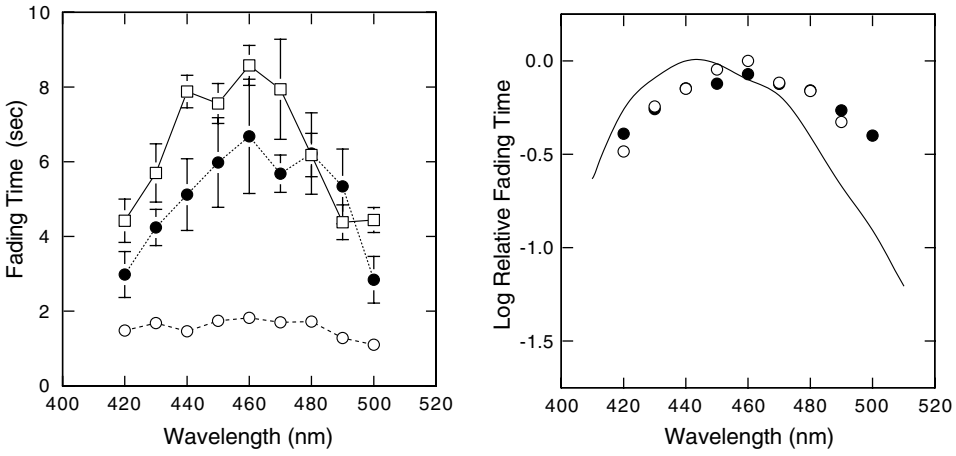

Fig. 3. Filling-in times of the central bright spot, or hole, in the negative afterimage plotted as a function of the wavelength of the adapting field. Left panel shows results for three individual observers. Error bars denote ±1 standard error of the mean. Right panel (filled symbols) shows results averaged for two observers and plotted as log relative fading time; curve as in Fig. 2. Open symbols are data from Magnussen et al. (2001, Fig. 2) representing *fading time* of the foveal blue scotoma as a function of the wavelength of a temporally modulated field.

modulated temporally as in Experiment 1. Fading was timed by the observer using an electronic stopwatch; the watch was started the moment the central white spot became visible (the offset of the adapting field) and stopped when it disappeared, merging into the background. The time was read off by the experimenter. Trials were separated by a minimum of 2 min to permit the previous afterimage to decay completely. Each observer was tested five times at each wavelength in random order.

3.2. Results

Mean filling-in times varied between 1.1 and 8.6 s depending upon the wavelength of the adapting stimulus, with substantial inter-individual differences. The data for individual observers are shown in the left panel of Fig. 3; the grand means are plotted in terms of log relative filling-in time in the right panel (filled symbols). Also shown in Fig. 3 is the relative sensitivity function of the S-cones and previous estimates of the fading time of the dark spot reported on a short-wave field (Magnussen et al., 2001, Fig. 2). Only two of the three observers are included in the mean data of the right panel because of a floor effect in measuring fading time for one observer (open circles, left panel). The correspondence between the S-cone sensitivity and filling-in times is quite good, considering that a precise match between spectral sensitivity and fading times, or between sensitivity and rating scale values, is not expected.

4. Experiment 3: Relations between the foveal blue scotoma, spatial distribution of S-cones and macular pigment density

The central blue scotoma unveiled in the negative afterimage has a diameter similar to the area of the foveola that is devoid of S-cones (Curcio et al., 1991) and also the retinal area that usually has the peak macular pigment density (Werner et al., 1987). Because individuals vary in both their S-cone and macular pigment distributions, it is not possible from the previous experiments to be certain whether one of these factors is relatively more important in producing the foveal blue scotoma. This experiment was designed to correlate the bright spot observed in the center of the negative afterimage produced by a short-wave test field with the spatial variations in macular pigment density and the area that is devoid of S-cones, as assessed by color confusions characteristic of tritanopia.

4.1. Methods

Three trichromatic observers (ages 29–39 years) participated in each condition of this experiment; they had not participated in the prior experiments. Practice sessions were provided prior to formal data collection. There were four test conditions: (1) measurement of the size of the bright center spot in the negative afterimage following extinction of a short-wave adapting field as in Experiment 1; (2) determination of tritan pairs for individual observers (i.e., lights that differ only in terms of S-cone excitation, but not M- and L-cone excitation); (3) comparison of discriminability of tritan pairs for stimuli of varying diameter (smaller and larger than the diameter of the bright central area of the negative afterimage); and (4) measurement of the spatial distribution of macular pigment density. The first three test conditions were made possible using a five-channel Maxwellian-view optical system similar to that used for Experiments 1 and 2. Trial lenses were inserted to correct for refractive error. Details of the apparatus and calibrations are described elsewhere (Werner, Bieber, & Schefrin, 2000).

Each condition of testing was initiated following 10 min of dark adaptation. A reticle placed in a collimated path of the white, temporally modulated background was used for measuring the size of the central white zone of the negative afterimage as in Experiment 1.

To identify individual pairs of lights falling on a tritanopic confusion line, subjects matched the appearance of a middle-wavelength light to a 420 nm reference. Color-matching commenced following five minutes of adaptation to a 5.4°, 420 nm field having a retinal illuminance of 115 Td. This adapting field was selected to suppress the relative sensitivity of S-cones and was viewed continuously during the matching experiment. Then, a 2.4° bipartite test field was superimposed onto the adapting field; the right half was composed of the 420 nm standard (400 Td) and the left was composed of a variable wavelength. The wavelength and radiance of the left hemi-field were controlled by the experimenter and the observer, respectively. The subject's task was to vary the radiance of the variable wavelength to see if a match could be found with the 420 nm standard. The wavelength of this metamer and the short-wavelength standard defined the individual's tritan pair.

The next task was designed to determine the size of the tritanopic area of the foveola. Following dark adaptation, the tritan pairs were presented in a bipartite field at various retinal subtenses on a dark background. The field sizes were 2.4° (the size at which the tritan pairs were determined) and four smaller field sizes ranging from 18 to 37.9 arcmin. The subject's task was to indicate whether the two half-fields matched, as expected if the bipartite field fell upon a tritanopic region of retina, but not if they stimulated S-cones. Field size was varied randomly.

The optical density and distribution of the macular pigment at 15, 30 min, 1°, 1.75° and 7° retinal eccentricity was assessed using heterochromatic flicker photometry on a short-wave adapting field (Werner et al., 1987). For this study we employed the densitometer by Macular Metrics, Providence, RI (Wooten, Hammond, Land, & Snodderly, 1999). A 10°, 3.0 cd/m^2, 470 nm, adapting background was presented continuously and one of the following five test stimuli was superimposed on its center: two test spots of 15 min and 30 min diameter, two circular rings of 1° and 1.75° and a 2° circle for the peripheral measurement. The test stimuli were composed of two narrow-band lights (from LEDs) having dominant wavelengths of 460 and 550 nm, that were alternated in square-wave counterphase at 16–23 Hz for the four central stimuli and 10–12 Hz for the peripheral one. The flicker frequency was based on preliminary tests of individual flicker sensitivity at each retinal eccentricity. The subject's task was to eliminate or minimize the flicker by turning a dial that changed the radiance ratio of the two wavelengths while maintaining a constant overall luminance. The subject viewed the stimulus in free view from a chin and forehead rest and with refractive correction. Four measurements were obtained at each retinal eccentricity.

4.2. Results

All observers described the negative afterimage similarly to the three observers tested in Experiments 1 and 2. Two of the three observers, however, reported that the bright center spot in the negative afterimage was a somewhat irregular or jagged circle. This was more clearly observed with a 440 nm inducing field (the peak sensitivity of S-cones, specified at the cornea) than with a 460 nm inducing field (the peak density of the macular pigment absorption spectrum). In the latter case, the edges were less discrete. Regardless of wavelength, the border defining the outer rim of the annulus was relatively subtle compared to the perimeter of the central bright spot.

The size of the central white spot with a 440 nm adapting field had a mean diameter of 33 arcmin (range = 24.8–44.3 arcmin), and is consistent with the size shown in Fig. 1 based on three other observers, considering that the range of estimates within subjects for these three observers was ~11 arcmin. The reason for this range is perhaps due to slight eye movements and a change in the size over the duration of the afterimage. Two observers reported that the central white portion of the negative afterimage may have been slightly larger in the early afterimage.

The mean matching wavelength to the 420 nm standard for the three observers was 531 nm (range = 529–532.5 nm), consistent with a previous study (Schefrin, Shinomori, & Werner, 1995). When the tritan pairs were presented in the absence of the short-wave adapting field, the two sides of the bipartite field were discriminable at the size for which they were determined (2.4°) and much smaller sizes, but never for sizes $\leqslant$ 20 arcmin. If fixation was shifted or the stimulus diameter was increased slightly above the maximum size at which the hemi-fields matched (by as little as 10 arcmin), the match was upset. The mean midpoint between the largest field diameter over which the hemifields matched and the smallest diameter at which they did not match was 27.3 arcmin (range = 24.3–33.3 arcmin), in close agreement with the 25 arcmin estimates of the tritanopic foveal area reported elsewhere (Williams, MacLeod, & Hayhoe, 1981a).

Fig. 4 plots, in separate panels, each observer's macular pigment density as a function of retinal eccentricity. The insets expand the central 1° radius for comparison of each observer's central bright spot in the negative afterimage (dashed line) with their corresponding tritanopic area of the fovea (shaded area). The mean difference in diameter between the central spot of the negative afterimage and the diameter of the same observer's tritanopic region was 7.1 arcmin (range = 0.05–20 arcmin). For two

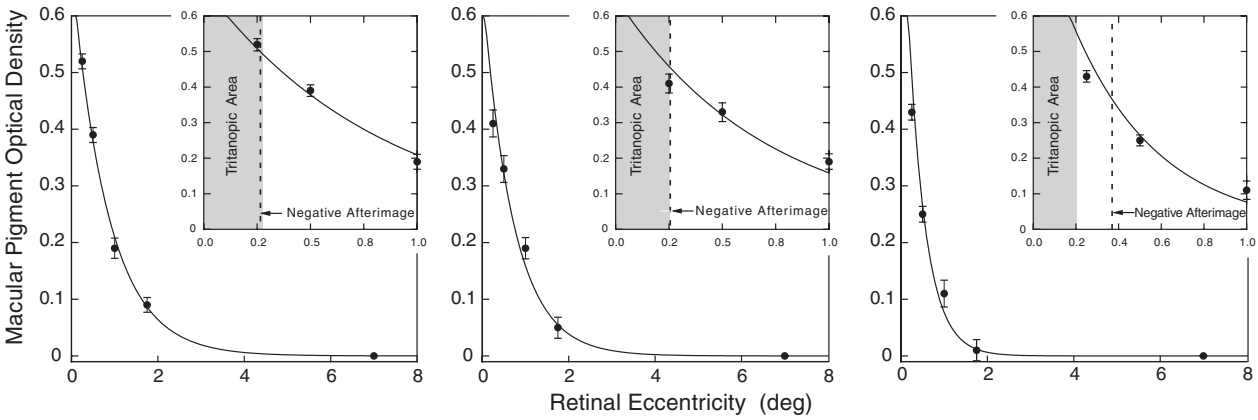

Fig. 4. Macular pigment density is plotted as a function of retinal eccentricity (deg) in separate panels for three observers. Insets show macular pigment density for the central 1° radius compared to the radius of the same observer's tritanopic retinal area (shaded) and the central portion of the negative afterimage (dashed line). Error bars represent ±1 standard error of the mean.

of three observers, the agreement between the two regions was nearly perfect. The third observer reported the greatest difficulty estimating the size of the bright center spot of the negative afterimage. Even in his case, however, the difference between the two sets of estimates encompasses a retinal region containing only about 3–4 S-cones (Curcio et al., 1991; Williams et al., 1981b). These results are consistent with the conclusion that the central zone of the negative afterimage is tritanopic (i.e., devoid of S-cones), but the surrounding area is trichromatic.

The spatial distribution of macular pigment can be described by an exponential for these observers as shown by fitted functions in each panel. Although macular pigment density is highest in the central zone of the negative afterimage, it is present at substantial density outside this zone and thus cannot be responsible for the central bright spot in the negative afterimage. The macular pigment distribution approaches an asymptotic level, however, at an eccentricity that appears to correspond to the outer diameter of the lighter annular region of the negative afterimage.

5. Discussion

Under ordinary viewing conditions the foveal blue scotoma is not visible to the human observer because of rapid filling-in (Magnussen et al., 2001). This filling-in process may be counteracted by restoring neural activity along the border defined by the retinal area where S-cones are absent and the surround where they are present. Thus, in analogy with stabilized retinal images (Barlow & Sparrock, 1964; Krauskopf, 1963), flickering a monochromatic short-wavelength background field prevents filling-in and makes the scotoma visible as a tiny *dark* spot in the central fovea (Magnussen et al., 2001). In the present study we have shown that the blue scotoma is visible in the negative afterimage of such an adapting field as a *bright* white spot and its size corresponds to the tritanopic area of the central foveola. The center of the negative afterimage thus mirrors the absence of the S-cones and not the uniform physical stimulus or its uniform appearance when presented as a steady field. The bright spot in the negative afterimage resulting from the lack of S-cones has no counterpart in normal vision. The uniform blue experienced in the area corresponding to the S-cone scotoma must, therefore, be assigned by lateral processes beyond the receptors (i.e., filling-in).

In addition to the absence of S-cones in the central foveola, short-wave sensitivity is attenuated by the presence of the yellow pigmentation of the macula. The peak macular pigment absorption is at 460 nm (Bone, Landrum, & Cains, 1992) and was shown here to have its highest density in the foveola, in agreement with previous studies (Hammond et al., 1997; Werner et al., 1987, 2000). The macular pigment is thought to be responsible for the entoptic phenomenon of Maxwell's spot (Nussbaum et al., 1981) which has an overall diameter of approximately 2.5°–3° visual angle (Miles, 1954; Spencer, 1967). Macular pigmentation may have contributed to the results presented in Figs. 2 and 3 by shifting the visibility curves for the bright center spot to longer wavelengths compared to the S-cone sensitivity function, but its principle effect is on the appearance of the afterimage in which the region of Maxwell's spot was visible as an inner surround.

The spectral dependence of visibility and filling-in times follow approximately the spectral sensitivity function of the S-cones (Magnussen et al., 2001; present study). Depending upon changes in the state of the receptors, an afterimage is a perfectly stabilized retinal event. So why is it not filled-in instantaneously? The answer is that afterimages are spatially, but not temporally, stabilized: In the negative afterimage, filling-in is temporarily prevented in the early phases of the afterimage because of the spatio-temporal activity gradient along

the border between the non-adapted foveal center and the rapidly recovering sensitivity of the adapted surround. When the recovery process slows down, the activity becomes less and the hole in the afterimage fills in.

In conclusion, the present results, together with the results of our previous study (Magnussen et al., 2001), provide strong evidence that the lack of visibility of the foveal S-cone scotoma in normal viewing is the result of post-receptoral—neural—filling-in processes.

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