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A new look at the Bezold–Brücke hue shift in the peripheral retina

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Abstract

Experiments were conducted with a bipartite field to better understand the Bezold–Brücke hue shift in the peripheral retina. The first experiment measured hue shift in the fovea and at 1° and 8° along the horizontal meridian of the nasal retina for nominal test wavelengths of 430, 450, 490, 520 and 610 nm. Peripheral measurements were obtained under two adaptation conditions: after 30 min dark adaptation and following a rod-bleach. Results indicated that foveal hue shifts differed from those obtained after a rod-bleach. Data from the rod-bleach and no-bleach conditions in the periphery were similar, indicating that rods could not account for the differences between the foveal data and the rod-bleach peripheral data. Hue shifts obtained for the 520 nm test stimulus, and to a smaller extent other test wavelengths, at 8° nasal retinal eccentricity revealed that the wavelength of the matching stimulus depended upon the lateral position of the matching and test fields, and this effect was greater in the no-bleach condition than the rod-bleach condition. Several factors were investigated in experiments 2 and 3 to explain the results with the 520 nm test field. It appears that differential rod density under the two half fields and the compression of photoreceptors by the optic disk may partially, but not fully, account for the 520 nm effect.

Keywords: Bezold–Brücke; Color; Rod; Cone; Vision

1. Introduction

The Bezold–Brücke hue shift is a perceptual change in hue when the intensity of a stimulus is increased or decreased. Research on the Bezold–Brücke hue shift has focused primarily on the hue shifts perceived with foveally presented stimuli. Results from these studies indicate a predictable direction in hue shift with changes in intensity (Boynton & Gordon, 1965; Cohen, 1975; Coren & Keith, 1970; Ejima & Takahashi, 1984; Jacobs & Wascher, 1967; Judd, 1951; Luria, 1967; Nagy, 1980; Nagy & Zacks, 1977; Purdy, 1931, 1937; Savoie, 1973; van der Wildt & Bouman, 1968). Specifically, with increasing intensity, longer wavelengths appear more yellow and shorter wavelengths appear more blue. When intensity is decreased, shorter and longer wavelengths become redder in appearance while middle-wavelengths appear greener.

Weale (1964) explained the Bezold–Brücke hue shifts in terms of differential bleaching, or adaptation, of photopigment. He proposed that the photopigment most sensitive to a particular stimulus adapted as the intensity of a stimulus increased. As one cone type adapted to a greater extent than the other two, the probability increased that another cone type, initially less sensitive to the test stimulus, would absorb light photons, and thus produce a change in the ratio of cone activities, and a commensurate change in perceived hue. Vos (1986) further elaborated on this notion of receptor adaptation to explain the Bezold–Brücke hue shift.

Several post-receptoral explanations have also been proposed to account for this perceptual effect: (1) the red/green (R/G) mechanism has a lower threshold than the yellow/blue (Y/B) mechanism (Judd, 1951; Yager & Taylor, 1970), (2) the response function of the Y/B mechanism has a faster growth rate than that of the R/G mechanism (Hurvich & Jameson, 1957; Yager & Taylor, 1970), (3) the response function of the Y/B mechanism is non-linear (Ejima & Takahashi, 1984), and (4) response saturation occurs at a post-receptoral site rather than at the receptoral level (Walraven, 1961). Regardless of the model, each presumes that as intensity increases, the Y/B signal increasingly dominates the R/G signal.

Unlike previously cited research that examined the Bezold–Brücke hue shift in the fovea, Stabell and Stabell

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(1979a, 1982) investigated this perceptual experience in the peripheral retina. Their first study measured the Bezold–Brücke hue shift at four eccentricities (1.5°, 6°, 9°, 14°) in the temporal retina under two conditions: after a rod-bleach and after 30 min dark adaptation. The peripheral test stimulus was presented at one of several intensity levels (1–1000 td); the foveal comparison stimulus was maintained at approximately 10 td. They found changes with retinal eccentricity such that the closer the stimulus was to the fovea the more similar the hue shift was to that reported in the fovea. Furthermore, at more eccentric locations, greater differences were shown between hue shifts measured after a rod-bleach vs. those measured after 30 min dark adaptation. These differences were most notable at the lower intensity levels, with the most pronounced effect being an increase in the perception of yellowness in the peripheral retina after 30 min dark adaptation. Stabell and Stabell (1979a) attributed their results to the involvement of rods in hue perception.

In a similar study, Stabell and Stabell (1982) investigated hue shifts after a rod-bleach in the far periphery of the temporal (40° and 70°) and nasal retinas (25°, 40°, 60°). At these eccentricities, peripheral stimuli from 490 to 650 nm appeared mostly yellowish at the three lowest intensity levels. As stimulus intensity increased, the peripheral stimuli appeared greener or redder. These hue shifts were in the opposite direction from those reported in the foveal studies.

Some procedural factors, however, may have influenced the results that Stabell and Stabell (1979a, 1982) obtained in their two studies. First, only one stimulus size was used at the different eccentricities in each study ($1° \times 1°$ in the 1979a study and $1° \times 2°$ in the 1982 study). It is possible that at the retinal eccentricities they investigated the stimulus was too small to fill the perceptive field sizes of the four elemental hues. In particular, it is known that the perceptive field size for green is three to five times larger than those of the other hues (Abramov, Gordon, & Chan, 1991). This may explain the appearance of yellow rather than green at the low intensity levels. The higher stimulus intensities may have compensated for the small stimulus size and allowed the perception of green. Second, as Purdy (1931) noted, the greater the difference between the test and matching fields in intensity, the more difficult the task is for observers to match hues; and when the intensity ratio between the fields exceed 20:1, Purdy claimed it was impossible for observers to obtain a hue match. In both Stabell and Stabell studies (1979a,1982), the intensity of the matching field was the same despite changes in the intensity of the test field. For example, a 1000 td test field in the periphery was matched to a 10 td foveal matching field. Likewise, a 1 td test field in the periphery was also matched to the 10 td foveal field. So in some instances, the test field was of higher intensity than the matching field, and in others the test field was of lower intensity than the matching field. To make hue judgments easier for observers, other researchers (e.g., Nagy, 1980; Nagy & Zacks, 1977; Savoie, 1973) maintained a constant difference between the test and matching fields as intensity increased and reported results comparable to those of Purdy (1931) rather than Stabell and Stabell (1979a, 1982). With this technique there is no switch in the intensity relationship between the test and matching fields, i.e., the test is either at a higher or lower intensity than the matching field throughout the experiment. A third factor that may have influenced the results from Stabell and Stabell is that they employed an asymmetric hue-matching technique rather than the use of two fields presented to the same retinal area (e.g., Purdy, 1931). In an asymmetric matching procedure, regardless of the retinal placement of the test stimulus, the observer's task is to match its hue to the hue of the stimulus presented in the fovea. It is well documented that the receptor mosaic differs across the retina (Curcio et al., 1991; Curcio, Sloan, Kalina, & Hendrickson, 1990). In particular, the distribution of rods and short-wavelength-sensitive (S) cones changes dramatically within the retinal region tested by Stabell and Stabell (1979a, 1982). Differences in the receptor complement underlying the test stimulus from that underlying the matching stimulus could have contributed to differences in hue perception.

Findings from other psychophysical studies suggest that rods may contribute a blueness perception (Ambler & Proctor, 1976; Buck, Knight, & Bechtold, 2000; Trezona, 1974). It has been demonstrated that rod and short-wavelength signals linearly summate (Naarendorp, Rice, & Sieving, 1996), implying a rod interaction or influence on cone signals and the subsequent chromatic pathway. Similarly, there is physiological evidence to suggest "cross-talk" between rods and cones. For example, there are known gap junctions between rods and cones, which are activated at light levels between cone and rod thresholds (Daw, Jensen, & Brunken, 1990) and rod modulation of the membrane potential of cones (Schneeweis & Schnapf, 1995). Farther along the pathway, rod signals are known to travel along a cone pathway via amacrine cells (Daw et al., 1990), and rod signals have been detected in recordings from parvocellular cells (Lee, Smith, Pokorny, & Kremers, 1997). Since rods interact with more than just S cones, one might conclude that rods contribute more than a blueness perception. Studies of unique hues and hue perception in the peripheral retina (Angel, 2003; Buck, Knight, Fowler, & Hunt, 1998, 2000; Nerger, Volbrecht, & Haase, 2003; Nerger, Volbrecht, & Ayde, 1995; Nerger, Volbrecht, Ayde, & Imhoff, 1998; Volbrecht, Nerger, Imhoff, & Ayde, 2000) support this contention.

Physiological and psychophysical evidence suggests the Bezold–Brücke hue shift may differ in the peripheral

retina as compared to the fovea due to the influence of rods. Hue matches made in the peripheral retina may, for example, show more blueness perception at lower luminance levels but less blue as intensity levels increase and rods saturate. On the other hand, if the parvocellular cells are the mediators of the R/G opponent mechanism, as some two-stage models of color perception propose, perhaps the amount of redness or greenness will differ at the lower luminance levels when rods are activated. Although difficult to address from the physiological findings, psychophysical studies (e.g., Buck et al., 1998; Stabell & Stabell, 1979a, 1982, 1996) provide evidence that rods may also influence the perception of yellow. This study, in three different experiments, systematically examines the Bezold–Brücke effect in the peripheral retina under conditions chosen to elucidate the contribution of rods to hue shifts.

2. Experiment 1

2.1. Observers

Two females and one male served as observers in this experiment. All participants had normal or corrected-to-normal visual acuity and normal trichromatic color vision as assessed by the Neitz anomaloscope, the F-2 tritan plate, and a series of three panel tests: D-15, Adams desaturated D-15, and Farnsworth–Munsell 100-hue. The Colorado State University institutional review board for human subject research approved the procedures used in this experiment as well as in the subsequent experiments.

2.2. Apparatus

All experiments were conducted on a three-channel Maxwellian-view optical system, with a 300-W (5500 K) xenon arc lamp regulated at 290 W by a dc power supply (Oriel). After passing through infrared heat-absorbing filters, two collimating lenses captured the light from the two exit ports of the lamp housing. Throughout the system, pairs of achromatic, doublet lenses were used to focus and collimate the light of the three channels. Light from channel 1 was focused onto the entrance slit of a grating monochromator (Instruments SA, Inc., Model H20, 4 nm half-bandpass) and produced the matching half of the bipartite field. Channel 2 generated the test half of the bipartite field; the spectral composition of this channel was defined by narrowband interference filters (Ditric Optics) placed in collimated light. Channel 3 created the fixation arrays and produced the broadband (5500 K) bleaching field. Intensity levels of all three channels were manipulated by neutral density filters and/or neutral density wedges. Field stops placed in collimated portions of light defined shape and size of stimuli and fixation points. A shutter and driver system (Uniblitz) placed at a focal point where lights from channels 1 and 2 were combined controlled the stimulus presentation. The final size of the Maxwellian image, defined by an artificial pupil, was <2 mm. Observers aligned their right eye to the optical system using a dental impression bite bar capable of movement in the X, Y, and Z planes.

2.3. Stimuli

Three retinal locations were studied: 0° (fovea), and 1° and 8° in the nasal retina. Circular stimuli (0.4° in the fovea, 0.2 and 0.9° at 1° retinal eccentricity, 0.4° and 1.5° at 8° retinal eccentricity) were vertically divided to produce two juxtaposed half fields. One half was the ''test field'' and was set at a fixed wavelength via the interference filters; the other half was the ''matching field'' in which wavelength was manipulated via the grating monochromator. The lateral positioning of the test and matching fields was counterbalanced across experimental sessions. The circular diameter of the largest stimuli just filled the perceptive fields of the four elementary hues at all three retinal locations (Abramov et al., 1991). The half fields were separated by a small vertical gap to avoid brightness induction effects (Purdy, 1931). This gap also helped observers to differentiate perceptually between the two fields (Nagy, 1980; Stabell & Stabell, 1977a, 1977b). To compensate for decreased acuity in the peripheral retinal, the hairline gap used in the fovea was increased slightly with retinal eccentricity.

Five wavelengths were chosen for the test field: 430, 450, 490, 520 and 610 nm. The three shorter wavelengths were chosen to investigate the influence of rods on blueness perception as well as on short-wavelength redness. The two longer wavelengths were selected to examine the changes in the perception of greenness, yellowness, and long-wavelength redness with rod input. Two of the three observers were tested with all five wavelengths and a third was tested on all wavelengths except 520 nm.

Following from the work of Nagy (1980) and Savoie (1973), the test field was maintained at an intensity level 0.5 log units higher than the matching field. Four intensity pairings were used: 0.7 and 1.2, 1.2 and 1.7, 1.7 and 2.2, and 2.2 and 2.7 log tds. In all conditions, stimuli were presented for 1 s every 7 s; and observers were permitted to view the stimuli as many times as needed to make a hue judgment.

A 6.7 log scotopic td, broadband (5500 K), circular field measuring 14.5° in diameter was used as the bleaching field in the rod-bleach conditions. A 10 s adaptation period to this field was calculated to bleach 99% of the rod pigment (Alpern, 1971; Rushton & Powell, 1972).

2.4. Calibration

Radiometric measures were made with an EG&G Gamma Scientific radiometer (DR-1500 A). Photometric measures for the rod-bleaching field and at one reference point, 540 nm, were obtained with a Minolta Chroma Meter (CS-100). Retinal illuminances were computed using the method outlined by Westheimer (1966). Neutral density wedges and filters were calibrated from 400 to 700 nm in 10 nm increments. The monochromator was calibrated to a He–Ne laser (Spectra-Physics; 632.8 nm). The nominal values of the interference filters were: 430, 450, 490, 520, and 610 nm. Spectroradiometric measurements were made for the five interference filters from 400 to 700 nm in 1 nm steps. The spectral transmittances of the narrowband interference filters are shown in Fig. 1. The wavelength of peak transmission as well as the half bandwidth of each filter is noted in the figure.

2.5. Procedure

2.5.1. Foveal and rod-bleach conditions

At the start of each experimental session, observers dark adapted for 10 min. Presentation of foveal stimuli immediately followed the dark adaptation period. At 1° and 8° nasal retinal eccentricity, the bleaching field was presented to minimize rod contribution to the hue signal in the peripheral retina. Following the 10 s bleach, observers dark adapted for an additional 4.5 min to ensure the stimulus presentations commenced along the time period associated with the cone plateau. The maximum testing period for the rod-bleach condition was 10 min post-bleach.

Employing the forced-choice procedures of Nagy (1980), Nagy and Zacks (1977) and Savoie (1973), observers made binary hue decisions between the test and matching fields of the bipartite stimulus. For example, if the test field was set at 610 nm (orange), the observer decided whether the matching field appeared more red or more yellow than the test field. If the test field was fixed at either 430 or 450 nm, the hue decision was between red and blue. For 490 nm, the hue choices were green and blue, and for 520 nm green and yellow.

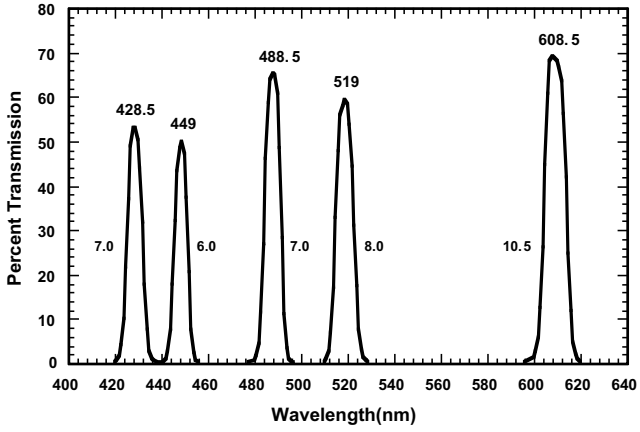

Fig. 1. Percent transmission is plotted as a function of wavelength (nm). Each curve denotes the spectral transmission for each interference filter used to generate the test half fields. The wavelength of peak transmission is noted at the peak of each function. The half bandwidth of each interference filter is specified on the side of each function.

The wavelength of the monochromatic matching field was presented using a double random-staircase procedure. Starting points for each of the two staircases bracketed the region containing the hue match. These points were selected so that initial hue judgments could be made easily. After presentation of the anchors, wavelengths were decreased or increased, based on the response given by the observer. Decreases in wavelength step size continued until reaching a size of 2 nm. Each staircase was terminated after four response reversals at this smallest step size. For the peripheral locations, combinations of intensity level, test size, and retinal eccentricity were randomly selected for each experimental session. For the fovea, intensity levels were always presented in ascending order to avoid differential adaptation of the retina. Approximately 30, 2-h sessions were required for each observer.

2.5.2. No-bleach condition

The effects of rod signals on the Bezold–Brücke hue shift were further investigated with two of the observers. Prior to the beginning of a session, observers adapted to the dark for 30 min. Half of the experimental sessions began at 1° nasal retinal eccentricity followed by presentations at 8° in the nasal retina; in the other half of the sessions, the order of peripheral locations was reversed. Because neither observer could differentiate hue in the smaller half fields, only the large stimuli (0.9° at 1° nasal retinal eccentricity and 1.5° at 8° nasal eccentricity) were used in the no-bleach condition. Other than the changes noted in this section, the experimental procedure was the same as that described for the fovea and rod-bleach conditions.

2.6. Results and discussion

The mean wavelength of the matching stimulus was computed for each test wavelength at each luminance pairing for each observer in each experimental condition. Only the data from the large stimuli are presented since there was no difference in wavelength shifts between the small and large test stimuli across retinal eccentricities and test wavelengths in the rod-bleach condition. Recall, that only the larger stimulus sizes were employed in the no-bleach condition. Similarly, only the foveal and 8° retinal eccentricity data are presented since there is no difference between the data ob-

tained from the 1° and 8° nasal eccentricities in the rod-bleach condition.

2.6.1. Fovea vs. rod-bleach condition

In Figs. 2 and 3 the intensity of the matching stimulus (log td) is specified as a function of the mean matching wavelength (nm) for the fovea (left panels) and the 8° nasal rod-bleach condition (right panels). Each row of panels represents a particular test wavelength (nominal value of the interference filter); different symbols denote the different observers. The vertical dashed line specifies the wavelength at peak transmission for the interference filter that generated the test stimulus. Error bars represent ±1 standard error of the means (SEM) based on between session variability of the matching wavelength.

In general, the results from Fig. 2 indicate that the measurements for the rod-bleach condition differ from the measurements made in the fovea for the 430 test stimuli. For 430 nm, the foveal matching data (upper left panel) are relatively invariant with increasing intensity while the rod-bleach data (upper right panel) show a shift to shorter wavelengths with increasing intensity. Since the test stimulus is 0.5 log td more intense than the matching stimulus, the test stimulus should become bluer as intensity increases (traditional Bezold–Brücke hue shift); and the wavelength of the matching stimulus should shift to a longer wavelength to compensate for the change in hue. This pattern is observed in the fovea for all three observers and in the peripheral retina at the three lower luminance levels for one observer (closed triangles). Thus, the results from the fovea follow the conventional Bezold–Brücke pattern while the data from the 8° retinal eccentricity in the rod-bleach condition deviate from the conventional hue shift for two of the three observers (closed circles and closed squares). It is difficult to compare the 430 nm foveal results of this study to previous studies since none of them used a wavelength as short as 430 nm; however, the shift is in the same direction as that reported by Boynton and Gordon (1965) for a 440 nm stimulus. Stabell and Stabell's (1979a) shortest test wavelength at 6° and 9° temporal eccentricity was 440 nm at 1 and 3 tds. Under these conditions the test stimulus was less intense than the matching field in the fovea, so according to predictions from the Bezold–Brücke hue shift, the test stimulus should appear redder than the matching field. Consequently, the matching wavelength should shift shorter than 440 nm. The wavelength of the

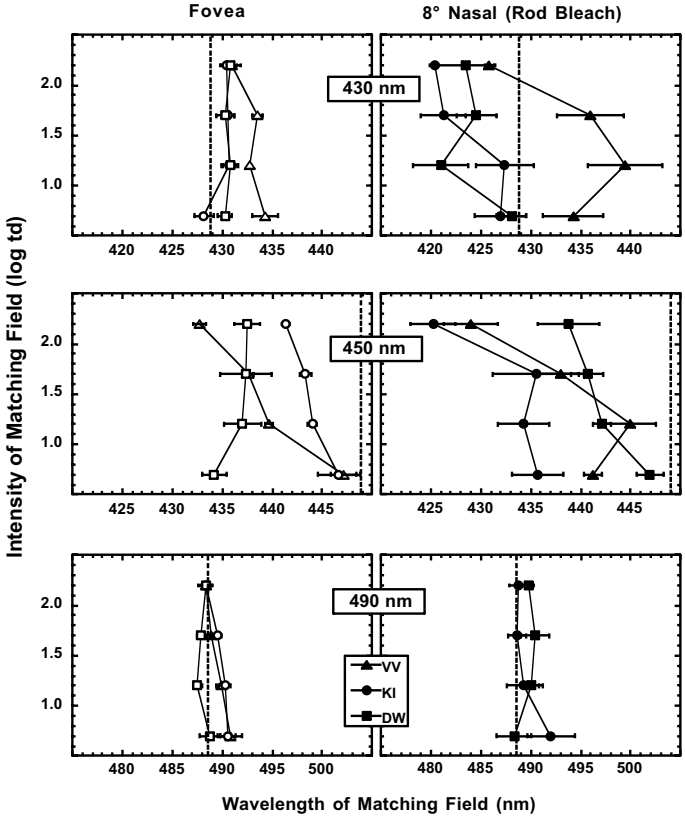

Fig. 2. Matching field intensity plotted as a function of mean matching wavelength (nm) for the fovea (left column) and the rod-bleach condition at 8° nasal eccentricity (right column). Each row denotes a particular test wavelength, and different symbols specify different psychophysical observers. The vertical dashed line indicates the wavelength of peak transmission. Error bars represent ±1 standard error of the mean (SEM).

matching field in the Stabell and Stabell study, though, shifted to longer wavelengths in the rod-bleach condition, contrary to the Bezold–Brücke prediction.

Similar to the 430 nm test stimulus, the wavelength of the matching stimulus for the 450 nm stimulus should be longer than 450 nm, consistent with the traditional Bezold–Brücke perception. Neither the data from the fovea (Fig. 2, middle left panel) nor from the 8° nasal retina (Fig. 2, middle right panel) reveal this pattern. The foveal results are contrary to previous studies using stimuli between 445 and 460 nm (e.g., Boynton & Gordon, 1965; Cohen, 1975; Luria, 1967; Purdy, 1931, 1937; van der Wildt & Bouman, 1968). Stabell and Stabell (1979a), however, showed no shift in the matching wavelength for a 460 nm stimulus when the foveal matching field (10 td) was more intense than the foveal test field (1 and 3 tds). Unlike the foveal results, Stabell and Stabell (1979a) reported a substantial shift to longer wavelengths in the foveal matching field for the 460 nm stimuli presented at 6° and 9° temporal eccentricity. Again the foveal matching stimulus in the Stabell and Stabell study was more intense than the rod-bleach test stimulus, so following from the traditional Bezold–Brücke predictions, the wavelength of the matching stimulus would be expected to be shorter than the wavelength of the test stimulus. Like the results reported here, Stabell and Stabell's results are opposite to the traditional prediction.

In Fig. 2, the foveal (lower left panel) and rod-bleach (lower right panel) data from the 490 nm test stimulus show a different pattern from the two other shorter wavelengths. For all three observers, the functions are relatively invariant with increasing intensity in both the fovea and 8° nasal eccentricity. The wavelength of the matching stimulus for the two experimental conditions is at the wavelength of peak transmission or shifted to a wavelength slightly shorter or slightly longer than the peak wavelength (approximately −1 to 4 nm). (No measurements were made for observer VV at 8° nasal retinal eccentricity in the rod-bleach condition.) Others have also reported minimal hue shifts within this region of the visible spectrum when stimuli are presented to the fovea (e.g., Boynton & Gordon, 1965; Cohen, 1975; Jacobs & Wascher, 1967; Nagy, 1980; Purdy, 1931, 1937; Stabell & Stabell, 1979a; van der Wildt & Bouman, 1968), as well as relative invariance in matching wavelength with increasing intensity (Cohen, 1975; Nagy, 1980; Purdy, 1937; van der Wildt & Bouman, 1968). One possible explanation is that 490 nm represents an invariant binary hue (blue–green) for our observers (Ayama, Nakatsue, & Kaiser, 1987; Vos, 1986).

Results for the two longer test wavelengths are shown in Fig. 3. The data are plotted in the same manner as in Fig. 2. For the 520 nm stimulus (Fig. 3, upper row), an increase in intensity should produce a perception of more yellow. One would, then, expect the wavelength of the matching stimulus to shift to increasingly longer wavelengths with increasing intensity. For both observers, the wavelength of the matching stimulus in the foveal and rod-bleach conditions was longer than that of the test stimulus, although the shift was not necessarily greater for the higher luminances. The foveal data are consistent with previous findings with a 520 or 525 nm stimulus (Boynton & Gordon, 1965; Cohen, 1975; Jacobs & Wascher, 1967; Luria, 1967; Nagy, 1980; Purdy, 1931, 1937; Stabell & Stabell, 1979a; van der Wildt & Bouman, 1968), although Boynton and Gordon

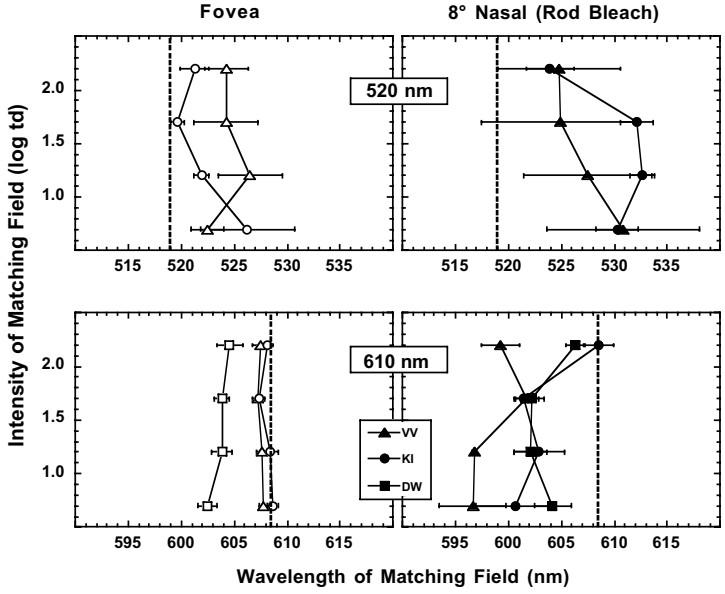

Fig. 3. Data are plotted as in Fig. 2 for the two longer test wavelengths.

(1965) reported some shifts to wavelengths shorter than 520 nm. Stabell and Stabell (1979a) also demonstrated a shift to longer wavelengths when the test field was either more (30, 100, 300, 1000 td) or less (1, 3 td) intense than the foveal matching field at both 6° and 9° temporal eccentricity. Thus, our results for the 520 nm test stimulus appear, at least at first glance, to be consistent with previous studies.

If the 610 nm test stimulus appeared more yellow than the matching stimulus, then the wavelength of the matching stimulus should have shifted to shorter wavelengths. As seen in Fig. 3, this was the case for all three observers in the fovea (lower left panel), although the degree of the shifts was less for two of the observers given the peak transmission (vertical dashed line) of the 610 nm filter. The wavelength for the matching stimulus in the 8° rod-bleach condition (lower right panel) also shifted to shorter wavelengths; this was, in general, most pronounced at the lower luminance levels. The foveal shift noted by others between 600 and 610 nm is overall similar to that shown in the lower row of Fig. 3 (e.g., Boynton & Gordon, 1965; Cohen, 1975; Jacobs & Wascher, 1967; Luria, 1967; Purdy, 1931, 1937; Savoie, 1973; Stabell & Stabell, 1979a; van der Wildt & Bouman, 1968). In the peripheral retina under rod-bleach conditions, Stabell and Stabell (1979a) demonstrated a shift to shorter wavelengths for both a 600 and 620 nm test, despite the intensity relation between the foveal matching and peripheral test fields, i.e., the test field being either more or less intense than the foveal matching field.

Overall, except for the foveal 450 nm test stimulus, our foveal data resembled findings from previous studies and followed the predictions for a Bezold–Brücke hue shift. This is somewhat surprising giving the diversity in stimuli size, duration, and configuration; luminance ratios between test and matching stimuli; and experimental procedures used to investigate the Bezold–Brücke hue shift by the various researchers. It is unclear why our foveal results at 450 nm deviate from previous studies. Only two of the studies have directly and systematically assessed a hue shift with a 450 nm stimulus. In these studies (Boynton & Gordon, 1965; Cohen, 1975), the test field was 10 times more intense than the matching field. In our study the test field was only three times more intense than the matching field. Luria (1967) demonstrated a reduced hue shift with a longer stimulus duration (300 vs. 2 ms) at 445 nm. The stimulus duration in our study was longer (1000 ms) than that in Luria's. Perhaps, the longer duration produced the shift to wavelengths less than 450 nm. Cohen (1975), however, reported no effect of stimulus duration (150–2000 ms) on wavelength shift with a 450 nm stimulus. While it is possible that the luminance ratio or stimulus duration may explain our 450 nm results, it seems unlikely given the apparent robustness of the foveal findings across studies for the other test wavelengths.

Since the measurements at 8° in the nasal retina were made following a rod-bleach, one might assume that the peripheral matches should have been the same as that in the fovea. In some cases, there was little difference between the foveal and 8° rod-bleach data (490 nm); but in most cases, the values did differ (450, 520 and 610 nm), and in one case (430 nm) the hue shifts were in opposite directions. These differences suggest that: (1) there is some rod input into the measurements, (2) there are adaptation effects from the 5500 K bleaching field, (3) the cone mechanisms from the peripheral retina differ from those in the fovea, and/or (4) photopigment optical density differs between the two retinal locations and affects hue perception. It seems unlikely there was rod intrusion in the fovea given the small size (0.4°) of the foveal stimulus. If there was rod input in either the foveal or rod-bleach condition, then the rod input should have been reduced as the intensity level of the test and matching stimuli increased. A review of Figs. 2 and 3 (right panels) shows, however, that there was no consistent difference at the lower intensity levels, nor was it necessarily the case that the wavelength value of the matching stimulus approached the same value as that in the fovea at the higher luminances. It, therefore, seems improbable that rod input was a factor in the rod-bleach condition. Control experiments from previous studies in our laboratory have demonstrated that the 5500 K bleaching field used in this study does not differentially adapt the cone types as evidence by unique hue loci (Nerger et al., 1995) and color-naming functions (Angel, 2003). While Stabell and Stabell (1979a) concluded that their rod-bleach data were similar to their foveal data, and only represented cone input, careful examination of their 6° and 9° temporal data reveal differences between their foveal and rod-bleach data. Other studies on color perception (e.g., Nerger et al., 2003; Stabell & Stabell, 1979b) have also reported differences between data from the fovea and the peripheral retina after a rod-bleach. Taken together, these findings suggest that either the cone mechanisms operate differently in the fovea than in the peripheral retina or cone-photopigment optical density differences between the fovea and the peripheral retina (Burns & Elsner, 1985; Elsner, Burns, & Webb, 1993; Pokorny, Smith, & Starr, 1976) influence hue perception.

2.6.2. Rod-bleach vs. no-bleach

A comparison of the rod-bleach (open symbols) and no-bleach (closed symbols) conditions at 8° nasal retinal eccentricity is presented in Fig. 4. As in the previous figures, the matching stimulus intensity is plotted as a function of the mean matching wavelength. Different symbols denote the two observers (triangles and circles). Error bars are ±1 SEM. The

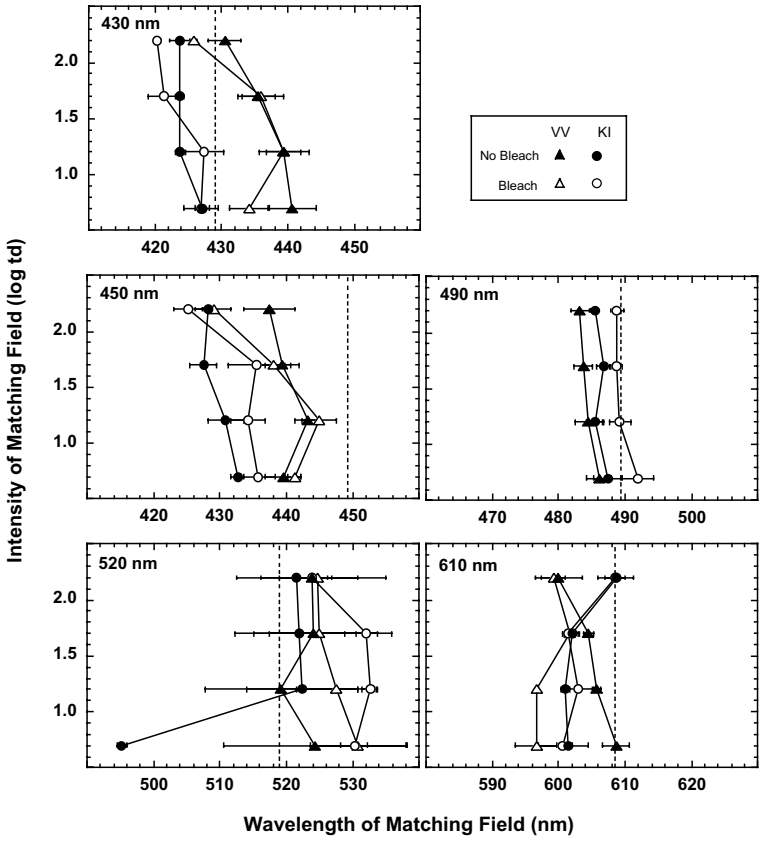

Fig. 4. Matching field intensity plotted as a function of mean matching wavelength (nm) for the no-bleach (closed symbols) and rod-bleach (open symbols) conditions at 8° nasal eccentricity for 430 and 450 nm. Different symbols specify different psychophysical observers. The vertical dashed line indicates the wavelength of peak transmission. Error bars represent ±1 SEM.

vertical dashed line represents the wavelength of peak transmission.

As Fig. 4 indicates, for each observer, the matching wavelength values for the rod-bleach and no-bleach conditions often overlap, in particular at the two shorter test wavelengths, 430 and 450 nm. The greatest differences in wavelength shift between the rod-bleach and no-bleach conditions occur at 490 and 520 nm for observer KI (circles) and at 610 nm for observer VV (triangles). If rod input to hue judgments was greater at the lower intensity levels, one might expect a greater difference between the matching values of the rod-bleach and no-bleach conditions at the lower luminance levels. At 490 nm, the wavelength shift was greater for the no-bleach condition at all intensity levels, but for the 520 and 610 nm test stimuli the wavelength difference in the shift between the two conditions was greater at the lower intensity pairings. In Stabell and Stabell (1979a) study, there was little difference between the rod-bleach and no-bleach conditions in wavelength shift for the 440 and 460 nm test stimuli at 6° temporal eccentricity while the differences between the two conditions at 1 and 3 tds for 440 nm did differ at 9° temporal eccentricity.

Another means to assess the effect of rods is to compare wavelength shifts at different retinal eccentricities. Because the number of rods is greater at 8° nasal retinal eccentricity than at 1° nasal retinal eccentricity (e.g., Curcio et al., 1990), one might expect that wavelength shifts would be greater at 8° than at 1° in the no-bleach condition. This comparison is illustrated in Fig. 5 for the 430 and 450 nm test stimuli. In this figure, open symbols denote data obtained at 1° nasal retinal eccentricity and closed symbols represent data obtained at 8° nasal eccentricity in the no-bleach condition. Different symbols (triangles and circles) within a panel distinguish the two observers, and error bars represent ±1 SEM. As Fig. 5 highlights, there is a greater wavelength shift at 8° (closed symbols) for both the 430 and 450 nm; the greatest difference appears at the lower luminance levels. For the test stimuli at the three longer wavelengths, there was no consistent difference between the two peripheral eccentricities.

In general, conditions chosen to manipulate rod input—stimulus intensity, bleach conditions, and retinal eccentricity—did not show a systematic effect of rods for every wavelength. For example, stimulus intensity by itself did not appear to modulate rod input, the no-bleach condition appeared to affect the wavelength shift with the longer test stimuli at the lower luminance levels, and retinal eccentricity was

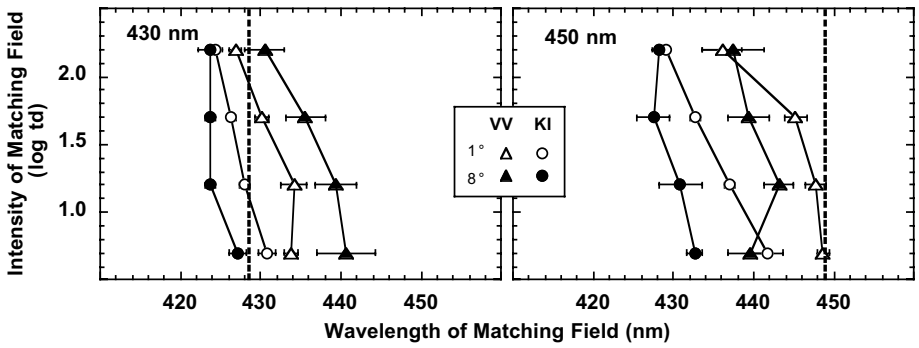

Fig. 5. Comparison of the mean matching wavelengths (nm) between the 1° (open circles) and 8° (closed circles) nasal retinal eccentricities in the no-bleach condition. Each panel denotes a different test wavelength, and different symbols specify different psychophysical observers. The vertical dashed line indicates the wavelength of peak transmission. The error bars represent ±1 SEM.

only a factor for the two shorter test stimuli at the lower luminance levels.

As noted above, the intensity difference between the test and matching stimuli was based on previous studies (Nagy, 1980; Savoie, 1973). Furthermore, Smith, Pokorny, Cohen, and Perera (1968) demonstrated that a 0.5 log td difference in intensity between a test and matching stimulus was sufficient to elicit a Bezold–Brücke hue shift. These studies, though, only investigated hue shifts in the fovea. It is therefore possible that outside the fovea a 0.5 log td difference between the matching and test stimuli was not adequate to induce a hue shift that was not only cone based but also rod-based. This seems unlikely since Stabell and Stabell (1979a) demonstrated wavelength shifts at 6° and 9° temporal eccentricity when the peripheral test field was set at 3 or 30 td and the foveal matching field was 10 td. They, however, utilized an asymmetrical matching procedure, and possibly a 0.5 log td difference was sufficient for their procedure.

2.6.3. Field placement

The variability for the matching wavelengths of the 520 nm test stimulus differed from the other test wavelengths. In particular, as Figs. 3 and 4 illustrate, the SEMs were much greater for the 520 nm matching stimulus, both in the no-bleach and the rod-bleach conditions. For example, in the no-bleach condition at 8° retinal eccentricity for observers VV and KI, the mean SEM (range of SEMs) was 1.90 (0.60–3.72) for 430 nm, 2.16 (0.90–3.84) for 450 nm, 1.42 (0.50–2.05) for 490 nm, 8.69 (0.66–13.88) for 520 nm, and 1.47 (0.60–3.58) for 610 nm. As this comparison illustrates, the mean SEM for the 520 nm condition was approximately four to six times larger than that of the other test wavelengths. A closer analysis reveals that placement of the matching field in relation to the test field influenced the magnitude and/or direction of the wavelength shift of the matching stimulus. This curious result is shown in Fig. 6 for one observer (VV), where matching stimulus intensity (log td) is plotted as a function of matching wavelength (nm) for the rod-bleach (triangles) and no-bleach (circles) condition. Open (closed) symbols denote the placement of the matching field to the left (right) of the test field, and the vertical dashed line specifies the wavelength of peak transmission. Placement of the test and matching field, relative to each other, altered the degree of the wavelength shift in both the rod-bleach and no-bleach conditions for all test stimuli, but the effect was most pronounced at 520 nm. Observer KI (not shown) showed the same pattern of results. No effect of field placement was observed in the fovea or at 1° nasal eccentricity. This effect has not been reported in the literature, though others have used a bipartite field (e.g., Purdy, 1931, 1937; van der Wildt & Bouman, 1968) or two stimuli in close proximity to each other in the fovea (e.g., Nagy, 1980; Nagy & Zacks, 1977; Savoie, 1973). None have reported counterbalancing the test and matching fields, nor have they presented data to show the effects of test and matching field placement. It could be that the effect was present in the earlier studies but not revealed in the analyses employed by the investigators.

Perhaps differences in macular pigment density with matching field locations at 8° nasal retinal eccentricity contributed to the differences in matching wavelength. When the matching field is closer to the fovea relative to the test field, macular pigment density might be greater in the matching field than the test field, but less when the location of the two fields is reversed. These differential density distributions across the two fields would not be a concern in the fovea since the two hemifields are concentrically located with respect to macular pigment. If this is a factor, then differences in matching wavelengths should also be observed at the three shorter wavelengths (430, 450 and 490 nm), where macular pigment absorption is greater compared to the two longer wavelengths. Furthermore, the different bleach

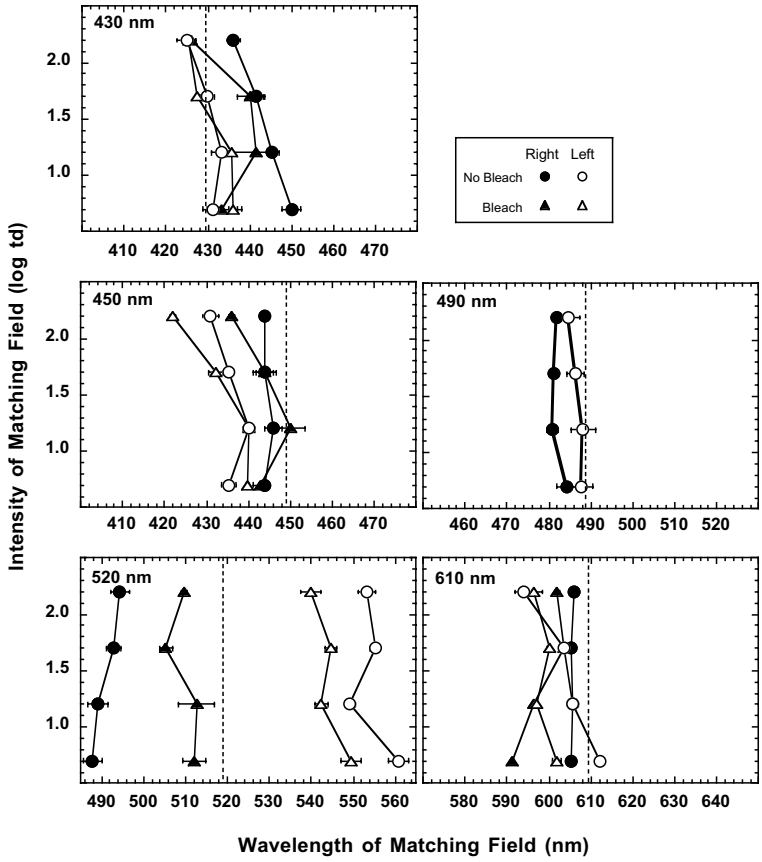

Fig. 6. Matching field intensity plotted as a function of mean matching wavelength (nm) for the left (open symbols) and right (closed symbols) placement of the matching field relative to the test field. Each panel presents a different test wavelength. Different symbols represent the two different bleach conditions: rod-bleach (triangles) and no-bleach (circles). The dashed line is the peak transmission of the 520 nm interference filter. Error bars represent ±1 SEM. The data are from observer VV.

conditions should not have affected these differences, i.e. the differences in matching wavelength with field placement should have been seen in both the bleach and no-bleach conditions. The data in Fig. 6 for the three shorter wavelengths suggest that this interpretation might be plausible, though many studies report that macular pigment density is negligible beyond 6°–7° retinal eccentricity (Bone, Landrum, Fernandez, & Tarsis, 1988; Hammond, Wooten, & Snodderly, 1997; Werner, Bieber, & Schefrin, 2000; Werner, Donnelly, & Kliegl, 1987). Furthermore, the 520 nm stimulus displayed a greater placement effect than the 430, 450, and 490 nm stimuli, a result not consistent with a macular pigment explanation.

A potential concern regarding the field placement finding in Fig. 6 is that the physical characteristics of the matching and test stimuli contributed to this effect. In particular, the matching wavelength was generated by a grating monochromator whereas an interference filter defined the test wavelength. Other studies have used two interference wedges (e.g., Nagy & Zacks, 1977), two monochromators (e.g., Nagy, 1980) or an interference wedge and interference filters (e.g., van der Wildt & Bouman, 1968) to generate the matching and test fields in foveal Bezold–Brücke experiments. While none utilized an interference filter and monochromator to create the stimuli, the positioning of the test field (interference filter) relative to the matching field (monochromator) should not cause the field placement effect seen in Fig. 6. Based on the physical characteristics of the narrowband interference filters used in this study (Fig. 1), it is concluded that the difference in spectral production of the two half fields cannot account for the findings in Fig. 6.

3. Experiment 2

In experiment 2, the field placement effect was further investigated by eliminating the intensity difference between test and matching fields, i.e., the two halves of the bipartite field were equated to the same retinal illuminance.

3.1. Observers

Two females served as psychophysical observers, and each had normal or corrected-to-normal visual acuity and normal trichromatic color vision as determined by the Neitz anomaloscope, a series of three panel tests (D-15, Adams desaturated D-15, and Farnsworth–Munsell 100-hue), and the F-2 tritan plate. One of the two observers, VV, also participated in experiment 1.

3.2. Stimuli

Wavelength matches were obtained in the fovea using a 0.9° and 1.5° vertically divided bipartite field and at 8° nasal eccentricity using a 1.5° vertically divided bipartite field. The smaller bipartite field in the fovea was chosen to include only cones in the measurements while the larger field was selected to include some input from rods. One half was the 520 nm "test field" and was specified by an interference filter; the other half was the "matching field" which was produced by a monochromator. The 520 nm stimulus was selected since it generated the largest field placement effect. The positioning of the test and matching fields was counterbalanced across experimental sessions. The half fields were separated by a hairline gap in the fovea; this gap was slightly increased in the peripheral retina.

Both the test and matching fields were set at 0.7, 1.7, and 2.7 log tds and presented for 1 s every 7 s. Observers were permitted to view the stimuli as many times as needed to make a hue judgment.

3.3. Procedure

The foveal and no-bleach procedures outlined in experiment 1 were employed here. Observers made binary hue judgments between the test and matching fields using a double-random staircase procedure. The intensity of the stimuli was presented in ascending order at both retinal eccentricities.

3.4. Results and discussion

Fig. 7 presents results from one of the observers (VV) for the 0.9° (upper panel) and 1.5° (middle panel) bipartite fields in the fovea and for the 1.5° bipartite field at 8° (lower panel) nasal eccentricity. The data from the other observer were similar to that of VV. The intensity of the matching stimulus (log td) is plotted as a function of the matching wavelength (nm) with placement of the matching field relative to the test field specified by open and closed circles. The vertical dashed lines indicate the peak transmission of the 520 nm interference filter, and the other dashed line the mean matching wavelength.

Fig. 7 shows that placement of the matching field relative to the test field does not matter in the fovea;

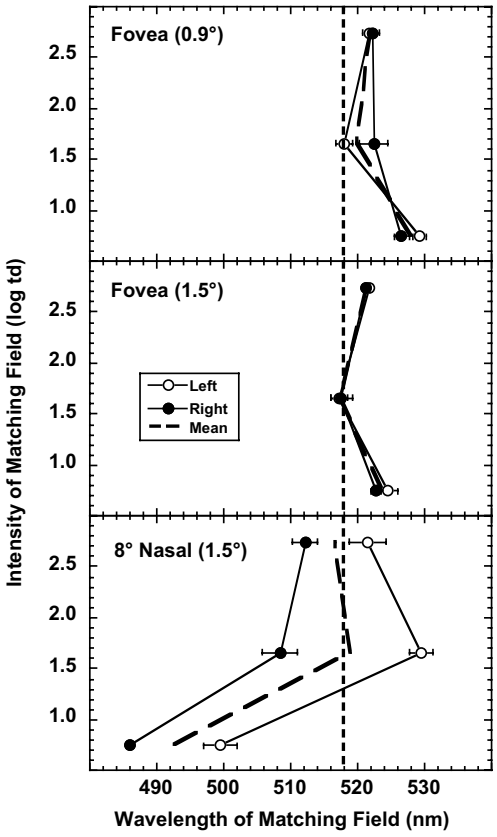

Fig. 7. Matching field intensity plotted as a function of mean matching wavelength (nm) for the left (open symbols) and right (closed symbols) placement of the matching field relative to the test field. Each panel denotes a particular eccentricity and a particular stimulus size for the foveal panels. The non-vertical dashed line indicates the mean wavelength shift across matching field location. The vertical dashed line is the peak transmission wavelength of the 520 nm interference filter. Error bars represent ±1 SEM. The data are from observer VV.

the matching wavelength is slightly longer than 520 nm regardless of field placement. The placement of the matching field, however, affects matching wavelength at 8° nasal retinal eccentricity (lower panel). Despite the fact that both half fields are equated in retinal illuminance, placement of the matching field changes the matching wavelength, showing a pattern similar to that in Fig. 6. If anything, the intensity difference between the two half fields (Fig. 6) appears to exacerbate the difference in the wavelength match with field placement.

Since the foveal results in Fig. 7 do not show a field placement effect, it seems unlikely that the physical attributes of the matching and test fields are contributing to the different wavelength shifts contingent on matching field placement relative to that of the test field. It is surprising, though, that the wavelength required to match the test field is slightly longer than that of the peak transmission wavelength at some of the luminance levels, but this shift occurs regardless of the location of

the matching field in the bipartite stimulus. It is very likely that the difference in the spectral production of the two stimuli yielded a matching wavelength that diverged from the wavelength of peak transmission. Consequently, the wavelength shifts as presented in the previous figures may be better judged by the monochromatic wavelength required to match the test stimulus at equal luminance. Although not measured, this deviation in the matching wavelength from the wavelength of peak transmission may explain why wavelength shifts at 450 nm did not follow the traditional Bezold–Brücke predictions (Fig. 2).

Stabell and Stabell (1979a) showed when the luminance level of the peripheral test field and the foveal matching field were both equated to approximately 10 td, the matching wavelength was not the same as the test wavelength. In the no-bleach condition at 6° temporal eccentricity the matching wavelength for the 520 nm test was approximately 535 nm and at 9° temporal eccentricity it was approximately 550 nm. It is possible that the foveal matching field in their study reflected a perceptual difference in hue perception between the foveal and temporal retina due to differences in underlying neural mechanisms (e.g., rod contribution vs. no rod contribution, photopigment density differences between the foveal and peripheral retina).

4. Experiment 3

Another possible explanation for the 520 nm results in this study may be the underlying retinal mosaic. For example, due to the presence of the optic disk in the nasal retina, the density of retinal cells is more compressed near the optic disk. Thus, the density of photoreceptors underlying the half field closer to the optic disk is higher. Similarly, it is well documented that the number of rods is increasing quite rapidly outside the fovea (e.g., Curcio et al., 1990). Thus, the absolute number of rods underlying the half field farthest from the fovea is greater than the absolute number in the other half field; perhaps this difference affects the wavelength chosen to match the test field. The orientation of the bipartite field separated by a gap may accentuate both the compression and rod density differences between the two half fields and may produce differences in the appearance of the two half fields. If this argument is valid, then a horizontally divided field should negate the differences. If the results from the 520 nm stimulus at 8° nasal retina are due to an imbalance in the rod density between the two halves, and not due to compression differences, then similar results should be obtained at 8° in the temporal retina. The only anticipated difference between the nasal and temporal results is the matching wavelengths in the temporal retina for the left and right field placements should be opposite to those obtained in the nasal retina.

Therefore, in this experiment two orientations of the bipartite field were compared in the fovea and at 8° nasal and temporal retinal eccentricities. One condition reexamined the same bipartite field configuration used in experiments 1 and 2, and the other condition investigated a bipartite field horizontally divided so that the two half fields were vertically displaced. This later bipartite field eliminated any effects due to rod density differences along the horizontal meridian as well as the effects associated with compression.

4.1. Observers

Four females participated in this study. All participants had normal or corrected-to-normal visual acuity and normal trichromatic color vision as determined by the Neitz anomaloscope, F-2 tritan plate, and a series of three panel tests: D-15, Adams desaturated D-15, and Farnsworth–Munsell 100-hue. Two of the observers (VV and KAH) also participated in experiment 2.

4.2. Stimuli

Hue shifts were obtained in the fovea and at 8° nasal and temporal eccentricities using a 1.5° bipartite field. In one condition the field was vertically divided as in experiments 1 and 2, and in the other condition the bipartite field was horizontally divided. One half was the ''test field'' set at 520 nm by a narrowband interference filter (see Fig. 1); the other half was the ''matching field'' generated by the grating monochromator. The lateral and vertical positioning of the test and matching fields was counterbalanced across experimental sessions. The half fields were separated by a hairline gap in the fovea; this gap was slightly increased in the peripheral retina.

As in experiment 1, the 520 nm test field was maintained at an intensity level 0.5 log units higher than the matching field. Two of the observers received three intensity pairings: 0.25 and 0.75, 1.2 and 1.7, and 2.2 and 2.7 log tds. The other two observers viewed these same intensity pairings as well as two additional pairings: 0.7 and 1.2, 1.7 and 2.2 log tds. The 0.25 and 0.75 log td pairing was introduced in this experiment to increase the probability of rod participation. In all conditions, stimuli were presented for 1 s every 7 s; and observers were permitted to view the stimuli as many times as needed to make a hue judgment.

4.3. Procedure

The same procedures as outlined in experiment 1 for the fovea and the no-bleach condition were used in this experiment. No measurements were made after a rod-

bleach since the greatest effect with the matching field location was observed after 30 min of dark adaptation (see Fig. 6). Observers again made binary hue judgments between the test and matching fields using a double-random staircase procedure. Intensity pairings were presented in ascending order in both the fovea and peripheral retina.

4.4. Results and discussion

Results for all four observers in experiment 3 are presented in Figs. 8 (fovea), 9 (8° nasal) and 10 (8° temporal). Matching stimulus intensity (log td) is specified as a function of mean matching wavelength (nm). Each row of panels denotes a different observer. The left panels represent wavelength shifts when the bipartite field was vertically divided and the right panels when the bipartite field was horizontally divided. The dashed line indicates the mean wavelength shift, and the open and closed circles indicate the different placements of the matching field relative to the test field. The vertical dashed line is the wavelength of peak transmission for the 520 nm interference filter; error bars denote ±1 SEM.

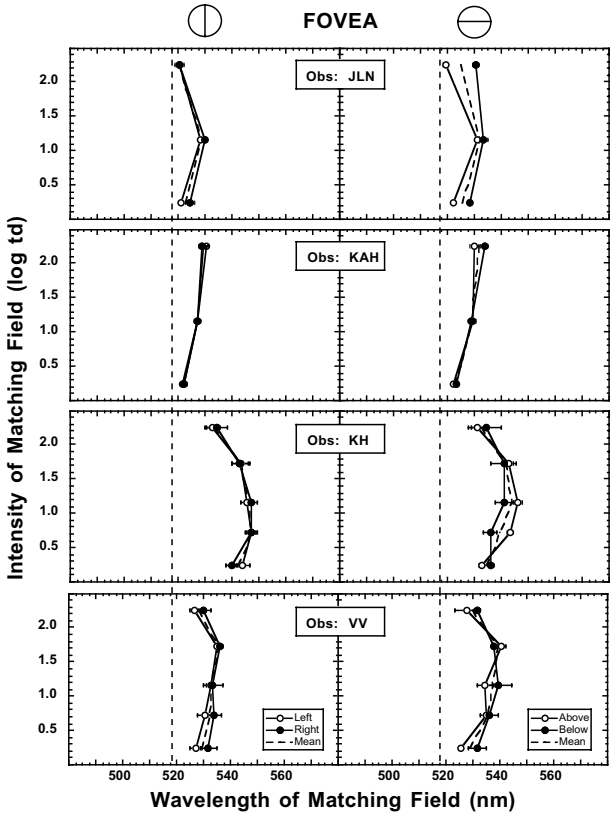

Fig. 8. Matching field intensity plotted as a function of mean matching wavelength (nm) for the fovea. Each row of panels denotes a different observer. The left panels represent the results for a vertically divided bipartite field, and the right panels for a horizontally divided bipartite field. Different symbols specify the placement of the matching field relative to the test field. The non-vertical dashed line indicates the mean wavelength shift across matching field location. The vertical dashed line is the peak transmission wavelength of the 520 nm interference filter. Error bars represent ±1 SEM.

In general, placement of the matching field in the fovea (Fig. 8) did not affect the matching wavelength for any of the four observers. Overall, the wavelength shift was to longer wavelengths as is expected with the Bezold–Brücke hue shift. The shifts were much greater than what was observed in Fig. 7 when the two half fields were equated in retinal illuminance. Fig. 9, though, reveals a different result at 8° nasal eccentricity. Placement of the matching field with the vertically divided bipartite field (left panels) influenced the matching wavelength for all four observers. In all cases, the wavelength shift was to longer wavelengths when the matching field was presented to the left of the test field. When the bipartite field was horizontally divided (right panels), three of the four observers showed no effect of half field placement. Thus, it appears that orientation of the half fields affects the Bezold–Brücke hue shift for the 520 nm stimulus in the nasal retina.

The finding of no difference in wavelength shift with the horizontally divided bipartite field is consistent with the idea that the difference in the number of rods and the number of cell bodies underlying each of the two half fields was minimized by this orientation; whereas, the vertically divided field maximized this distinction. To further support this possibility, measurements were also obtained in the temporal retina at 8° eccentricity. Results for the 520 nm stimulus in the temporal retina are presented in Fig. 10. The data from the temporal retina are less consistent among the four observers than that from the nasal retina. Two observers (KAH and VV) show some evidence that placement of the matching field in the vertically divided bipartite field creates different wavelength shifts. The wavelength shifts for these two observers are longer when the matching field is in the right hemifield than when it is in the left hemifield, the reverse of that found in the nasal retina (see Fig. 9, left panels). This is the result that would be expected if the underlying number of rods is a factor in the hue judgment. In general, for each observer, the wavelength shifts associated with placement of the matching field in the horizontally divided bipartite field were similar to results found in the nasal retina.

Figs. 9 and 10 demonstrate that field placement within the bipartite field and retinal quadrant can differentially influence wavelength shifts at 520 nm. The effects were largest in the nasal retina with the vertically divided field suggesting that asymmetric distribution of rods as well as the differential compression of photoreceptors underlying the two halves of the bipartite field influence hue perception.

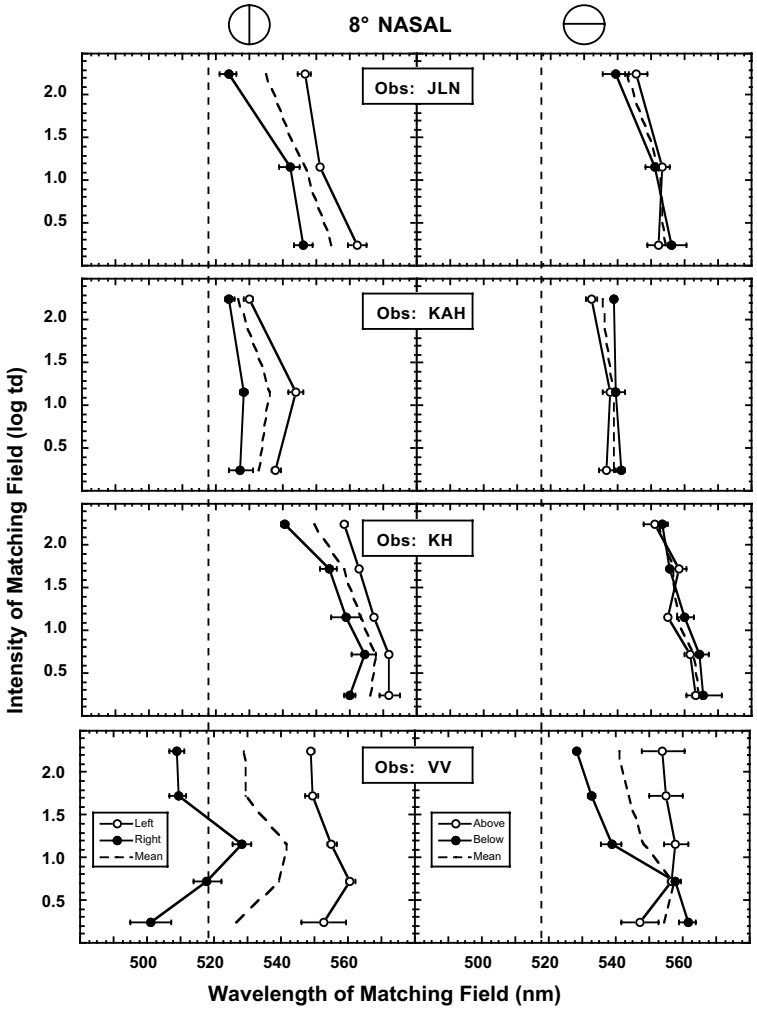

Fig. 9. The same as Fig. 8 except the results are from the 8° nasal retinal eccentricity.

5. Summary

Results from experiment 1 revealed that wavelength shifts in the rod-bleach condition differed from those in the fovea. This suggests that the peripheral cones may send signals differently to the chromatic-opponent processes than the foveal cones, and/or the Bezold–Brücke effect may capitalize on the photopigment optical density differences between foveal and peripheral receptors. There was a difference between the rod-bleach and no-bleach conditions at the lower intensity levels at 490, 520 and 610 nm. There was an effect of retinal eccentricity at the three shorter wavelengths in the no-bleach condition. The wavelength shift was greater at 8° nasal eccentricity than at 1° nasal eccentricity for the lower luminance levels. These results differ from those reported by Stabell and Stabell (1979a), but may be attributed to the differences between the procedures used by the two studies (see Section 1). Interestingly, our hue shifts from the fovea and rod-bleach condition were more similar to those reported by other investigators in the fovea, conforming to the predictions of the Bezold–Brücke hue shift, rather than those of Stabell and Stabell. The unexpected finding in the no-bleach condition was the effect of matching field location within the bipartite field on the matching wavelength for the rod-bleach and no-bleach conditions.

Experiment 2 revealed that an intensity difference between the 520 nm test and matching fields was not required to generate a difference in matching wavelengths with field placement in the nasal retina. While the difference in the spectral production of the test and matching fields may explain the deviation of the matching wavelength from the wavelength at peak transmission, it cannot account for the field placement effect.

In experiment 3 orientation of the bipartite field and placement of the matching field relative to the 520 nm test field in these orientations was explored in the fovea and at 8° eccentricity in the nasal and temporal retinas

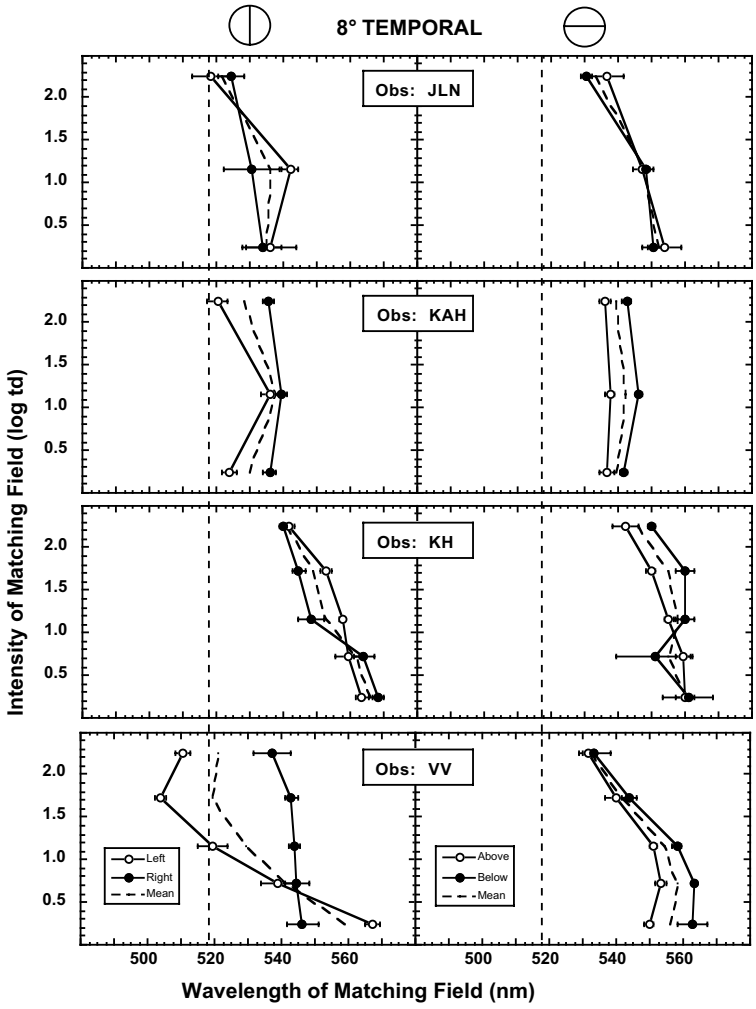

Fig. 10. The same as Fig. 8 except the results are from the 8° temporal retinal eccentricity.

after 30 min dark adaptation. The orientation of the bipartite field and placement of the matching field was critical in the nasal retina, but was not as important in the temporal retina.

Acknowledgements

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