THESIS

SCOTOPICALLY EQUATED STIMULI VERSUS PHOTOPICALLY EQUATED STIMULI IN UNIQUE HUE JUDGMENTS

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ABSTRACT

SCOTOPICALLY EQUATED STIMULI VERSUS PHOTOPICALLY EQUATED STIMULI IN UNIQUE HUE JUDGMENTS

One of the quandaries when studying color perception in the peripheral retina is whether to equate stimuli photopically to the cones or scotopically to the rods. Both methods are prevalent in the literature and while many of the findings are similar when using either method, there are some notable differences. The purpose of this study was to determine whether the differences in results can be at least partially attributed to the methodology used to equate experimental stimuli. Unique hue loci (blue, green, yellow) were measured in the fovea and at 10° temporal retinal eccentricity under bleach and no-bleach conditions for stimuli equated either photopically (0.3 and 2.3 log phot td) or scotopically (1.0 and 3.0 log scot td).

While some differences in unique hue loci exist depending on the method of equating stimuli, the overall pattern of results suggested that different conclusions cannot be drawn depending on the method of equating stimuli. Most likely, the differences reported among unique hue studies are not due to the method of equating stimuli. The findings from this study suggest the method used to equate stimuli can be discounted as a potential confound in interpretation of results from unique hue studies.

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INTRODUCTION

Background – Color Vision Theories

Human color vision has been of interest to people throughout history. Historical figures such as René Descartes (late 1500s to early 1600s) and Isaac Newton (mid 1600s to early 1700s) spoke of color vision (King et al., 2009), but it was not until Hermann von Helmholtz (Helmholtz, 1867/1962) and James Maxwell (Maxwell, 1860) that psychophysical evidence supported a trichromatic theory of color vision. The psychophysical results from Helmholtz and Maxwell showed that humans needed only blue, green, and red in order to match any other hue, which lead to the formulation of the trichromatic theory. The trichromatic theory states that there are three different sensory mechanisms which respond optimally to specific hues (blue, green, and red) (Helmholtz, 1867/1962), but it was not shown until later that the three sensory mechanisms corresponded to three cone photoreceptors [now known as short-wavelength-sensitive (S), middle-wavelength-sensitive (M), and long-wavelength-sensitive (L) cones] (Bowmaker et al. 1980; Dartnall et al., 1983; Wald, 1964).

While the trichromatic theory focused on physical stimuli reacting with sensory receptors, another theory of color vision was based on perceptual experience. An interesting pattern was observed between a stimulus and its afterimage. For example, after staring at a green stimulus and then looking at a white piece of paper, the paper appears reddish. This perceptual experience was also seen with blue and yellow as well as white and black. Hering (1878/1964) therefore proposed that color perception is the

result of activity from three neural opponent mechanisms and called these three opponent pairs: red/green (R/G), yellow/blue (Y/B), and white/black (Wh/Bk). Hering, through perceptual observation, noted that a chromatic opponent pair was mutually exclusive, i.e., a hue can not be perceived as both bluish and yellowish at the same time and in the same place (Hering, 1878/1964).

Hurvich and Jameson (1957) adopted Hering's perspective on color perception to develop the experimental procedure of hue cancellation. Hue cancellation experiments start with a given hue, and then the observer is required to add enough of the opposing hue to cancel out the chromatic information from the initial hue – resulting in a stimulus that is devoid of the particular opponent channel. As an example, an experiment might start with a blue/green stimulus, and the observer would add yellow to the mix until the blue is cancelled out; leaving only the green hue.

Combining the ideas of the trichromatic theory (three cone photoreceptors) with the ideas of the opponent-process theory (three neural opponent processes), Hurvich and Jameson (1957) proposed the two-stage model of color vision. S-, M-, and L- cone outputs are added and subtracted from each other to form the three opponent channels. The R/G channel is produced by the following cone outputs: (S+L) - M. The Y/B channel is produced from the following cone outputs: (M+L) - S. The last channel, the achromatic channel, comes from S+L+M signals.

Photoreceptors – Types and Distributions

Cones

There are two main types of photoreceptors: rods and cones. Helmholtz (1867/1962) could only speculate on the physiological existence of cones and their response properties. It was not until the 1960's that physiological evidence supported the existence of three cone types (Wald, 1967) and was later verified by more refined microspectrophotometric procedures (Bowmaker et al, 1980; Dartnall et al. 1983). In the 1980s and 1990s (Ahnelt, 1987; Curcio, 1990), S cones were shown to be physically different than M and L cones.

The density and distribution of human cone photoreceptors was first measured by Østerberg (1935). This was one of the first experiments showing that rods were virtually absent from the fovea. Figure 1.1 illustrates Østerberg's data and shows how cone density peaks in the center of the fovea and decreases rapidly around 1.25-degrees retinal eccentricity. Østerberg (1935) showed that cone density varies between the nasal and temporal regions, with a higher cone density in the nasal retina than the temporal retina [i.e. density is 40-45% higher in the nasal region (Curcio et al., 1990)]. Later studies by Curcio and colleagues (1990) also reported higher cone densities in the nasal retina than temporal retina and differences in density of cones in the superior retina versus the inferior retina.

Individual cone types also vary in their distribution (Ahnelt et al., 1987; Curcio et al., 1987; Nerger et al., 1992). S cones comprise approximately 7-10% of the total number of cones present in the retina (Ahnelt et al., 1987; Curcio et al., 1991). Curcio et al. (1991) found no S cones in the very center of the fovea, rather first

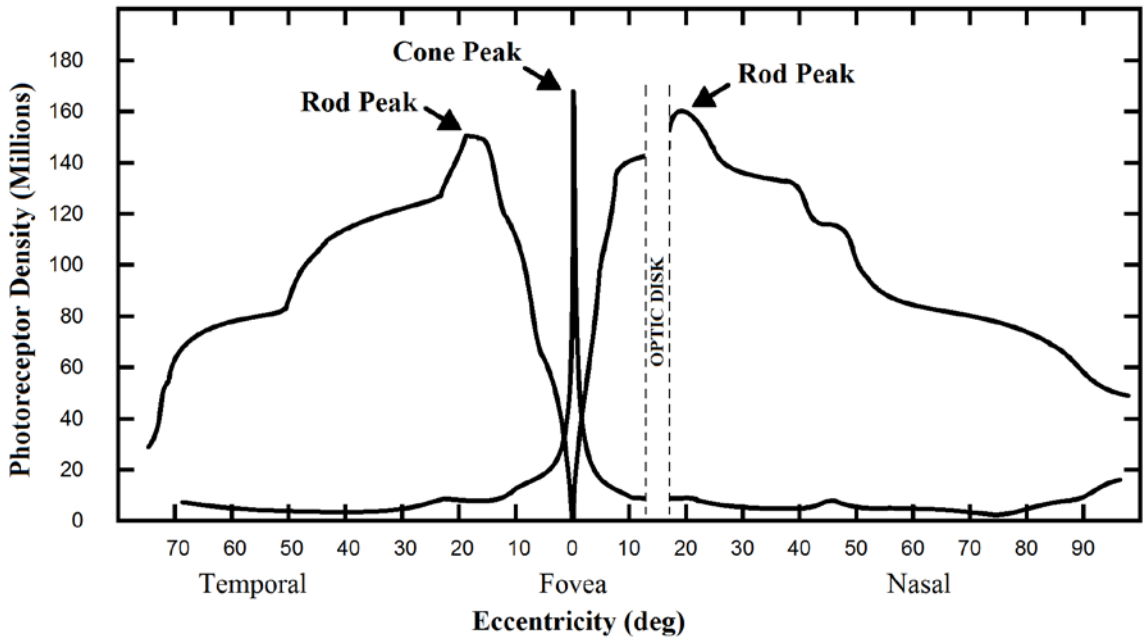

Figure 1.1. *Distribution of rod and cone photoreceptors as a function of retinal eccentricity. Based on Østerberg (1935).*

appearing at approximately 0.35 degrees from the center of the fovea. In contrast, Ahnelt et al. (1987) showed that S cones are present in the center of the fovea, although minimally and not necessarily consistently among eyes. Both groups agree that S cones reach their peak density at approximately 1 deg from the center of the fovea. S cone density remains fairly constant from 10 to 20 deg in the retina (Ahnelt et al., 1987).

M and L cones on the other hand make up a much larger proportion of the cones in the retina than S cones. The peak densities of both M and L cones occur in the fovea and decrease exponentially until approximately 7-8 degrees in the fovea, where the number of cones eventually stabilizes (Curcio et al., 1990). Nerger and Cicerone (1992) show that the ratio of L to M cones is roughly 2:1 from 1 to 4 degrees in the temporal retina. Otake and Cicerone (2000) suggest this ratio exists out until at least 28 degrees in

the peripheral retina. The adaptive optics imaging of the cone mosaic by Roorda et al. (1999) supports this notion (stable ratios past 20 deg), although they show greater variability in L:M cone ratios (e.g. 1.15:1 to 3.79:1) among observers.

Rods

The second type of photoreceptor is the rod photoreceptor, which is important for perception under conditions of dim illumination. This greater sensitivity is due to a greater neural convergence of rod signals on to one ganglion cell (Curcio and Allen, 1990). Curcio et al. (1990) reported a mean of approximately 92 million rod photoreceptors in the retina, in contrast to approximately 4.5 million cones in the retina. Curcio et al. (1990) found between 1.07 million ganglion cells on average in the human eye. Figure 1.1 illustrates the changes in the density of rods across the peripheral retina. As seen in Figure 1.1, rod density increases from the fovea and peaks around 15-25 degrees from the fovea (Osterberg, 1935). Curcio et al. (1990) describe this peak density section as the “rod ring”.

Bleach and No-Bleach Procedures

Because the peripheral retina consists of both rods and cones, one of the inherent issues when studying color vision in the peripheral retina is how to isolate the cone signals from the rod signals. In an experimental setting, bleach and no-bleach conditions can be used to maximize (no-bleach) and minimize (bleach) rod input, respectively, in the processing of color information (Stabell and Stabell, 1976). In a bleach condition, an individual is exposed to a very intense broadband (“white”) light, which inactivates most of the photopigment in the rods and cones. When light strikes the light sensitive pigment,

the shape of the pigment molecule changes and can no longer absorb light. The pigment is said to be bleached. Therefore, there is less photopigment available to absorb light. Consequently, the amount of available light needs to be increased in order to improve the probability that light is absorbed by the remaining active photopigment. After a photopigment is bleached, the molecule gradually returns to its original shape and can once again absorb light. This process is referred to as photopigment regeneration. It has been demonstrated that cone photopigment regenerates faster (approximately 4 min) than rod photopigment (approximately 20-30 min) (Alpern, 1971; Rushton & Powell, 1972). During an interval from 4-9 min post-bleach, rods are unable to contribute to vision at cone threshold levels and minimally at levels above cone threshold. Differences in rod and cone thresholds post-bleach are shown in Figure 1.2. Zero minutes on the figure represents the moment the bleaching field is terminated. The figure illustrates which photopigment (rod versus cone) has the lowest threshold for light detection (solid line) and subsequently, which photopigment is primarily responsible for detecting light at the given dark adaptation times. Thus, the bleaching condition minimizes rod contribution to color vision in the peripheral retina for a specific period of time – before the rod/cone break (see Figure 1.2). In the no-bleach condition, participants dark adapt for 30 min to ensure the rods are fully active, yielding rod contribution to color perception.

Unique Hues

Unique hues provide a way to study how rods influence color perception. Among the first to psychophysically measure unique hues were Hurvich & Jameson (1957). A unique hue is a wavelength of light that is the equilibrium point of a chromatic-opponent

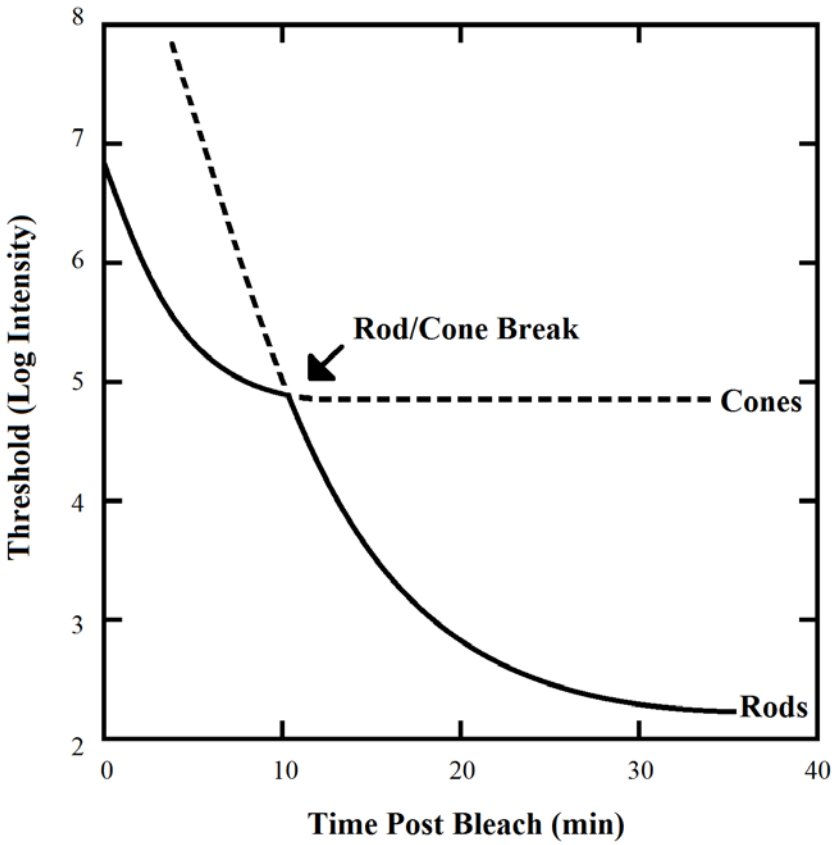

Figure 1.2. *Rod and cone thresholds after bleaching stimulus. Based on Pirenne (1962).*

process. Unique green, for example, is defined as the wavelength of monochromatic light where the Y/B opponent processes cancel each other, leaving the green process from the R/G channel to mediate perception in the middle-wavelength portion of the visible spectrum. Figure 1.3 presents the opponent-chromatic response functions measured with the hue-cancellation procedure and the loci of unique hues across the visible spectrum. It should be noted that there is no spectral unique red, since the longest wavelengths of light in the visible spectrum are perceived to be yellowish-red.

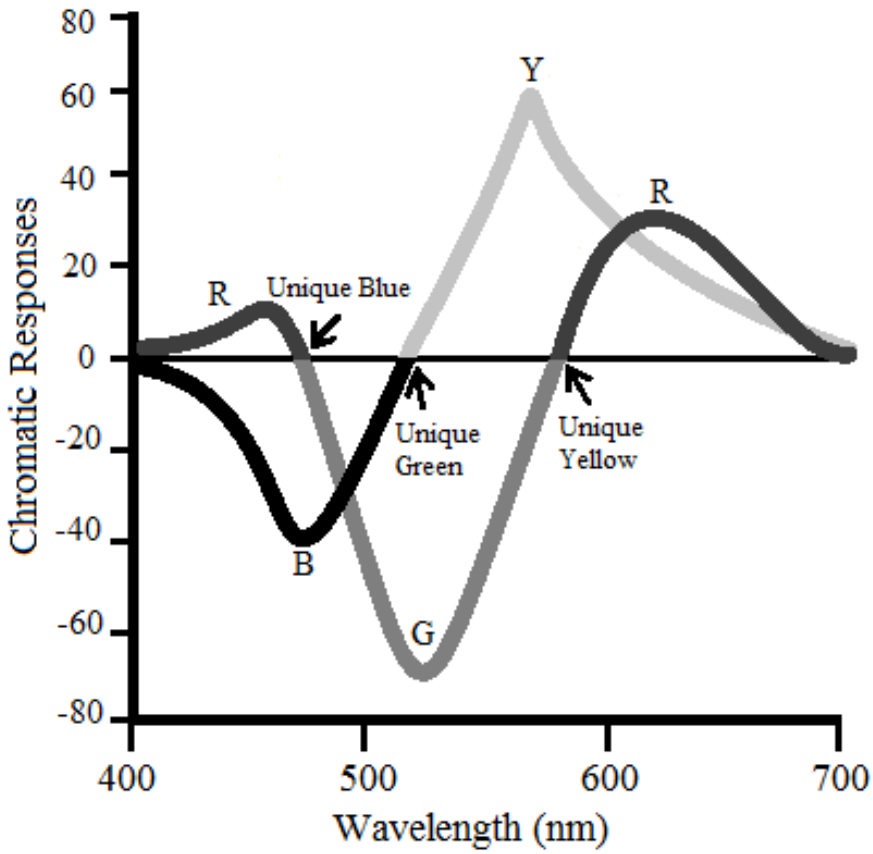

Figure 1.3. *Foveal chromatic-opponent response functions (based on Werner and Wooten, 1979). The points where the curves cross the zero line are the unique hues.*

Unique hues have traditionally been investigated in the fovea. Larimer, Krantz, and Cicerone (1975a, 1975b) did so by requiring participants to view colored stimuli, foveally, and make binary, forced choice responses. Their forced choice responses were "red" or "green" for determining unique blue and unique yellow loci if the stimuli appeared reddish blue or greenish blue and reddish yellow or greenish yellow, respectively (Larimer, et al., 1975a). Forced choice responses for unique green consisted of "blue" or "yellow" responses if the hue appeared bluish green or yellowish green (Larimer et al., 1975b). This procedure of forced choice responses has also been

employed in more recent unique hue research (eg. Nerger et al., 1998; Thomas et al., 2004; Volbrecht et al., 2000).

Since the fovea consists only of cone photoreceptors, unique hues have previously been investigated by equating the retinal illuminance of the stimulus photopically. When stimuli are equated photopically, each wavelength along the spectrum stimulates the M and L cones similarly; however, S-cone activity varies with wavelength. Figure 1.4 presents the photopic (V_λ) and scotopic (V'_λ) spectral luminosity functions. The photopic function represents the combined spectral sensitivity of the M and L cones, while the scotopic function represents the spectral sensitivity of the rods. The peak sensitivity of V_λ is 560 nm, and the peak for V'_λ is 500 nm. Wavelengths shorter and longer than the wavelength associated with the peak sensitivity require more physical energy to be equally luminous to wavelengths at peak efficiency. Equating stimuli photopically, and thereby equating M and L cone activity, can be problematic for studying peripheral color vision since the rods, like the S cones, are differentially activated across wavelengths by these stimuli. This effect is illustrated in Figure 1.5 where stimuli that have been equated to 0.3 log td have also been converted to their scotopic troland equivalent. As seen in Figure 1.5, equating the photopic system to 0.3 log trolands keeps luminance equal throughout the visible spectrum for the cones, but the shorter wavelengths appear much brighter and longer wavelengths appear much dimmer to the scotopic system. Conversely, Figure 1.6 shows stimuli equated to 1.0 log scot td and then converted to their photopic troland equivalent. When scotopically equated, stimuli appear dimmer at the shorter wavelengths and brighter at the longer wavelengths for the photopic (M and L cones) system.

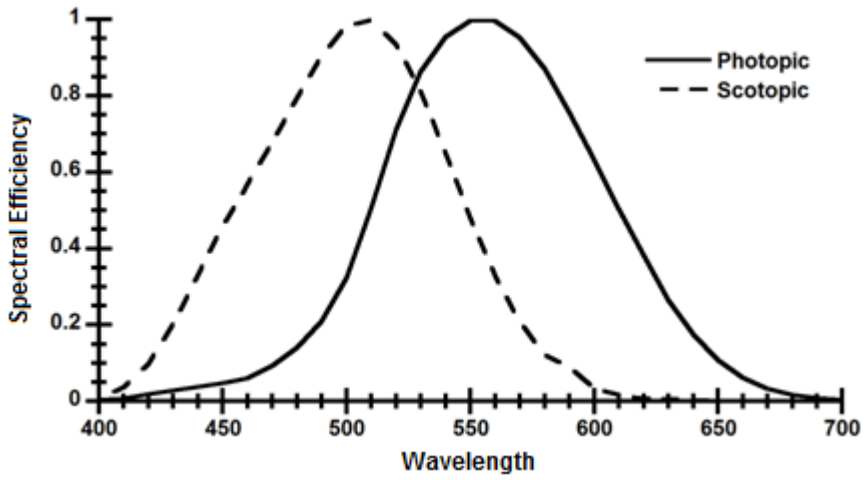

Figure 1.4. *Photopic (solid lines) and scotopic (dashed lines) spectral efficiency plotted as a function of wavelength. Photopic values are from Vos (1978) and scotopic values are from the 1951 CIE (Wyszecki & Stiles, 1982).*

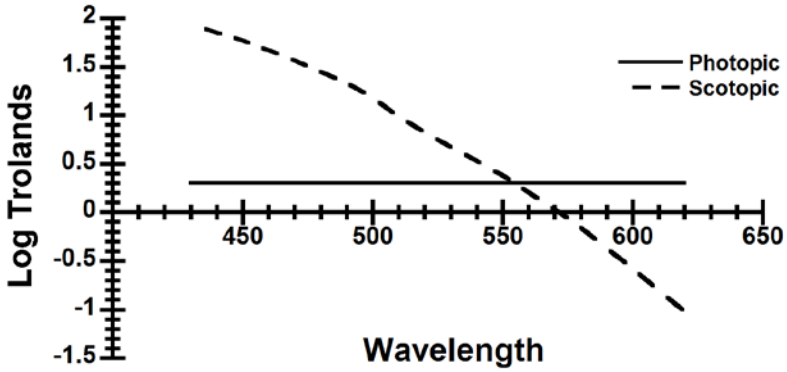

Figure 1.5. *The solid line presents wavelengths that have been equated to 0.3 log photopic trolands while the dashed line shows the scotopic troland equivalent for those wavelengths.*

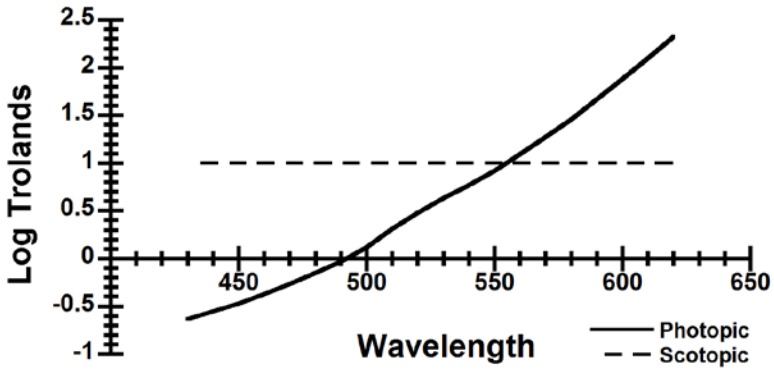

Figure 1.6. *The dashed line presents wavelengths that have been equated to 1.0 log scotopic troland while the solid line shows the photopic troland equivalent for those wavelengths.*

Recent studies have measured unique hues in the peripheral retina, and some vision researchers (Buck et al., 1997, 2000) have equated peripheral stimuli scotopically, rather than photopically. Scotopically equated stimuli stimulate the rods in the same way, but S-, M-, and L-cone activities vary with wavelength. Thus, scotopically equated stimuli are problematic for studying peripheral color vision because the cones respond to light differently depending on wavelength.

Research (Buck et al., 2000; Nerger et al., 1998; Volbrecht et al., 2000) investigating the effects of rods on unique hue loci have used both the bleach and no-bleach procedures. Buck et al. (2000) equated stimuli scotopically and found that 1) rod signals shifted unique blue, green, and red loci in the no-bleach condition when compared to the bleach condition, and 2) changes in retinal illuminance also shifted unique hue loci. In general, rods (no-bleach condition) shifted the loci of all three spectral unique hue judgments to longer wavelengths compared to the bleach condition with minimal rod contribution. Increases in retinal illuminance also caused the loci of unique hues to shift; however, these shifts were not always in the same direction as the shifts caused by rod

contribution. For example, in the no-bleach condition, unique blue and unique green loci shifted to shorter wavelengths as retinal illuminance increased. In the bleach condition, unique blue and green loci shifted to longer wavelengths as retinal illuminance increased.

Nerger et al. (1998) and Volbrecht et al (2000), who equated their stimuli photopically, also used bleach and no-bleach conditions to look at differences in color perception in the peripheral retina. Nerger et al. (1998) showed that, contingent on stimulus size, the locus of both unique blue and unique yellow shifted to longer wavelengths in the no-bleach condition when compared to the bleach condition; and this shift in loci was greater at the smaller test size (0.5 deg versus 2 deg). Volbrecht et al. (2000) found that the locus of unique green shifted to shorter wavelengths as eccentricity increased, but suggested that rod contribution was not responsible for this shift (i.e. the same shift to shorter wavelengths was observed under both the bleach and no-bleach conditions). While studies with photopically equated stimuli (e.g. Nerger et al., 1998; Volbrecht et al., 2000) and studies with scotopically equated stimuli (e.g. Buck et al., 2000) suggest a rod contribution, procedural differences make it difficult to directly compare the results. Procedural differences include differences in stimulus sizes, retinal eccentricity, retinal illuminances, and methods of equating stimuli. Buck et al. (2000) and Nerger et al. (1998) are in agreement with loci in the no-bleach condition showing shifts to longer wavelengths when compared to the bleach condition (for unique yellow and unique blue); however, contrary to Buck et al. (2000), Volbrecht et al. (2000) do not show this effect with the unique green loci.

This Study

Given the differences between previous studies, the question still remains: should peripheral color vision researchers equate their stimuli photopically or scotopically? There are no previous studies which compare the differences in loci of unique hues in the peripheral retina obtained when stimuli are scotopically equated versus photopically equated and with the same observers. The goal of this study was to determine if the two methods of equating stimuli yielded different results with the same experimental procedure and same observers.

METHODS

Observers

Three females (age 22, 23, and 52) and one male (age 24) served as observers in this study. All observers had normal or corrected to normal visual acuity and were assessed for trichromatic color vision using anomaloscopic matches (Neitz OT-II) and three panel tests (Farnsworth-Munsell 100-Hue, D-15, and Lanthony Desaturated D-15). All observers had some training on how to make unique hue judgments and did not see their own data until completing all experimental conditions. The observers also served as experimenters in this study.

Apparatus

The apparatus was a three-channel Maxwellian-view optical system, and a schematic of the system is presented in Fig. 2.1. A 300W xenon arc lamp (LS; Oriel, Model 66065, 5500K), maintained at 290W by a dc power supply (Oriel, Model 68811), served as the light source for the Maxwellian-view optical system. Light leaving the two exit ports of the lamp housing passed through heat-absorbing filters (H1 and H2) to form three channels within the optical system.

Light from channel 1 was collimated and then focused on a monochromator (MC; Instruments SA, Inc., Model H20, 4-nm half-amplitude bandpass). Light from the MC

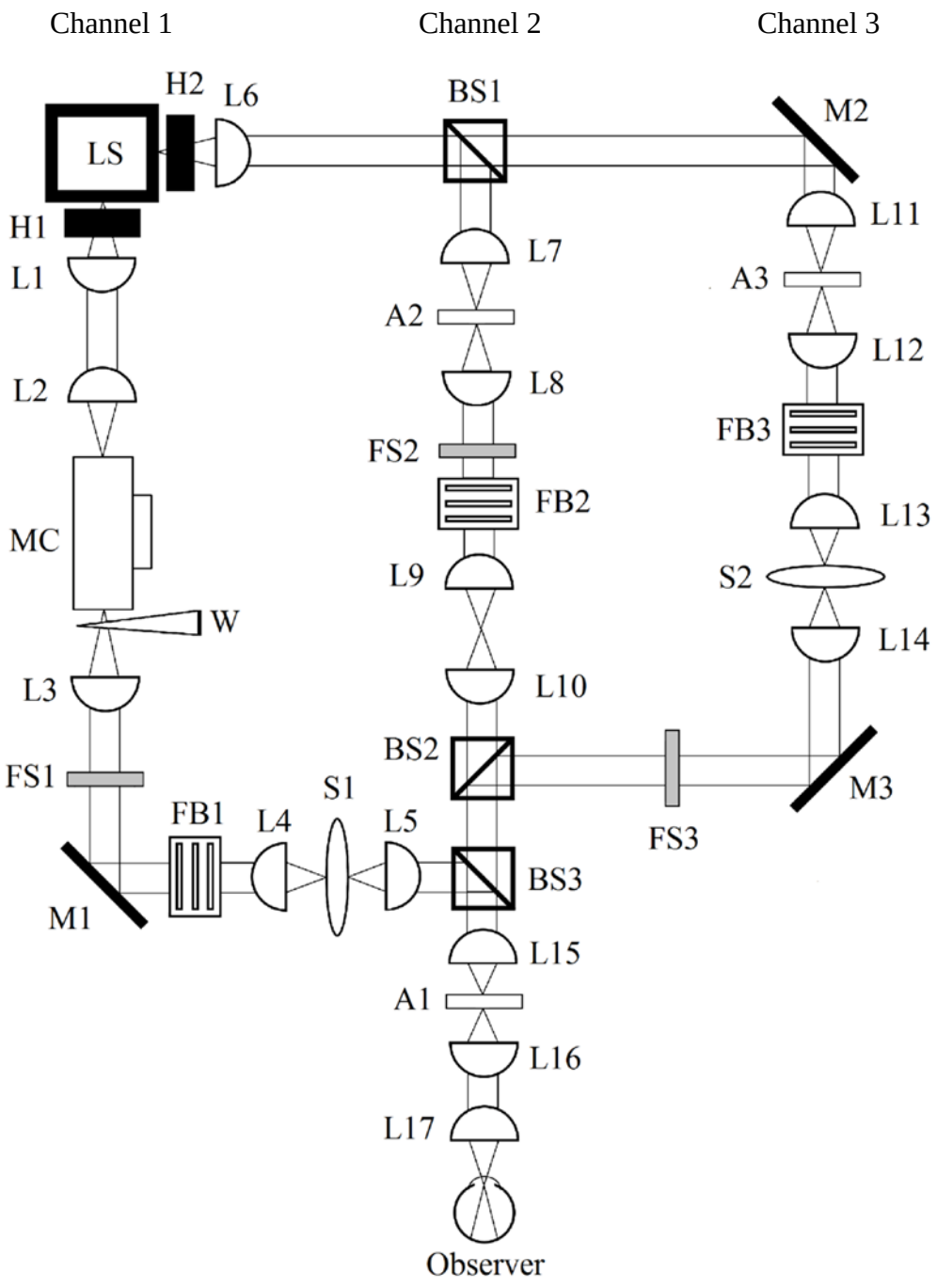

Figure 2.1. *Schematic of the three-channel Maxwellian-view optical system. Components are as follows: LS = Light Source; H = Infrared Heat Absorbing Filter; L = lens; BS = Beamsplitter; M = Mirror; MC = Monochromator; W = Neutral Density Wedge; FS = Field Stop; FB = Filter Box; S = Shutter; AP = Artificial Pupil, A = Aperture. The observer's position is indicated at the bottom of the figure.*

was focused on a two log-unit circular neutral density wedge (W; Ealing Electro-Optics). L3 collimated the light, which passed through a field stop (FS1) that defined the size of the test stimulus, and was reflected at a 90-deg angle by a mirror (M1). The collimated light passed through neutral density filters located in a filter box (FB1). The light was then refocused with a lens (L4), passed through a shutter (S1) controlled by a driver system (Uniblitz, model T132), was recollimated with another lens (L5), and passed through a beamsplitter (BS3) which combined the light from all three channels. Channel 1 controlled the wavelength, intensity, size, shape, and duration of the test.

Upon exiting a beamsplitter (BS1), light from channel 2 was focused with a lens (L7), passed through an aperture (A1) and then was recollimated using a lens (L8). The collimated light passed through a field stop (FS2) defining the fixation array and through a filter box (FB2) controlling the intensity of the fixation points, before being refocused by a lens (L9). Light was again recollimated (L10) and then combined with the other channels by means of beamsplitters (BS2 and BS3). Channel 2 generated the fixation points.

Upon exiting BS1, light in channel 3 was directed to and reflected from a mirror (M2) through a focusing lens (L11). An aperture (A2) was placed at the focal point to reduce stray light, and the light was then recollimated with a lens (L12) and passed through neutral density filters situated in a filter box (FB3) to the next focusing lens (L13). Light passed through a shutter (S2). The light was again collimated by a lens (L14) and reflected from a mirror (M3), and passed through a field stop, which defined the size of the bleaching field, and a beamsplitter (BS2), which combined light from channels 2 and 3. A second beamsplitter (BS3) in the collimated path recombined the

light from channel 1 with light from channels 2 and 3. Channel 3 provided the bleaching (5500K) stimulus used to minimize rod activity.

The light exiting BS3 was focused with a lens (L15) onto an artificial pupil (AP1) that defined the final size of the Maxwellian image (1.8 mm in diameter, which is smaller than the smallest pupil). A lens (L16) recollimated the light, and a final lens (L17) focused the light from all channels onto the plane of the observer's pupil. Observers aligned their right eye with respect to the optical axis of the Maxwellian-view system by means of a dental impression bite-bar assembly that permitted adjustments in three orthogonal directions.

Stimulus

Monochromatic stimuli were presented at 10-deg retinal eccentricity along the horizontal meridian of the temporal retina, as well as in the fovea. Stimuli were either photopically equated (0.3 and 2.3 log td) or scotopically equated (1.0 and 3.0 scot. log td). Tables 2.1 and 2.2 show the scotopic equivalent of the photopic stimuli (0.3 and 2.3 log td) and the photopic equivalent of the scotopic stimuli (1.0 and 3.0 log scot td), respectively. The retinal illuminance levels were chosen so that both rods and cones were stimulated. Stimulus sizes were 4 deg in the peripheral retina and 1 deg in the fovea. For all four elementary hues (blue, green, yellow, red), stimulus sizes of 3 deg or larger have been shown to fill the perceptive fields (Troup et al., 2005) at 0.3 log td in the temporal retina. Thus, it is possible some of the short- and middle-wavelength stimuli at 1.0 log scot td did not completely fill the perceptive fields for some of the elementary hues (see Table 2.2).

Table 2.1: *0.3 and 2.3 log phot td values and the log scot td equivalents for a range of wavelengths.*

λ	Log scot td. equivalent of 0.3 log td.	Log scot td. equivalent of 2.3 log td.
430	1.93	3.93
440	1.85	3.85
450	1.77	3.77
460	1.67	3.67
470	1.57	3.57
480	1.45	3.45
490	1.33	3.33
500	1.18	3.18
510	0.99	2.99
520	0.82	2.82
530	0.67	2.67
540	0.53	2.53
550	0.38	2.38
560	0.21	2.21
570	0.03	2.03
580	-0.16	1.84
590	-0.37	1.63
600	-0.58	1.42
610	-0.8	1.2
620	-1.02	0.98

Table 2.2: *1 and 3 log scot td values and the log phot td equivalents for a range of wavelengths.*

λ	Log phot td. equivalent of 1 log scot td.	Log phot. td. equivalent of 3 log scot td.
430	-0.63	1.37
440	-0.55	1.45
450	-0.47	1.53
460	-0.37	1.63
470	-0.27	1.73
480	-0.15	1.85
490	-0.03	1.97
500	0.12	2.12
510	0.31	2.31
520	0.48	2.48
530	0.63	2.63
540	0.77	2.77
550	0.92	2.92
560	1.09	3.09
570	1.27	3.27
580	1.46	3.46
590	1.67	3.67
600	1.88	3.88
610	2.1	4.1
620	2.32	4.32

Each stimulus was presented for 500 ms on a dark background with an interstimulus interval of at least 10 s to minimize any adaptation effects. A fixation array (see Fig. 2.2) with pin-sized holes was used to control retinal position of the stimulus in the temporal retina and fovea. For peripheral measurements, the stimulus was centered between the two vertical fixation points. A third fixation point, located on the horizontal axis and centered relative to the two vertical fixation points, was used to position the stimulus at 10-deg in the temporal retina. In the foveal condition, the vertical fixation points were used to align the stimulus, with the stimulus centered between the vertically displaced points (there was no horizontal point in the foveal condition). The intensity of the fixation points were adjusted so the observer could barely detect them – in order to minimize adaptation (Jameson & Hurvich, 1967).

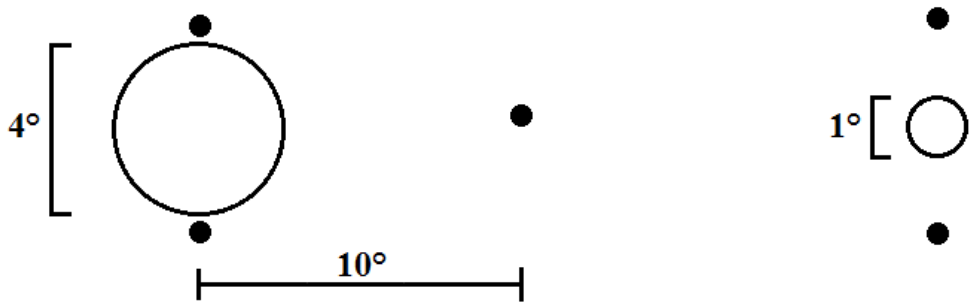

Figure 2.2. *Diagrams of the fixation arrays. Displayed on the left are fixation points in the peripheral condition; showing placement of the 4 deg stimulus. Displayed on the right are fixation points in the foveal condition; showing placement of the 1 deg stimulus.*

For the bleach condition, observers were exposed for 15 seconds to a 10.2 deg, 6.25 log scot td bleaching field centered over the peripheral location (10 deg). This bleaching field is calculated to bleach approximately 95% of rod photopigment (Alpern, 1971; Rushton & Powell, 1972).

Calibrations

The neutral density filters and wedge were calibrated by taking radiometric measurements from 400-620 nm in 10 nm steps. A photometric measurement was taken for channel 1 at a reference wavelength of 560 nm (peak spectral sensitivity of the photopic luminosity function) to enable conversion of radiometric measurements from 400 to 620 nm to photometric measurements. A photometric measurement was obtained for the bleaching field, calculated using the method of Westheimer (1966). Photopic troland values were converted to scotopic troland values using the conversion factors found in Wyszecki and Stiles (1982). Radiometric measurements were made with a UDT

Instruments radiometer (Model S370) and photometric measurements were made with a Minolta Chroma Meter (Model CS-100).

Procedure

In the bleach condition, at 10-deg in the temporal retina, observers adapted to the dark for 10 min, viewed the bleaching field for 15 s, and then adapted to the dark for an additional 4 min. Measurements were taken 4-9 min post-bleach – the time period associated with the cone plateau of the dark adaptation function. This time interval ensured recovery of cone sensitivity before unique hue judgments were obtained and the termination of measurements before the cone-rod break of the dark adaptation function. In the no-bleach condition, observers adapted to the dark for 30 min (the time period associated with the rod plateau) before measurements were taken in the peripheral retina. Foveal measurements were taken after 10 min of dark adaptation.

Each stimulus presentation required a forced choice response of “red” or “green” for both unique blue or unique yellow determinations and a response of “blue” or “yellow” for unique green determinations. For example, when a stimulus appeared reddish-blue in the unique blue condition, the observer responded “red”. Likewise, if the stimulus appeared greenish-blue, the observer responded “green”. A one-up, one-down, four-interleaved staircase procedure was used to determine unique hue judgments. The experimenter intentionally set the first two stimuli in each staircase so that the observer clearly perceived the two hue responses. The starting values varied for each staircase and were pseudo randomly chosen. After the initial response reversal in each staircase, the step size between wavelengths was reduced until a step size of 2 nm was reached. The

criterion for terminating a session was three response reversals at the smallest step size (2 nm). The mean of the last three reversals from each staircase and across two experimental sessions defined the locus of the unique hue for each experimental condition for three observers (AM, ND, and VV). The mean of the last three reversals from each staircase and from only one experimental session defined the locus of the unique hue for each experimental condition for observer KG.

One unique hue and method of equating retinal illuminance (photopically or scotopically) at one retinal illuminance was randomly selected for each experimental session. Fovea, no-bleach, and bleach conditions were all randomly presented in one session for that unique hue and retinal illuminance.

RESULTS

Analysis

For three observers (AM, ND, VV), the mean of the last three reversals from each staircase and across two experimental sessions defined the locus of the unique hue for each experimental condition. For KG, who participated in one experimental session instead of two, the mean of the last three reversals from each staircase defined the locus of the unique hue for each condition. As defined by previous studies (Nerger et al., 1998; Volbrecht et al., 2000), the criteria used to determine a shift in unique hue loci are: 1) means differ by a minimum of 3 nm and 2) the standard error of the means (SEM) do not overlap. This criterion is based on wavelength-discrimination functions of the fovea and peripheral retina (Stabell et al., 1984) and between-session variability of unique hue loci (e.g. Nerger et al., 1998; Volbrecht et al., 2000). In the following figures, all of the scotopic illuminance values were converted back into photopic trolands using conversion factors provided by Wyszecki and Stiles (1982). The conversion of scotopic trolands to photopic trolands permitted easier comparison between the two retinal illuminance conditions. The means from all three unique hue judgments for each observer were used to assess the influence of different methods of equating retinal illuminance on 1) scalar invariance of unique hue loci, 2) the relationship between unique hue loci measured in the bleach versus no-bleach conditions, and 3) the similarity between foveal unique hue loci and the peripheral unique hue loci from the respective bleach condition.

Unique Hue Loci

Unique hue loci for all observers and conditions are presented in Figures 3.1 – 3.4. Wavelength (nm) is denoted on the x-axis and retinal illuminance (in log photopic trolands) on the y-axis. It should be noted that retinal illuminance (our independent variable) is plotted on the y-axis to reflect how unique hues at various retinal illuminances have traditionally been presented (e.g., Larimer, Krantz, and Cicerone 1975a; 1975b; Nagy, 1979). Each panel represents one of the three experimental conditions: fovea (top panel), rod bleach (middle panel), and no-bleach (bottom panel). Solid lines connect the two unique hue loci obtained with photopically equated stimuli, and the dashed lines connect the two unique hue loci obtained with scotopically equated stimuli. These lines have been drawn for ease of comparison. Within a panel, the left most lines are unique blue loci, the middle are unique green loci, and the right most are unique yellow loci. The error bars represent ±1 SEM.

Unique Blue

Under the three conditions, unique blue loci are, in general, at longer wavelengths in the scotopic condition (dashed lines) than the photopic condition (solid lines). In the no-bleach condition, this difference in unique blue loci is dependent on retinal illuminance. For example, observer KG's and VV's scotopic unique blue locus compared to the photopic unique blue locus (Figures 3.3 and 3.4) is at longer wavelengths at the lower retinal illuminances, while ND's scotopic unique blue locus is at a longer wavelength at the higher retinal illuminance compared to the photopic unique blue loci.

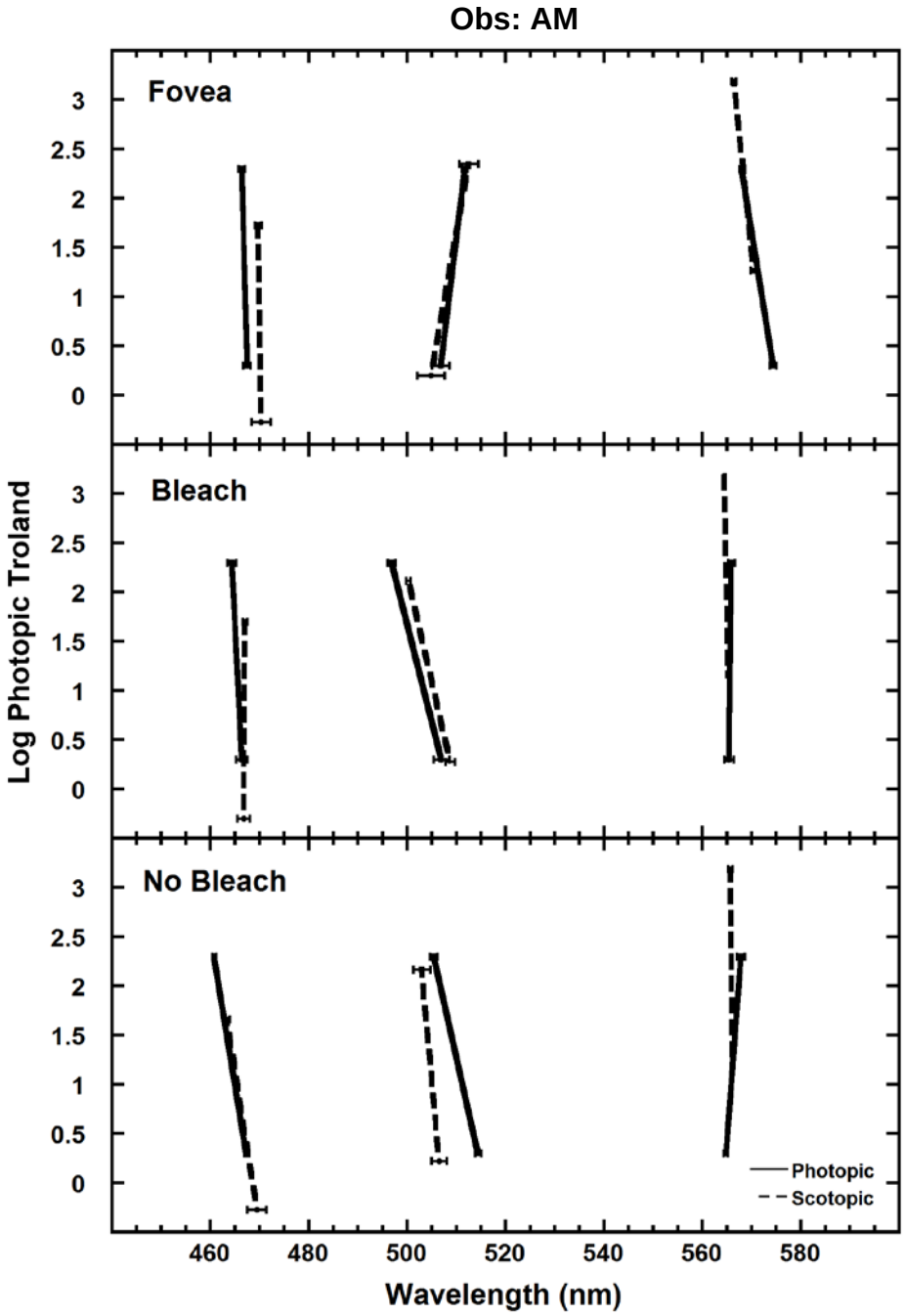

Figure 3.1. *Unique hue loci for AM. The figure shows both low and high retinal illuminance values for both scotopically (dashed line) and photopically (solid line) equated stimuli for all three conditions: fovea (top panel), bleach (middle panel), and no-bleach (bottom panel). Log scotopic trolands were converted into log photopic trolands for ease of comparison.*

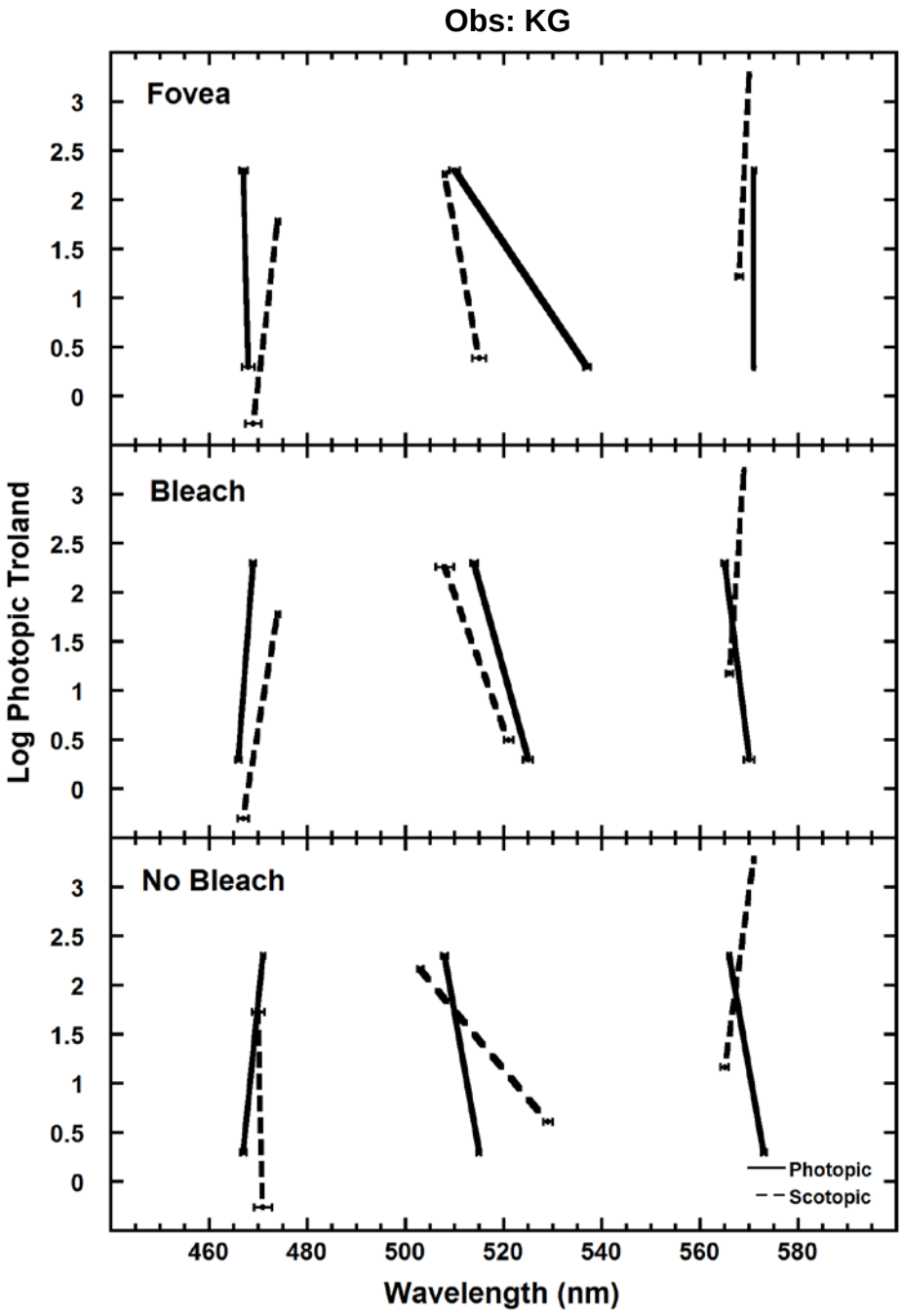

Figure 3.2. *Same as Figure 3.1, except for KG.*

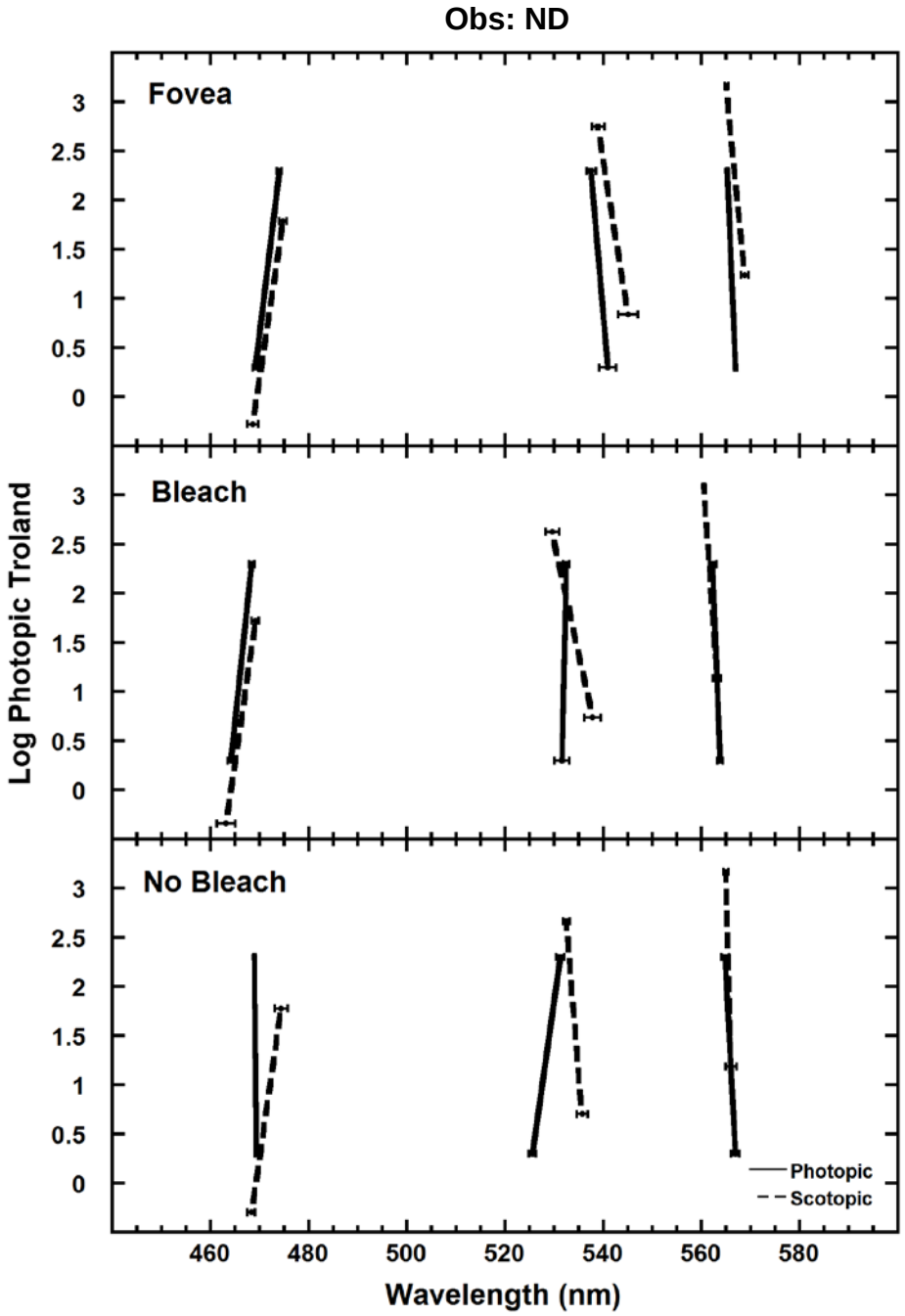

Figure 3.3. *Same as Figure 3.1, except for ND.*

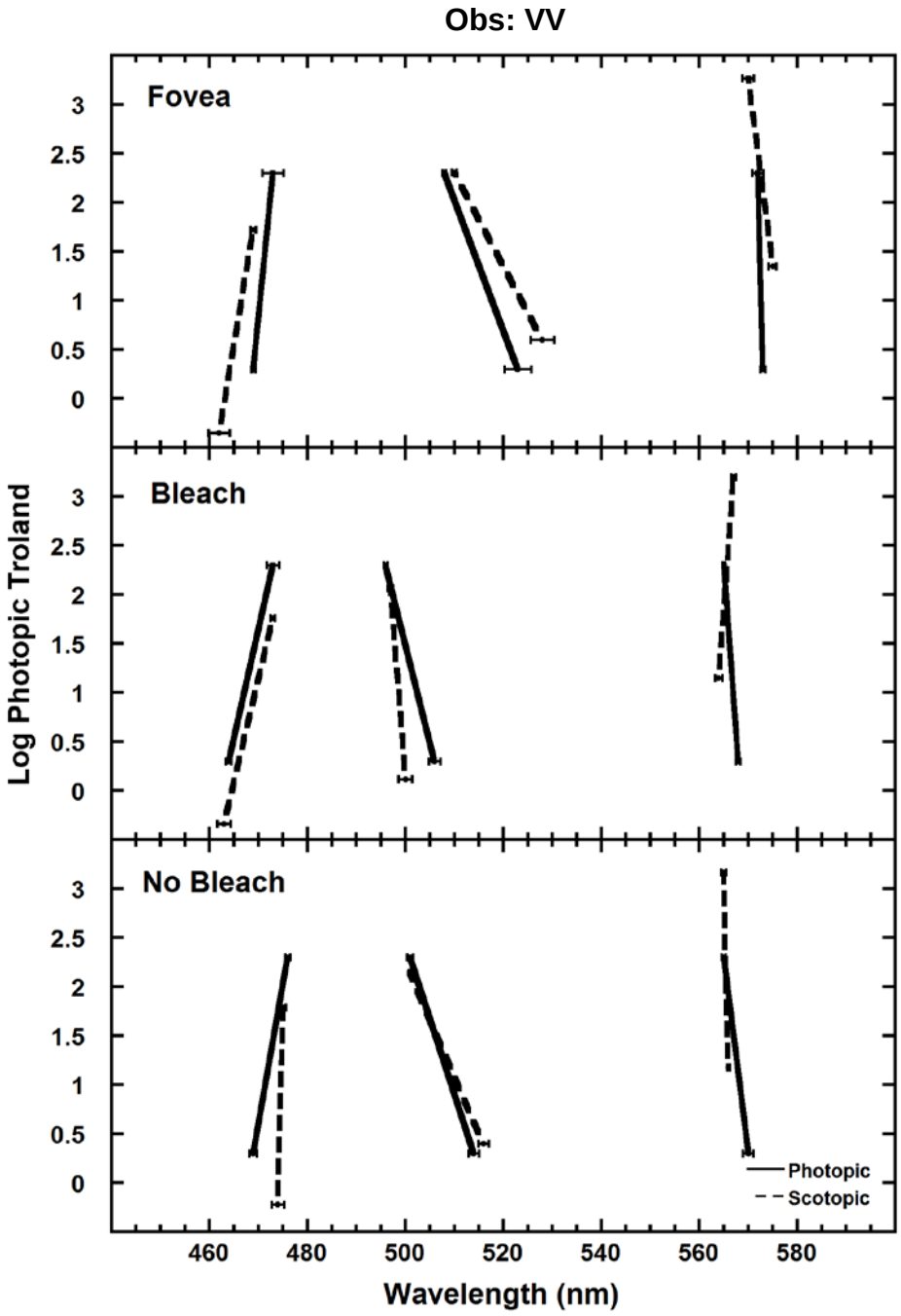

Figure 3.4. *Same as Figure 3.1, except for VV.*

Unique Green

Similarly, for two to three observers in each experimental condition, scotopic unique green loci (dashed line) were at longer wavelengths than unique green loci in the photopic condition (solid line). Under both bleach and no-bleach conditions, this difference was specific to either high or low retinal illuminance.

Unique Yellow

Comparing unique yellow conditions presents a challenge due to the large difference between retinal illuminance levels in photopically versus scotopically equated stimuli. For some observers (e.g. KG fovea), photopic unique yellow loci (solid line) are at longer wavelengths than scotopic loci (dashed line). For other observers (e.g. ND - fovea), the reverse relationship is seen; unique yellow loci obtained with scotopically equated stimuli are at longer wavelengths than those measured with photopically equated stimuli. As with unique green loci, the relationship between photopically equated and scotopically equated unique yellow loci in the bleach and no-bleach conditions is contingent on retinal illuminance.

Scalar Invariance

With scalar invariance, unique hue loci do not shift as a function of retinal illuminance. For example, unique blue loci obtained at the low and high retinal illuminances should be the same, showing no shift greater than 3 nm or by having overlapping error bars. If the loci differ between low and high retinal illuminance, scalar

invariance has been violated and unique hue loci shift to either longer or shorter wavelengths between lower and higher retinal illuminances (see Figures 3.1 – 3.4). A completely vertical line connecting the unique hue loci obtained at the low retinal illuminances to unique how loci obtained at higher retinal illuminances would in contrast indicate scalar invariance. Scalar invariance can be assessed in Figures 3.1 – 3.4 and Figures 3.5 – 3.8.

Figures 3.5 – 3.8 compare unique hue loci measured at the higher retinal illuminance to unique hue loci measured at the lower retinal illuminance. Solid symbols denote unique hue loci obtained with retinal illuminance equated photopically. Open symbols denote unique hue loci obtained with retinal illuminance equated scotopically. Each panel indicates a different unique hue. The solid line depicts where the unique hue loci at both the higher and lower retinal illuminance are the same and obey scalar invariance. The dashed lines represent the criterion of ±3 nm. Data points falling above the solid line indicate unique hue loci shifting to longer wavelengths with increasing retinal illuminance, while data points below the solid line indicate unique hue loci shifting to shorter wavelengths with increasing retinal illuminance.

Unique Blue

Unique blue loci (left panel) measured in the fovea (triangles) and bleach condition (circles) either showed no shift in locus with retinal illuminance (Figure 3.5) or they shifted to longer wavelengths with increasing retinal illuminance for both scotopically and photopically equated stimuli (ND and VV, Figures 3.7 and 3.8). As seen

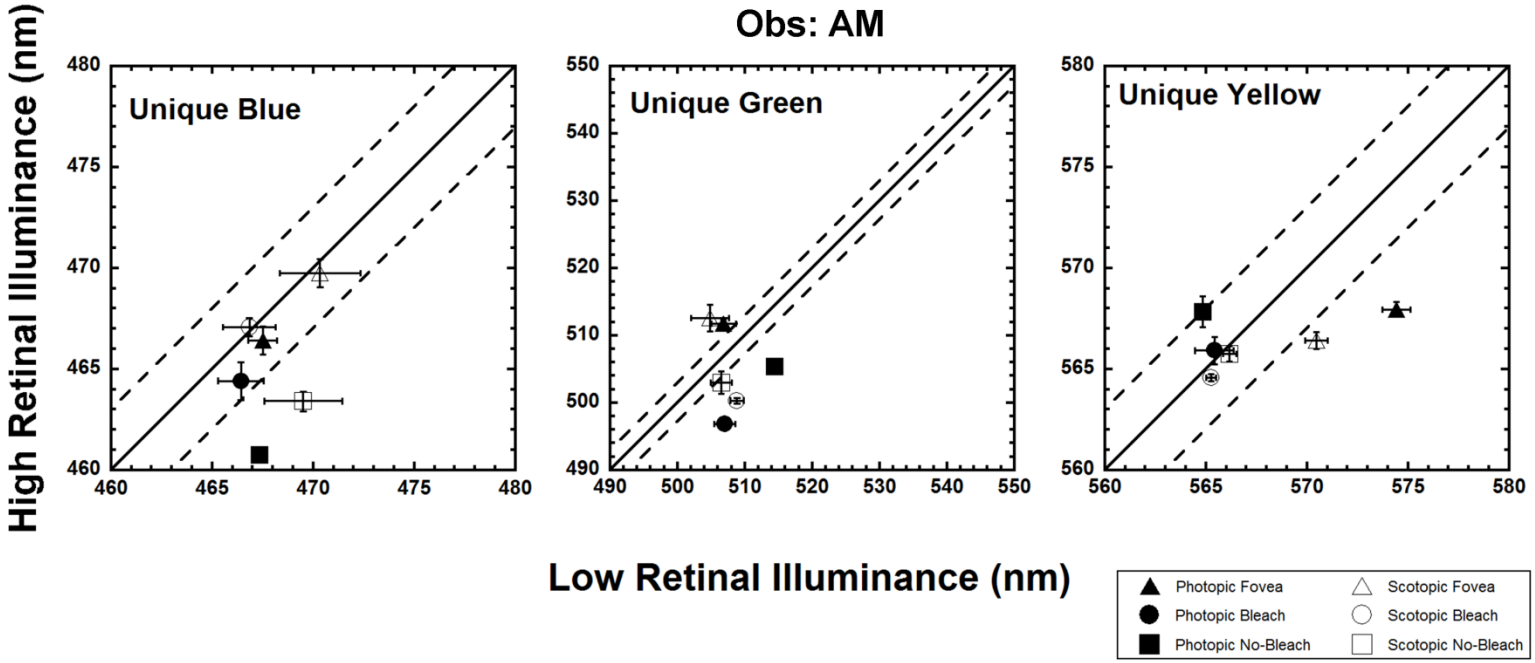

Figure 3.5. *Unique hue loci for observer AM obtained at low retinal illuminances have been plotted against unique hue loci obtained at high retinal illuminances. The solid line indicates no difference in the unique hue values. The dashed lines represent the criterion of ±3 nm.*

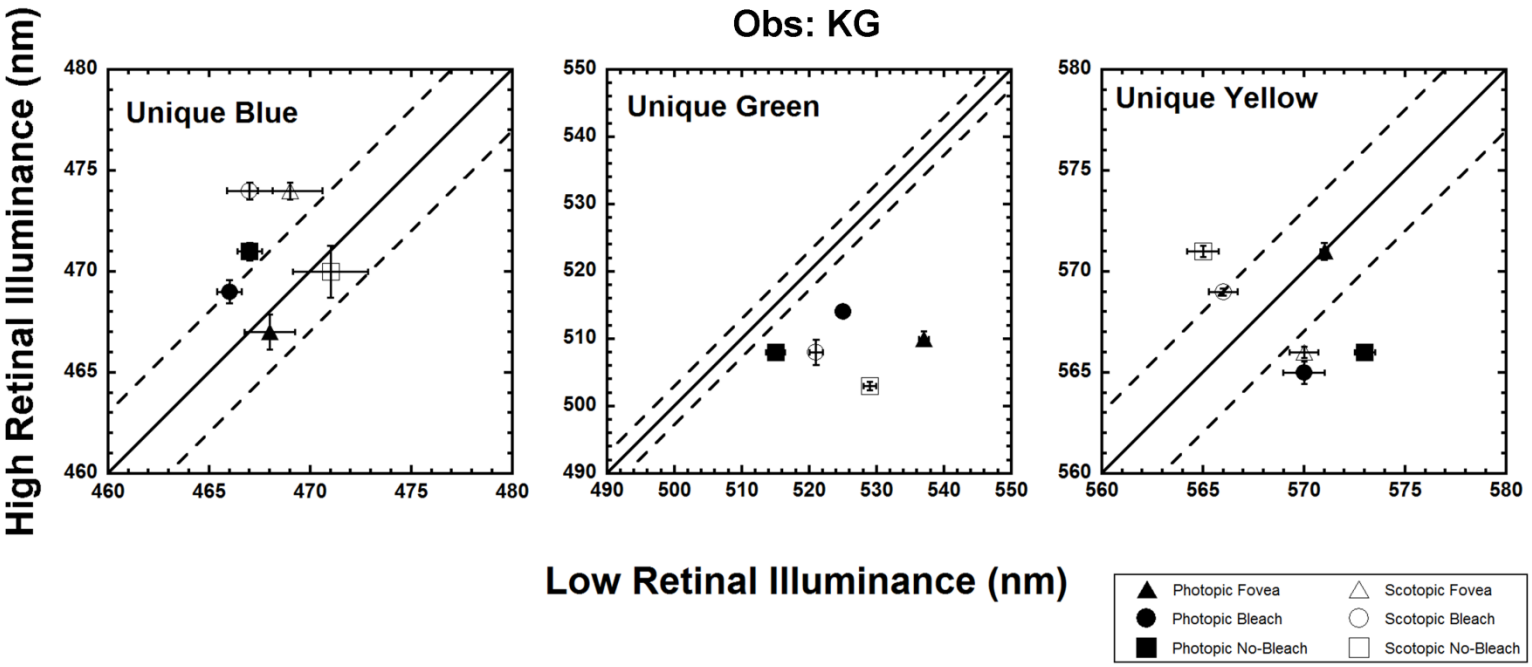

Figure 3.6. *Same as Figure 3.5, except for obs KG.*

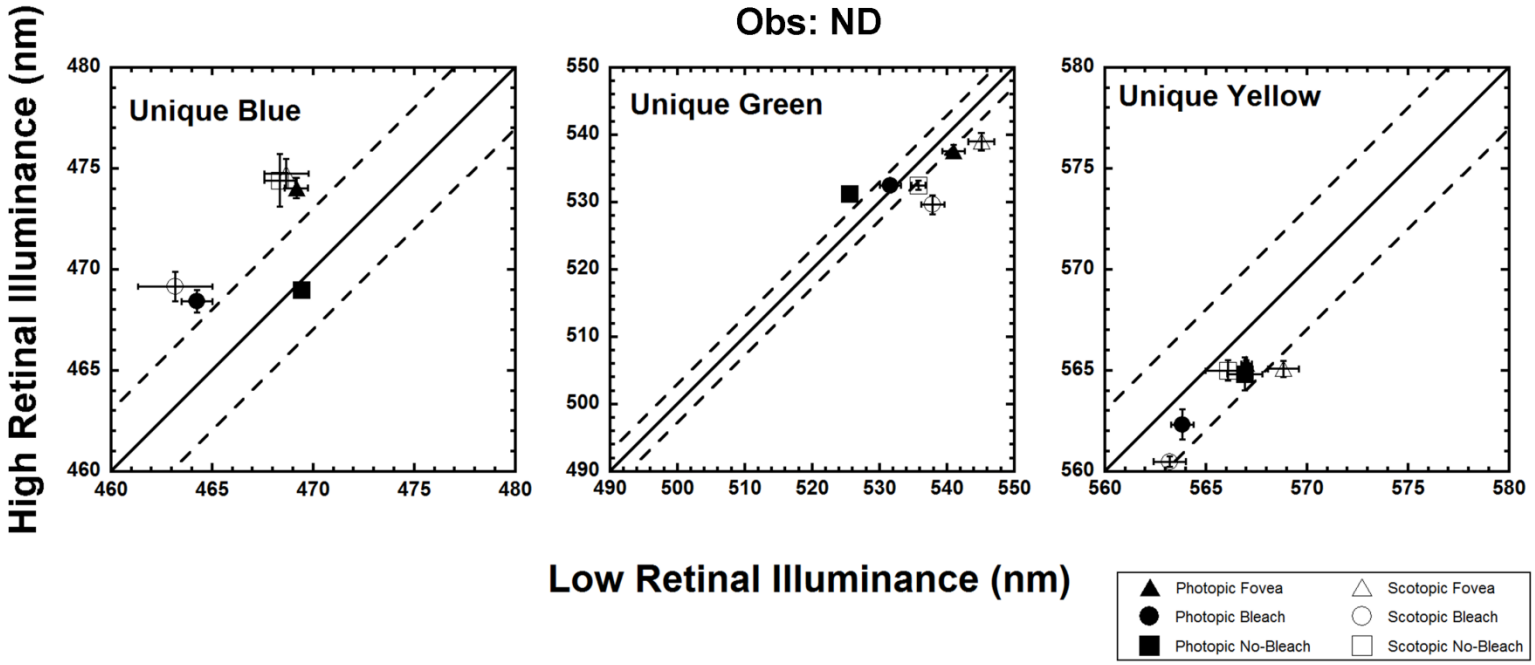

Figure 3.7. *Same as Figure 3.5, except for obs ND.*

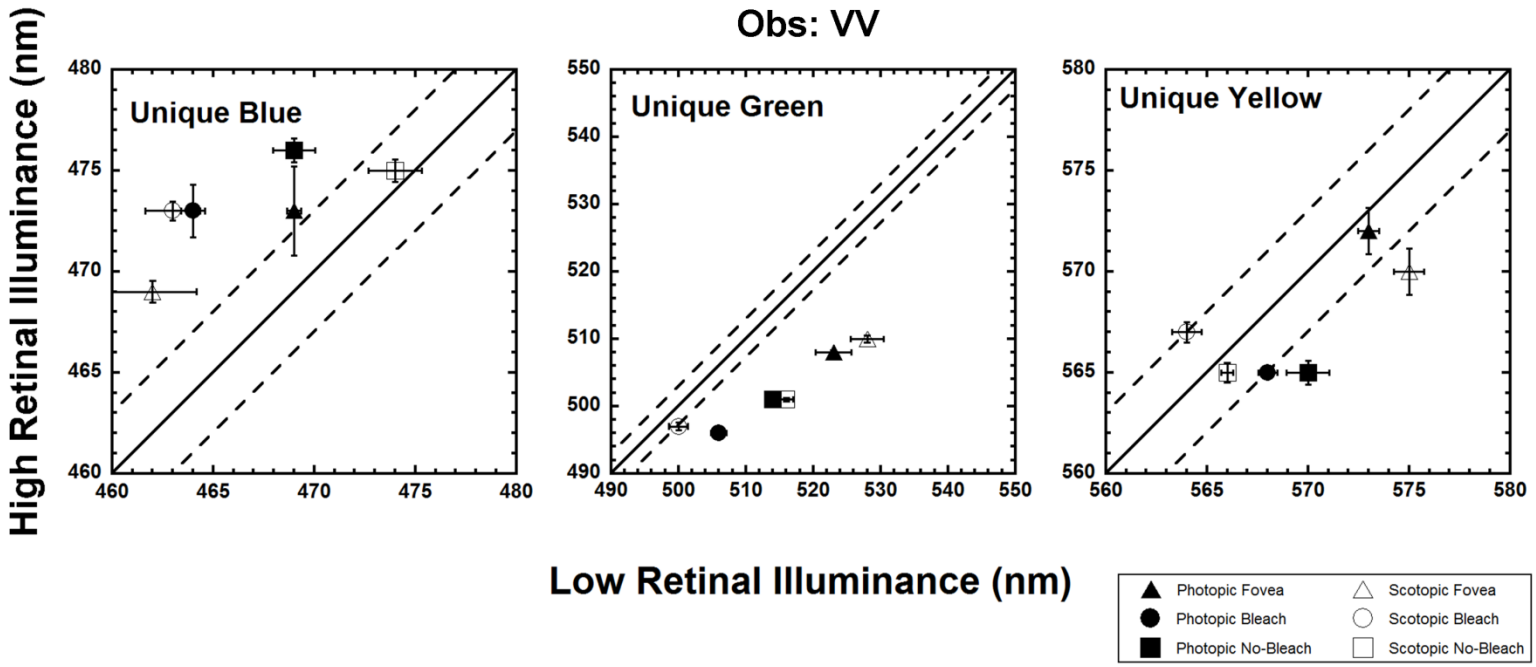

Figure 3.8. *Same as Figure 3.5, except for obs VV.*

in Figure 3.6, only one observer (KG) showed a difference between scotopically and photopically equated stimuli in the fovea and bleach conditions, i.e., unique blue loci measured with photopically equated stimuli were scalar invariant while unique blue loci measured with scotopically equated stimuli showed violations of invariance. In the no-bleach condition (squares), unique blue loci from three of four observers differ depending on the method of equating stimuli. For two observers (KG and VV, Figures 3.6 and 3.8), unique blue loci from the photopic condition (solid triangles) shifted to longer wavelengths with increasing retinal illuminance while unique blue loci from the scotopic condition (open triangles) were scalar invariant. For observer ND (Figure 3.7), the opposite result was seen; unique blue loci from the photopic condition were scalar invariant but loci measured scotopically showed violations of scalar variance. Because of this, the method of equating stimuli is only a factor in the interpretation of scalar invariance of unique blue loci in the no-bleach condition, where rod input is the greatest, but not in the fovea and bleach conditions.

Unique Green

For measurements of unique green loci (middle panel) made with photopically and scotopically equated stimuli in the fovea (triangles), data from three of four observers show violations of scalar invariance with unique green loci shifting to longer wavelengths (AM, Figure 3.5), or shorter wavelengths (KG and VV, Figures 3.6 and 3.8) with increasing retinal illuminance. In the bleach condition (circles), unique green loci from two observers (AM and KG, Figures 3.5 and 3.6) show shifts to shorter wavelengths with increasing retinal illuminance for both photopically and scotopically equated stimuli. The

unique green loci from VV (Figure 3.8) displayed scalar invariance with the scotopically equated stimuli, while unique green loci measured photopically (solid circles) shift shorter with increasing retinal illuminance. The opposite pattern is observed with data for ND (Figure 3.7). In the no-bleach condition (squares), unique green loci from three observers (AM, KG, and VV, Figures 3.5, 3.6, and 3.8) shift to shorter wavelengths with increasing retinal illuminance, regardless of the method used to equate stimuli. For measurements of unique green, scalar invariance does not seem to be influenced by the method used to equate stimuli.

Unique Yellow

Foveal measurements (triangles) of unique yellow loci (right panel) show that measurements obtained with photopically versus scotopically equated stimuli differ from each other for three observers (KG, ND, and VV, Figures 3.6, 3.7, and 3.8). Loci obtained with photopically equated stimuli (solid triangles) are scalar invariant but not those with scotopically equated stimuli (open triangles). In the bleach condition (circles), unique yellow loci for three of four observers (AM, ND, and VV, Figures 3.5, 3.7, and 3.8) are scalar invariant with both photopically and scotopically equated stimuli. The unique yellow loci from AM and ND (Figures 3.5 and 3.7) in the no-bleach condition (squares) are also scalar invariant for both photopically and scotopically equated stimuli. Unique yellow loci from KG and VV (Figures 3.6 and 3.8) differ, depending on whether stimuli were photopically or scotopically equated. The unique yellow loci measured with photopically equated stimuli shifted to shorter wavelengths with increasing retinal illuminance for both KG and VV, while loci measured with scotopically equated stimuli

shifted to longer wavelengths for KG while VV was scalar invariant. Thus, for some observers under the foveal and no-bleach conditions, the conclusions drawn regarding scalar invariance differed depending on whether stimuli were equated photopically or scotopically.

Bleach Versus No-bleach Conditions

Bleach (minimal rod input) and no-bleach (maximal rod input) conditions are compared in figures 3.9 – 3.13 to determine if rods alter the loci of unique hues and whether the method of equating stimuli alters the relationship between the bleach and no-bleach conditions. In figure 3.9, retinal illuminance is plotted as a function of unique hue loci. Columns on the left side correspond to photopic conditions while the right column corresponds to scotopic conditions. Each row represents a different observer. The lines connect the unique hue locus from the low retinal illuminance to the respective unique hue locus at the high retinal illuminance. The dashed line represents the no-bleach condition while the solid line represents the bleach condition. In each panel, the lines on the left are unique blue loci, the middle lines are unique green loci, and the far right lines are unique yellow loci. The error bars represent ±1 SEM.

Figures 3.10 – 3.13 plot unique hue loci obtained in the no-bleach condition as a function of unique hue loci in the respective bleach condition. Solid symbols represent unique hue loci obtained with photopically equated stimuli while open symbols represent scotopically equated unique hue loci. Loci from the low retinal illuminance condition are represented by circles, while high retinal illuminance is represented by squares. The error bars represent ±1 SEM. If unique hue loci from the respective bleach and no-bleach

condition are the same, they will fall on the solid line. If the loci fall above the line, no-bleach loci are at longer wavelengths than bleach loci. If the loci fall below the line, bleach loci are at longer wavelengths than the no-bleach loci. The dashed lines represent the ±3 nm criterion.

Unique Blue

Figures 3.9 – 3.13 show that in general for unique blue loci, the scotopic loci show a similar relationship between bleach and no-bleach conditions as the photopic loci. The exceptions are observers KG and ND (Figures 3.9 – middle rows, and Figures 3.11 and 3.12). The scotopic unique blue locus at the high retinal illuminance is shorter in the no-bleach condition than the bleach for KG (Figure 3.11), while the photopic bleach and no-bleach loci and the scotopic bleach and no-bleach loci at low retinal illuminance do not differ from each other. The unique blue loci at the high retinal illuminance do not differ between the bleach and no-bleach conditions for ND (Figure 3.12) for photopically equated stimuli, but do differ for scotopically equated stimuli, while the photopic loci at both illuminance levels and the scotopic low retinal illuminance show the loci at longer wavelengths in the no-bleach condition than the bleach condition. When a shift is observed between unique blue loci in the bleach and no-bleach conditions, the no-bleach locus can be either shorter (AM and KG, Figures 3.10 and 3.11) than the bleach or longer (ND and VV, Figures 3.12 and 3.13) than the bleach locus.

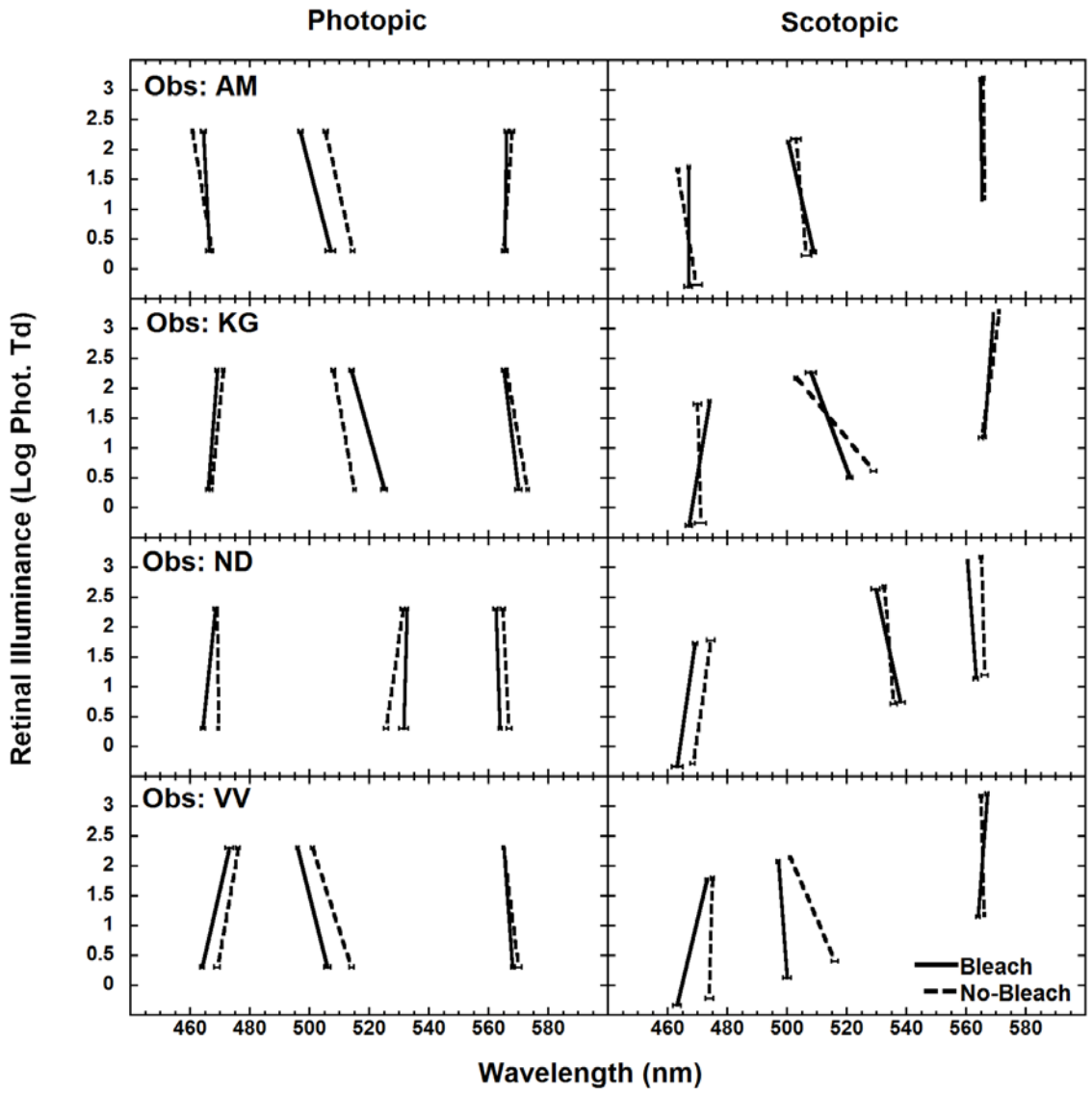

Figure 3.9: *Peripheral unique hue loci from the no-bleach (dashed lines) condition are compared to peripheral unique hue loci from the bleach (solid lines) condition for the four observers. The left column shows loci from the photopically equated condition and the right column shows loci from the scotopically equated condition. Error bars represent ±1 SEM.*

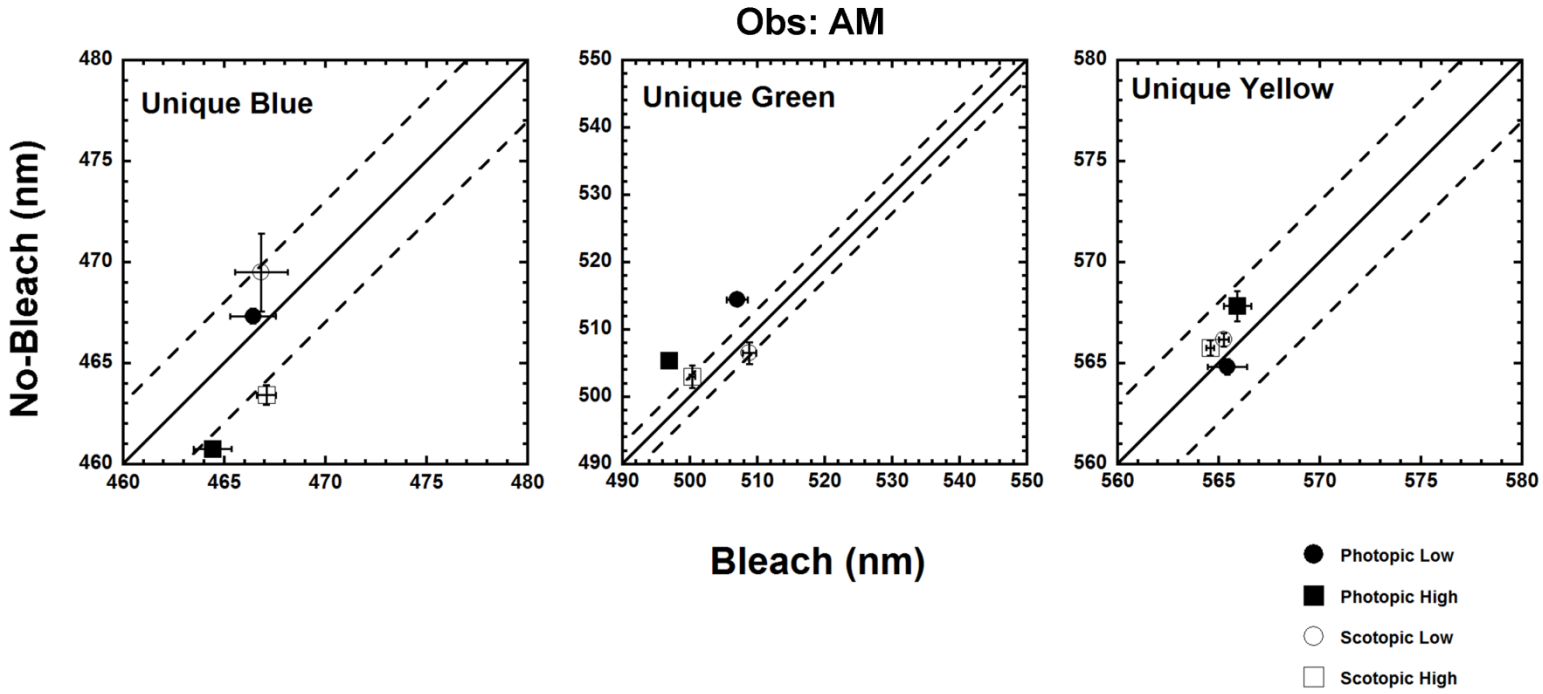

Figure 3.10. *Unique hue loci from the bleach condition are compared with unique hue loci from the respective no-bleach condition for observer AM. The solid line indicates no difference between the bleach and no-bleach loci. The dashed lines represent the criterion of ±3 nm.*

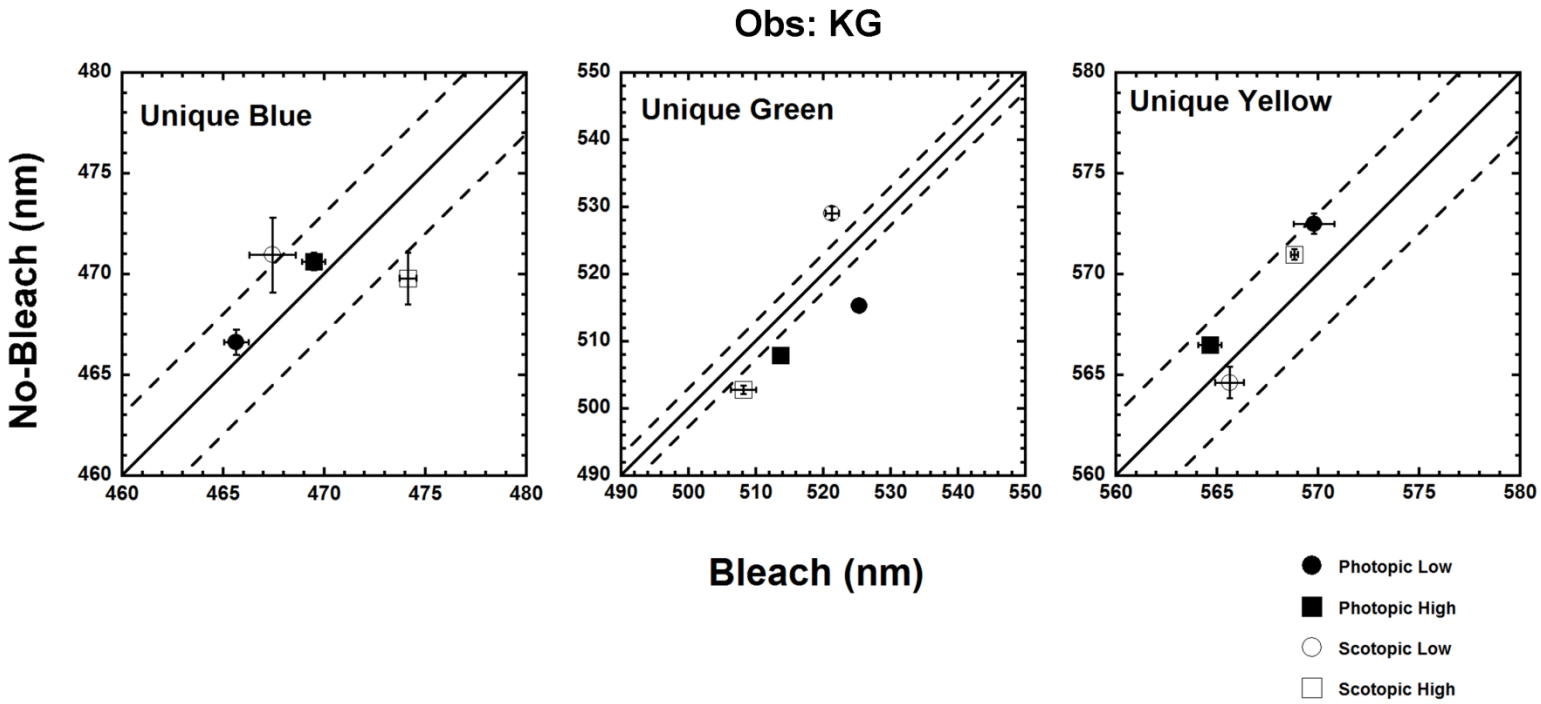

Figure 3.11. *Same as figure 3.10, except for observer KG.*

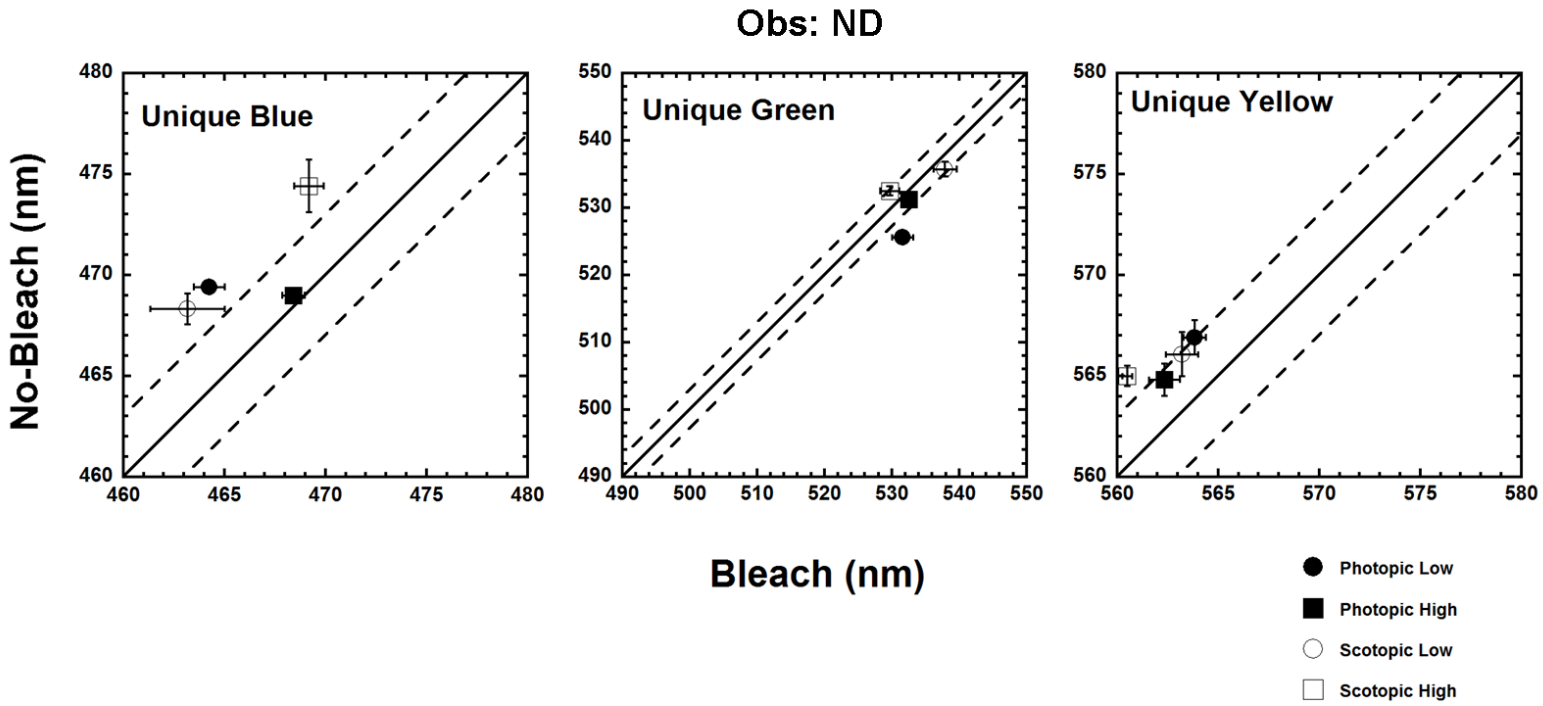

Figure 3.12. *Same as figure 3.10, except for observer ND.*

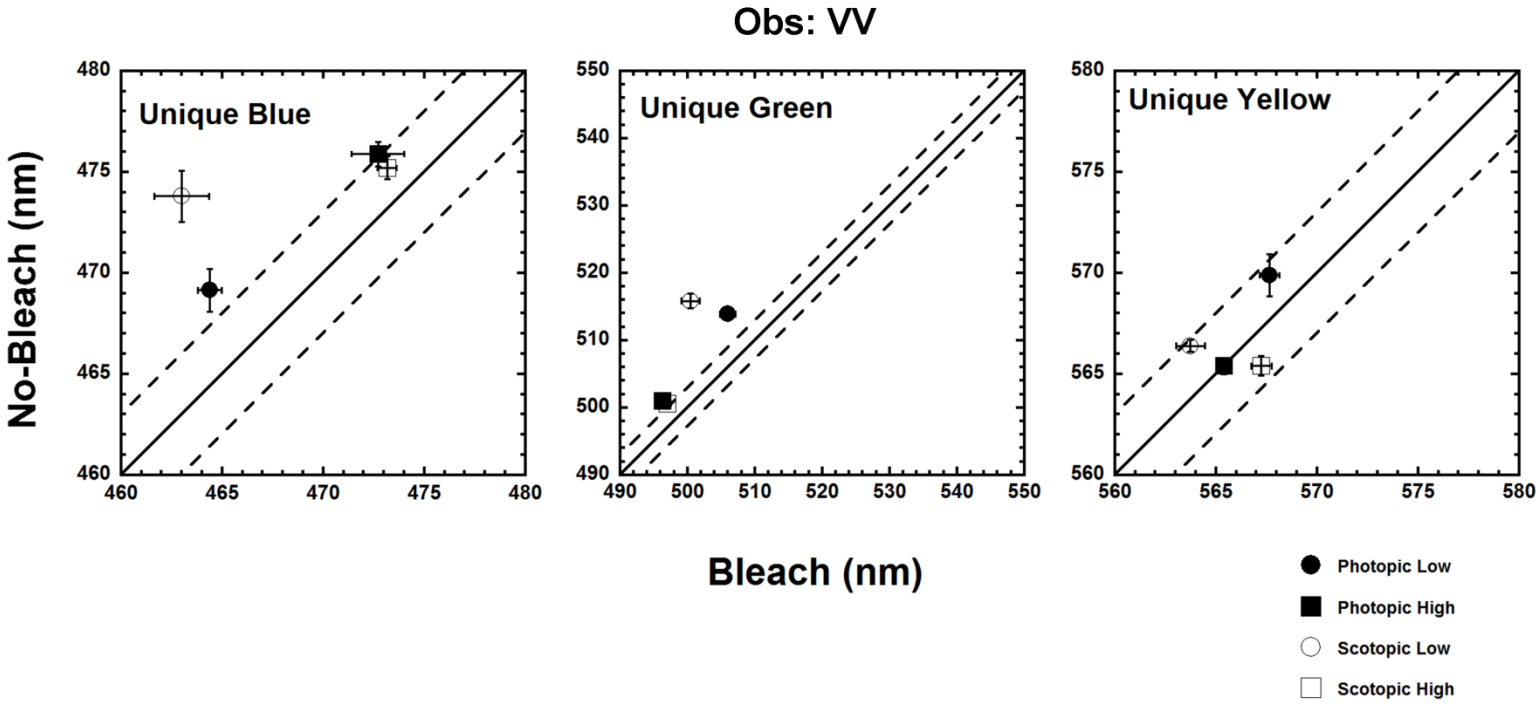

Figure 3.13. *Same as figure 3.10, except for observer VV.*

Unique Green

For unique green loci, each observer shows at least one difference between bleach and no-bleach conditions, depending on the method used to equate stimuli; however, there is no pattern among observers for photopically and scotopically equated stimuli. For example, with AM (Figures 3.9 and 3.10), the no-bleach unique green locus is at a longer wavelengths than the locus from the bleach condition when stimuli have been equated photopically for both retinal illuminances. With the scotopically equated stimuli, there is no difference between the no-bleach unique green loci and bleach unique green loci at both retinal illuminances. The unique green loci from AM and VV show the bleach unique green loci at longer wavelengths than bleach unique green loci. In contrast, the no-bleach loci obtained from KG and ND were more likely to shift to shorter wavelengths compared to the bleach loci.

Unique Yellow

Lastly, the unique yellow loci from the bleach and no-bleach conditions do not differ from each other for either the photopically or scotopically equated stimuli.

Foveal Versus Peripheral Cones

The relationship between cones in the fovea versus the cones in the peripheral retina was investigated by comparing foveal loci with unique hue loci obtained in the periphery under the bleach condition with minimal rod input. Figure 3.14 illustrates how the loci of unique hues vary for the foveal and peripheral cones. The column on the left side corresponds to unique hue loci obtained with photopically equated stimuli while the

right column corresponds to scotopically equated stimuli. The x-axis specifies unique hue loci while the y-axis shows the retinal illuminances. Each row of panels presents data from a different observer. The error bars represent ±1 SEM. Within a panel, the left lines depict unique blue loci at the two retinal illuminances, the middle lines depict unique green loci, and the right lines depict unique yellow loci. The solid lines represent unique hue loci measured in the fovea and the dashed lines denote unique hue loci obtained in the peripheral retina under bleach conditions. To assist in determining whether a shift in unique hue loci is observed, based on the criteria established at the beginning of this chapter, data have been replotted in a different format in Figures 3.15 – 3.18. In these figures, unique hue loci obtained in the fovea are plotted as a function of unique hue loci obtained in the peripheral retina under bleach conditions. Each panel presents a different unique hue. The solid line represents where the foveal unique hue locus is the same as the peripheral unique hue locus. If the loci fall above the line, foveal loci are at longer wavelengths than bleach loci. If the loci fall below the line, bleach loci are at longer wavelengths than the foveal loci. Dashed lines denote ±3 nm.

Unique Blue

As shown in Figures 3.14 – 3.17, the method used to equate the stimuli did not affect the pattern of results when comparing foveal unique blue loci to peripheral unique blue loci for three observers (AM, KG, and ND). For two of these observers (AM and KG), the unique blue loci from the two retinal locations did not differ from each other. For the third observer (ND), the foveal unique blue loci were longer than the peripheral bleach loci. The presence or absence of a shift for the fourth observer (VV, Figures 3.14

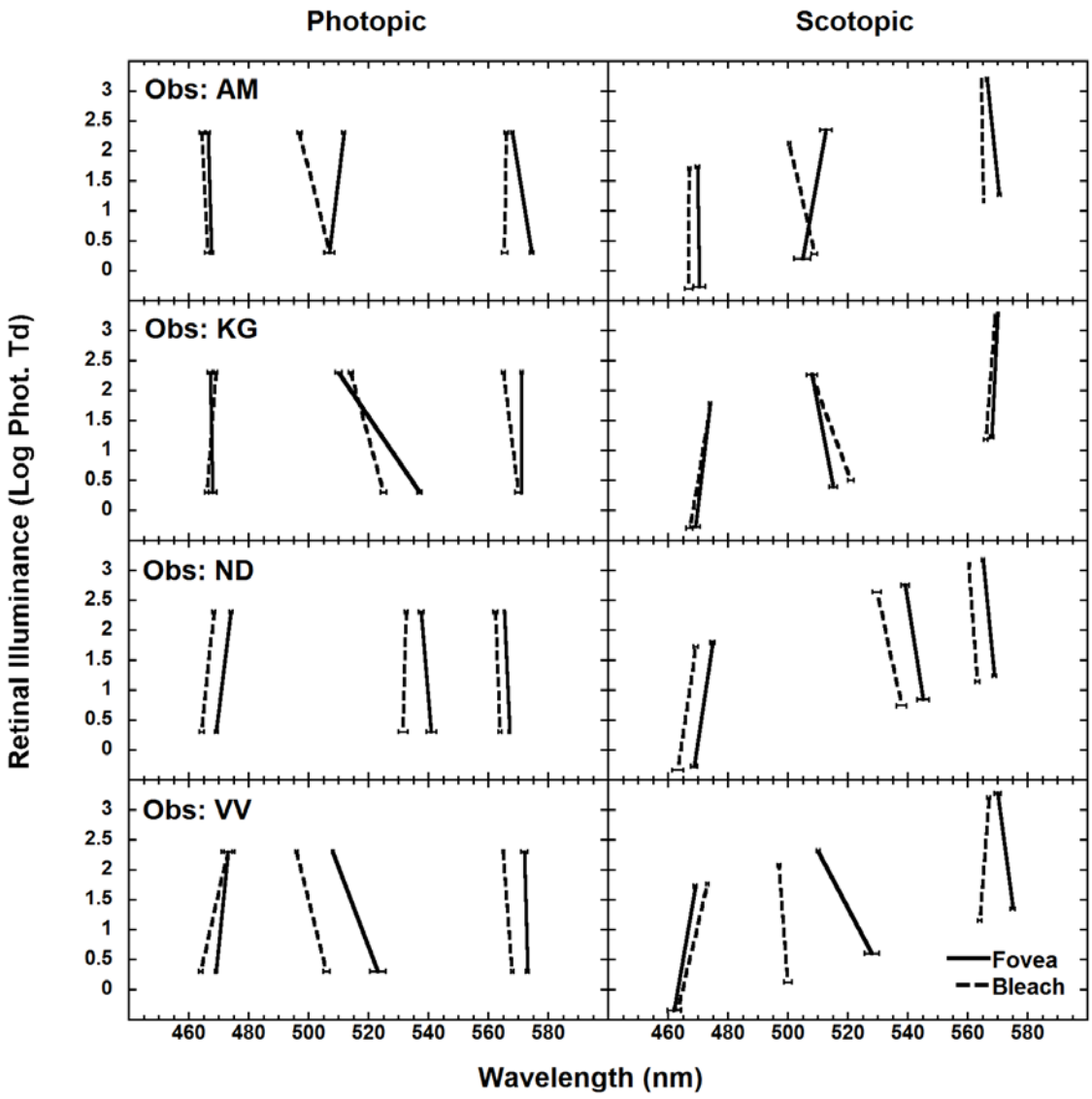

Figure 3.14: *Foveal unique hue loci (solid lines) are compared with peripheral unique hue loci (dashed lines) for all observers. The left column presents unique hue loci obtained with photopically equated stimuli while the right column shows unique hue loci obtained with scotopically equated stimuli. The error bars denote* ±1 SEM.

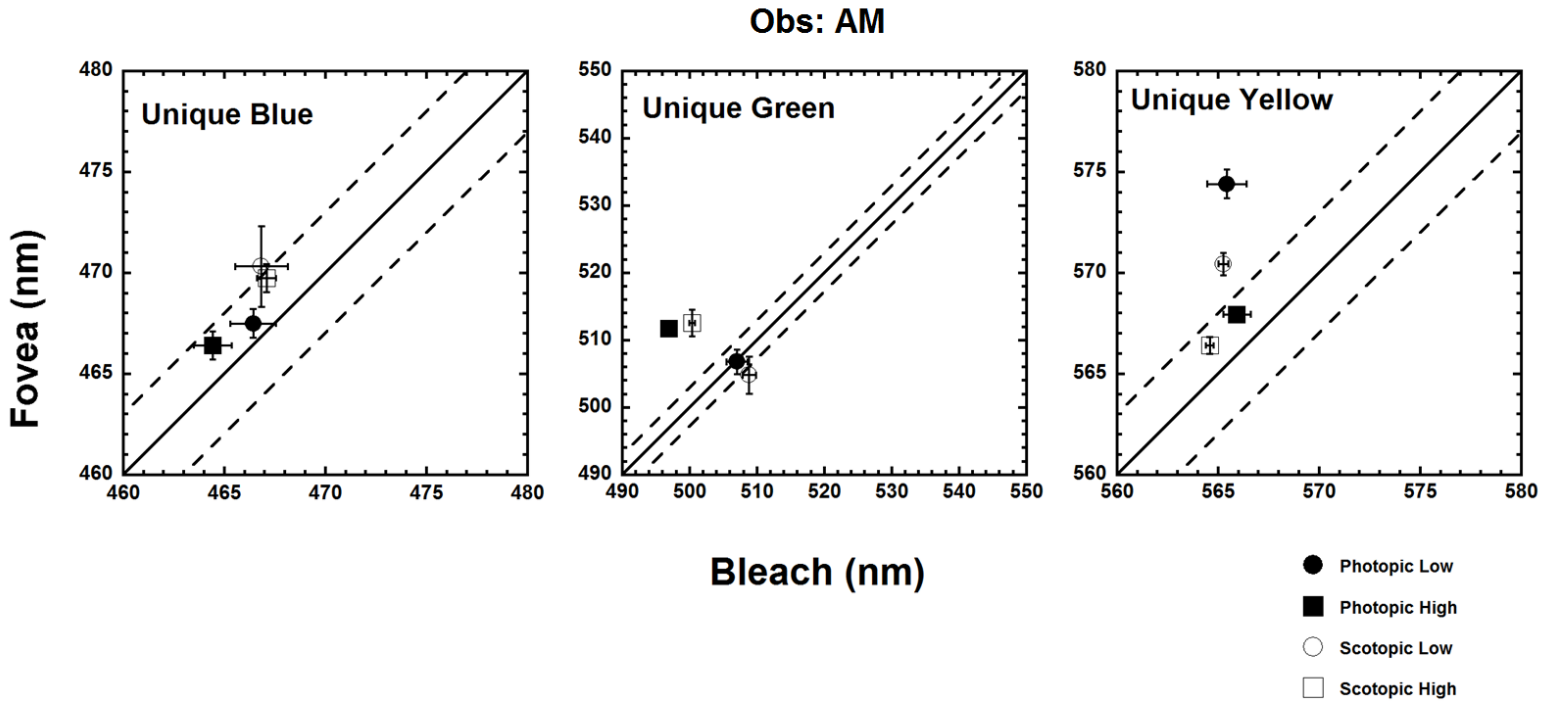

Figure 3.15. *Foveal unique hue loci are plotted as a function of peripheral bleach unique hue loci. Circles denote low retinal illuminance, while solid symbols denote photopically equated stimuli. Squares denote high retinal illuminance, while open symbols denote scotopically equated stimuli. If the unique hue loci from the fovea and peripheral bleach condition were the same, they would both fall on the solid diagonal line. The dashed line represents ±3 nm.*

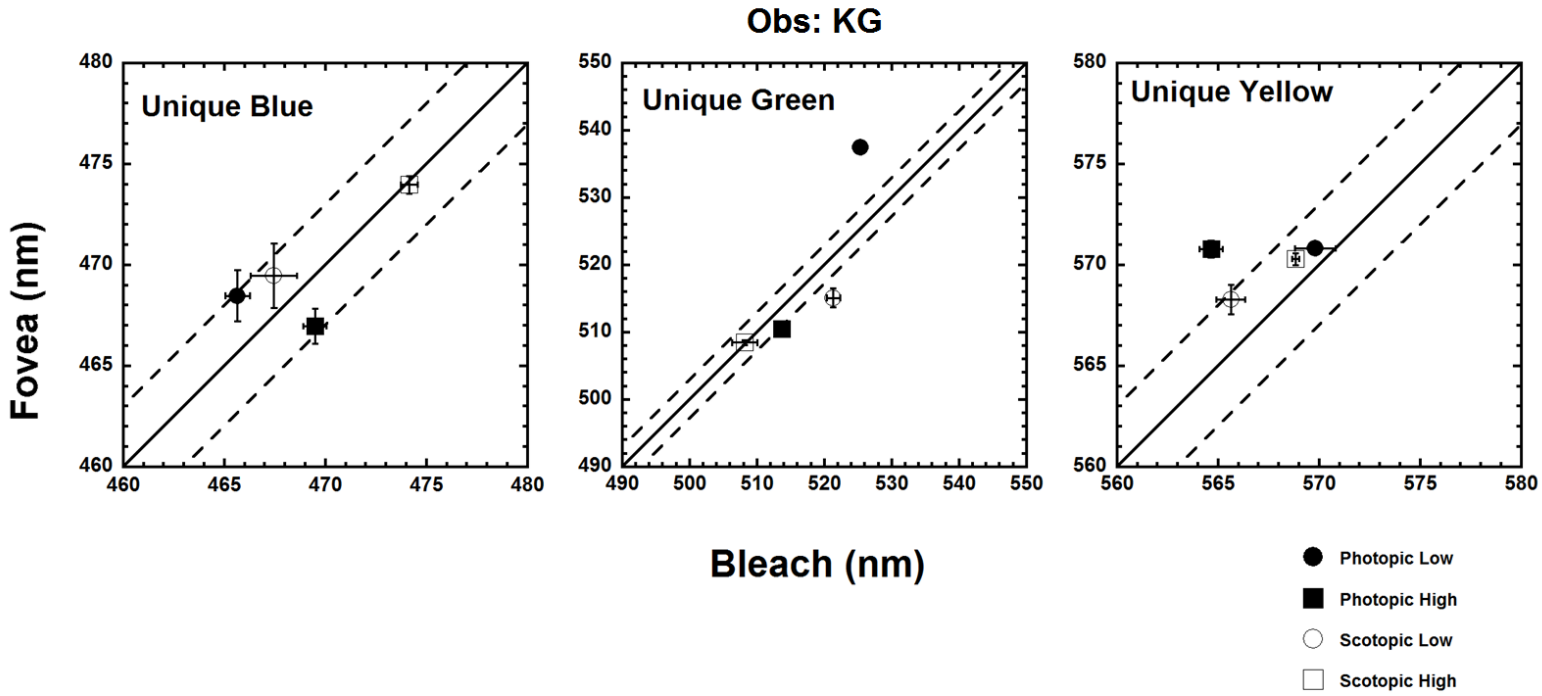

Figure 3.16. *Same format as Figure 3.15, except for observer KG.*

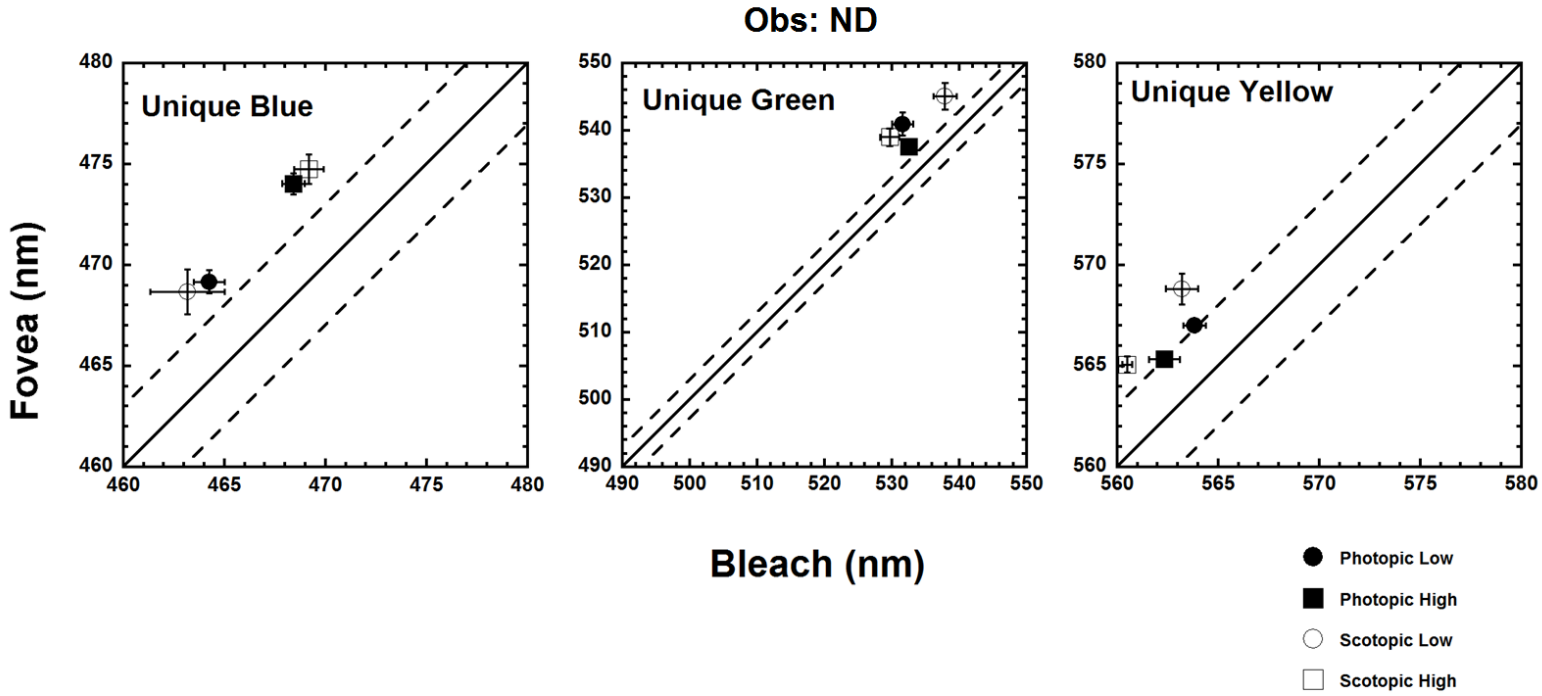

Figure 3.17. *Same format as Figure 3.15, except for observer ND.*

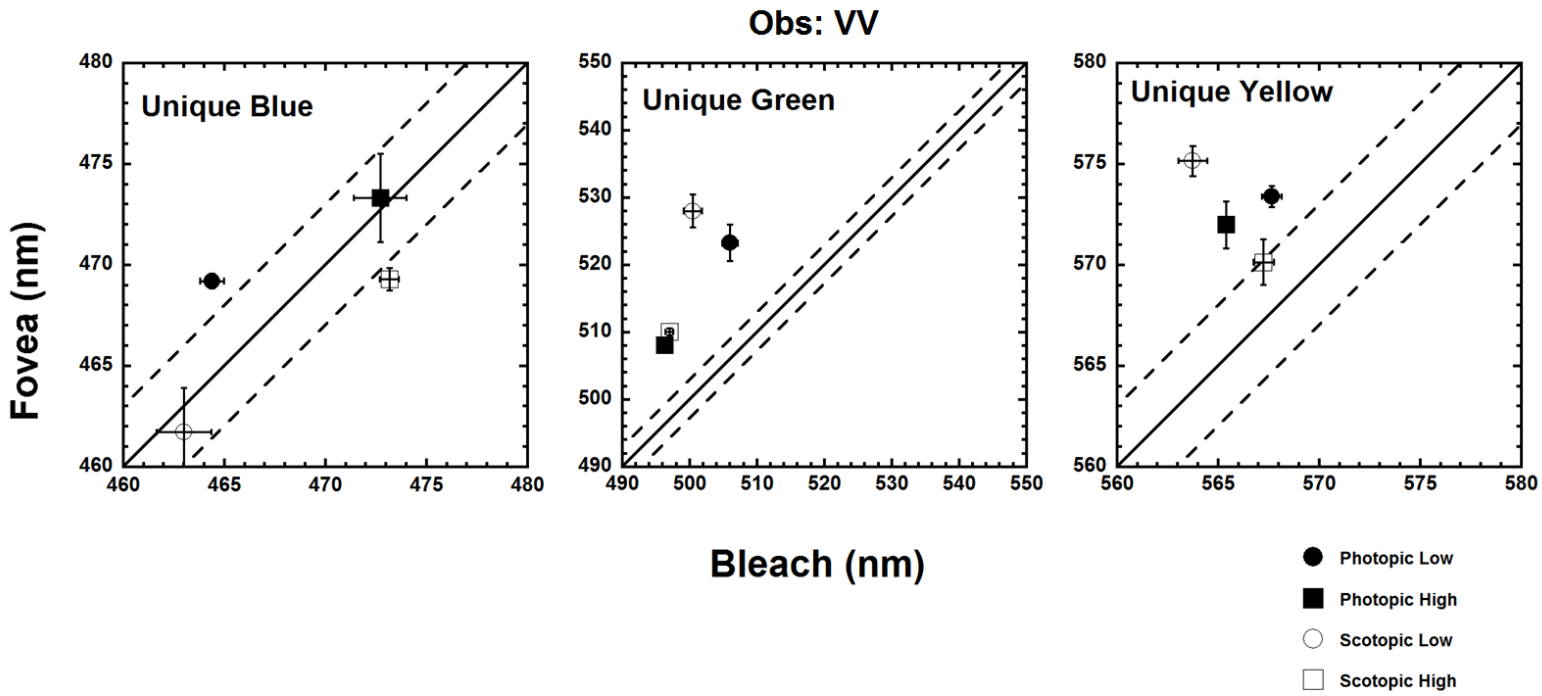

Figure 3.18. *Same format as Figure 3.15, except for observer VV.*

and 3.18) was dependent on retinal illuminance and the method of equating stimuli. Data from VV showed at the low retinal illuminance, photopically equated foveal locus shifted to a longer wavelength than the low retinal illuminance bleach locus. She showed the opposite for scotopically equated stimuli, where the high retinal illuminance bleach locus was at a longer wavelength than the high retinal illuminance foveal locus.

Unique Green

Similarly, Figures 3.14 – 3.18 show the method used to equate stimuli did not affect the results for unique green loci for three of the four observers (AM, ND, and VV). For all three observers, foveal unique green loci were at longer wavelengths than the peripheral bleach loci for the high retinal illuminance. For ND and VV, this difference was also present at the low retinal illuminance, while the unique green loci for AM showed no difference between the two retinal locations at the low retinal illuminance. For KG (Figure 3.16) at the lower retinal illuminance, the foveal unique green locus measured with photopically equated stimuli were longer than the peripheral bleach locus and this direction of shift was reversed with the scotopically equated stimuli.

Unique Yellow

As shown in Figures 3.14 and 3.16 – 3.18, the comparison for unique yellow was affected by the method used to equate stimuli for three of the four observers (KG, ND, and VV). Some of these differences were specific to a particular retinal illuminance. For example, the foveal unique yellow locus from KG (Figures 3.16) was similar to peripheral bleach locus for both retinal illuminances with scotopically equated stimuli but

only for the low retinal illuminance with photopically equated stimuli. At the high retinal illuminances for KG, the foveal unique yellow locus was at longer wavelengths than the peripheral bleach unique yellow locus. If a difference was observed between foveal and peripheral bleach unique yellow loci, under any of the experimental conditions, the foveal unique yellow loci were at longer wavelengths than peripheral bleach loci. Overall, the method of equating stimuli did not change the conclusion drawn about the relationship between foveal unique yellow loci and peripheral bleach unique yellow loci.

DISCUSSION

Summary of Results

Photopic versus Scotopic

In the foveal condition for unique blue loci, three of four observers showed differences between photopic and scotopic loci at higher retinal illuminances (see Figures 3.1 – 3.4). At least three of four observers show differences between unique green loci at the low retinal illuminances in all three experimental conditions (fovea, bleach, and no-bleach) when comparing the photopic loci to the scotopic loci. There were no differences in photopically and scotopically equated unique blue and unique yellow loci in the bleach and no-bleach conditions, and additionally, no differences in the fovea with unique yellow loci.

Scalar Invariance

Scalar invariance was observed in the fovea for unique blue and unique yellow loci when photopically equated, as well as for unique blue loci when scotopically equated (see Figures 3.5 – 3.8). Violations of scalar invariance were seen in the fovea with scotopically equated unique green and unique yellow loci and photopically equated unique green loci. Only in the case of unique yellow did the method of equating stimuli influence the outcome of scalar invariance.

In the bleach condition, scalar invariance was observed for photopically equated unique yellow loci and scotopically equated green and yellow unique hue loci (see Figures 3.5 – 3.8). Violations of scalar invariance were seen with scotopically equated

unique blue loci, and under photopic conditions for unique blue and unique green loci. Only in the case of unique green did the method of equating stimuli influence the outcome of scalar invariance.

In the no-bleach conditions, violations of scalar invariance were seen in the photopic conditions for all unique hues, and additionally in the scotopic condition for unique green loci (see Figures 3.5 – 3.8). Under scotopic conditions, both unique blue and unique yellow loci were scalar invariant. In the case of unique blue and unique yellow loci, the method of equating stimuli influenced the outcome of scalar invariance.

Bleach versus No-Bleach

Three of four observers showed the same pattern of results; the relationship between bleach and no-bleach loci differed depending on whether stimuli were equated photopically or equated scotopically for unique green loci at low retinal illuminances (see Figures 3.9 – 3.13). For unique blue and unique yellow loci, the method of equating stimuli was not a factor.

Fovea versus peripheral bleach:

Unique yellow loci measured at the high retinal illuminance is the only condition where you can draw different conclusions based on whether stimuli were equated photopically or scotopically when looking at loci in the fovea versus loci obtained after a peripheral bleach. When stimuli were equated photopically in the high retinal illuminance condition, two observers showed foveal loci at longer wavelengths than their bleach counterparts (see Figures 3.14 – 3.18). When stimuli were equated scotopically, these same two observers showed no differences between the loci of bleach and foveal data. One other observer showed differences in bleach and foveal loci depending on the

method of equating stimuli used (see Figures 3.14 – 3.18); however, this was opposite of the pattern shown by the other two observers. For unique blue and unique green loci, the method of equating stimuli had no effect on the relationship between foveal versus peripheral bleach comparisons.

Comparison to Previous Studies

Fovea versus Bleach

Foveal unique hue loci tended to be at longer wavelengths than their bleach counterparts for at least three of four observers with all unique hue loci, regardless of the method used to equate stimuli. Our data suggest that cones in the fovea are responding in a similar manner as cones in the peripheral retina to changes in retinal illuminance. For unique blue, unique green, and unique yellow loci, both photopic and scotopic conditions, showed that loci measured in the fovea and bleach conditions shifted in the same directions with increases in retinal illuminance, although the magnitude of these shifts varied among observers. As Figure 3.14 illustrates, in general, the foveal and bleach unique hue functions are relatively parallel to each other. The unresolved question is what is the mechanism responsible for creating this additive effect. One explanation is that there may be residual rod effects in the bleach condition, since no-bleach loci were often at longer wavelengths than their bleach counterparts.

Nerger et al. (1995) showed that at 20 degrees in the temporal retina, unique green loci were at longer wavelengths in the fovea than the peripheral retina for the bleach condition. Similarly, Nerger et al. (1998) have also reported unique blue loci in the fovea at longer wavelengths than loci at 1 deg and 8 deg in both the nasal and superior retinas

for the bleach condition. This was also shown for unique yellow loci, but only at 8 deg in both the nasal and superior retinas for the bleach condition. It should be noted, though, that unique yellow loci did not show this trend for stimuli larger than 2.0 deg. As mentioned above, for at least 3 of 4 observers in this study, unique green foveal loci were at longer wavelengths than bleach loci, which disagrees with data reported by Volbrecht et al. (2000), who showed no differences between foveal and bleach unique green loci.

Bleach versus No-Bleach

The direction and magnitude of unique hue loci shifts between the bleach and no-bleach conditions varied among and within observers, and consequently, there were no observable trends among observers concerning rod influence on unique hue loci. This is unexpected, as it would be assumed that conditions at low retinal illuminances would differ between bleach and no-bleach loci due to more rod input at the lower retinal illuminance in the no-bleach condition. At 10 deg retinal eccentricity, the number of rods is near its peak for all retinal meridians (Curcio et al., 1990). Nerger et al. (1998) obtained unique hue loci at 8 deg in the peripheral retina (nasal and superior) and reported no-bleach loci at longer wavelengths than bleach loci for unique blue and unique yellow loci; a similar pattern did not emerge for Volbrecht et al. (2000) with unique green loci and unique hue loci in this current study. In another study, Volbrecht et al. (2010) showed that unique green loci shifted to longer wavelengths as the time post-bleach increased; however, this trend only occurred with loci derived from hue naming data but not from unique green data acquired with a staircase procedure.

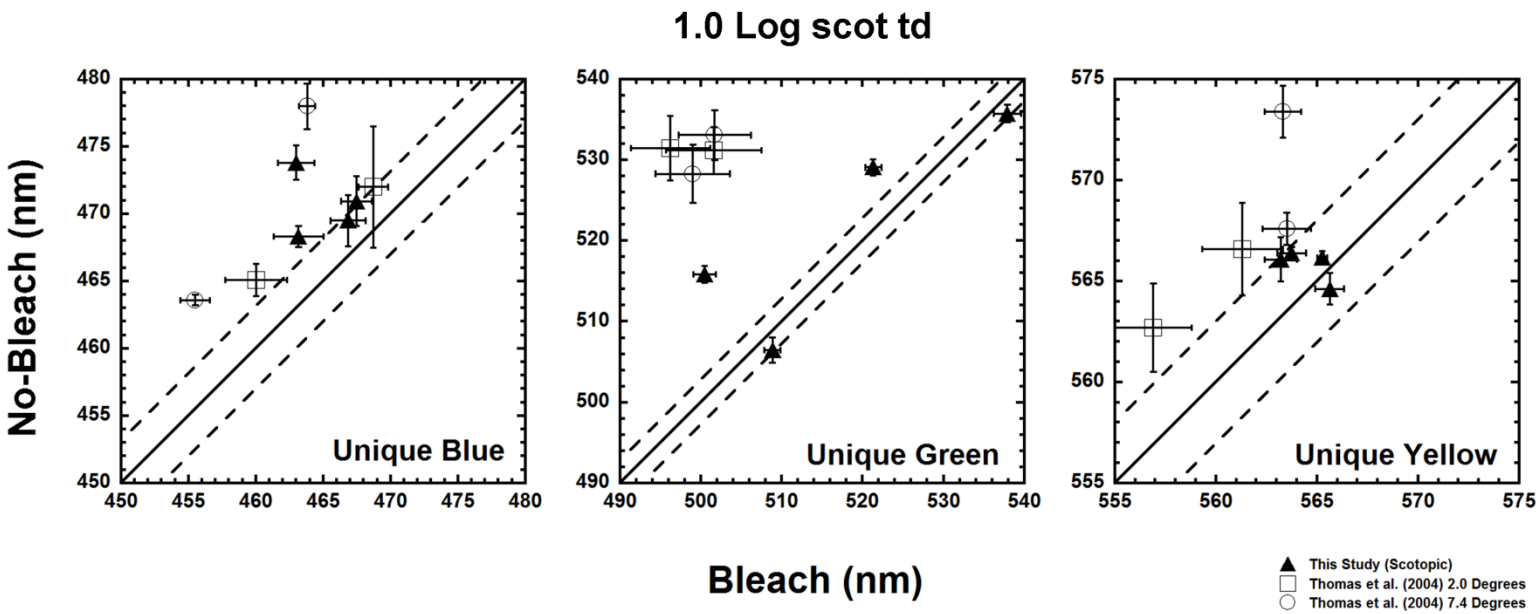

Figure 4.1. *Bleach and no-bleach data from this study (obtained at 1.0 log scot td) are compared with bleach and no-bleach data from Thomas et al. (2004) obtained at 1.0 log scot tds. Solid triangles represent loci from this study while open symbols represent loci from Thomas et al. (2004). Open Squares represent loci obtained with 2.0 degree stimuli and open circles represent loci obtained with 7.4 degree stimuli. The error bars denote ± 1 SEM. The solid line depicts where bleach and no-bleach loci are the same while dashed lines denote ±3 nm.*

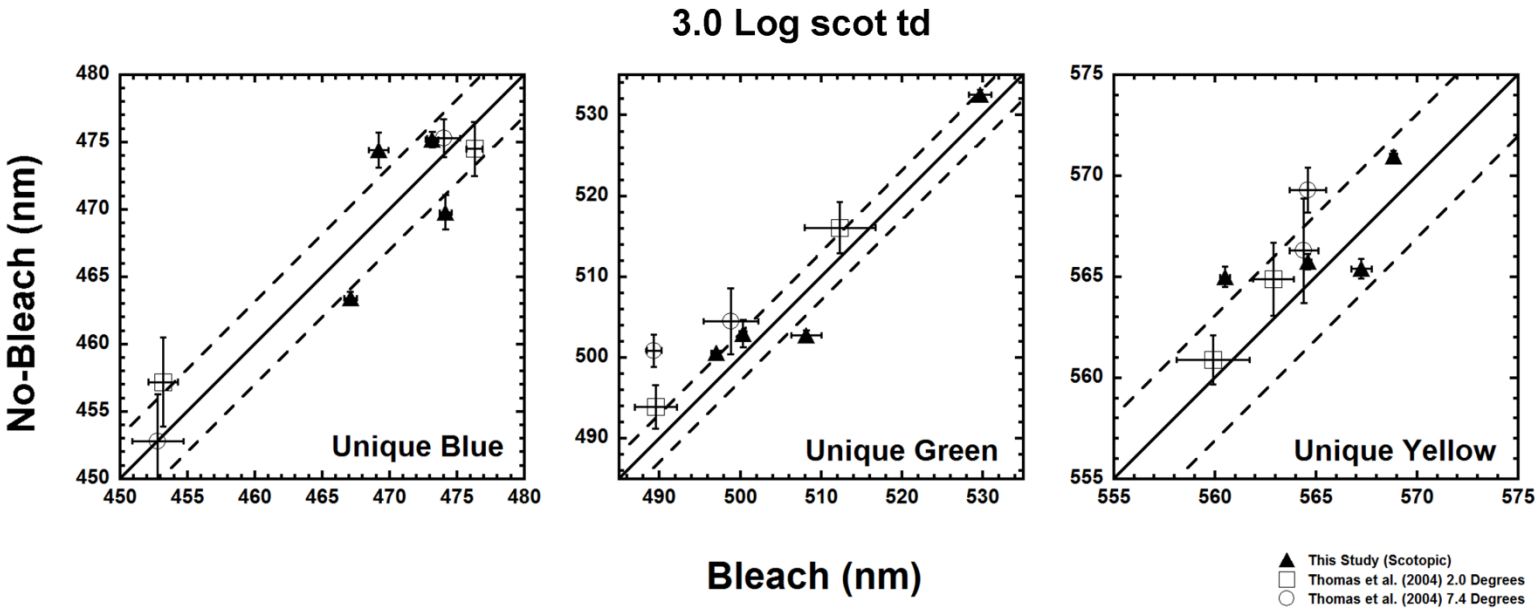

Figure 4.2. *Same format as Figure 4.1, except retinal illuminance is at 3.0 log scot tds for both studies.*

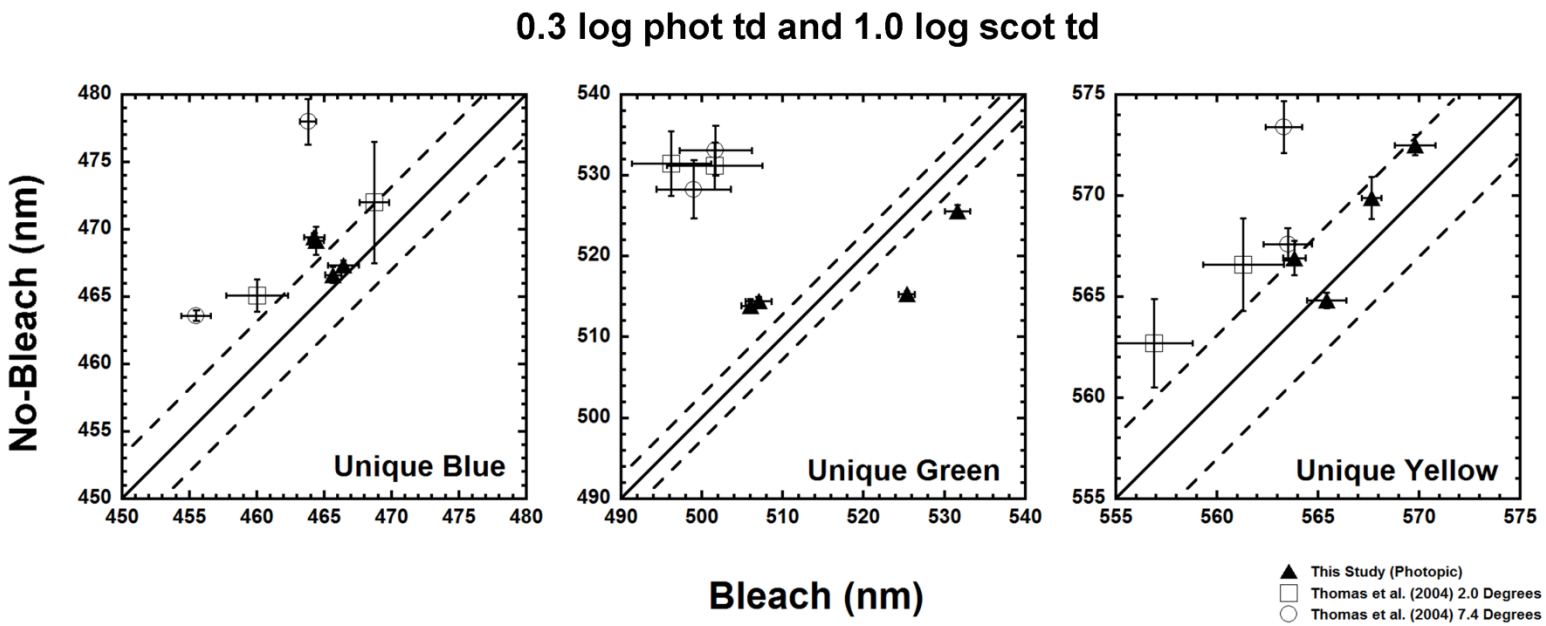

Figure 4.3. *Bleach and no-bleach obtained at 0.3 log phot tds in this study are compared with bleach and no-bleach data obtained at 1.0 log scot tds in Thomas et al. (2004) study. Solid triangles represent loci from this study while open symbols represent loci from Thomas et al. (2004). Opens squares represent loci obtained with 2.0-deg stimuli and open circles represent loci obtained with 7.4-deg stimuli. The error bars denote ±1 SEM. The solid line depicts where bleach and no-bleach loci are the same, while dashed lines denote ±3 nm.*

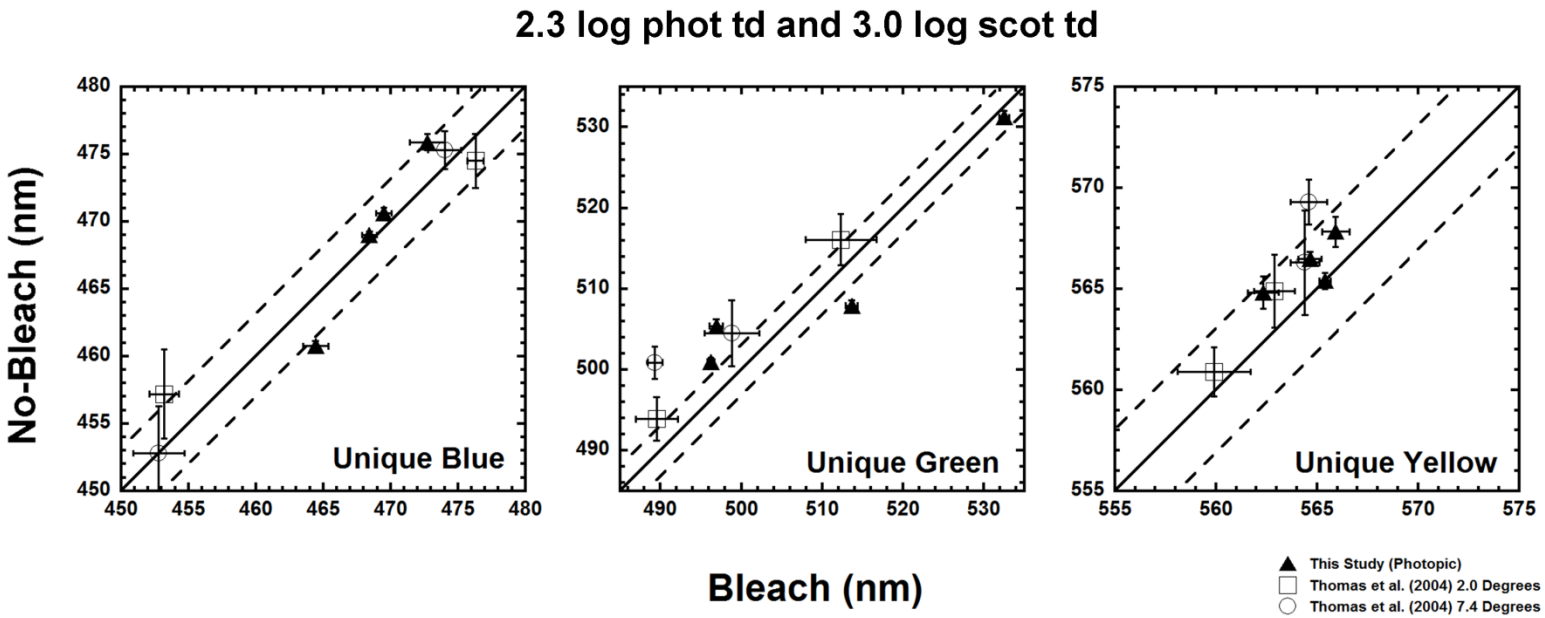

Figure 4.4. *Same format as Figure 4.3, except the retinal illuminance for this study is 2.3 log phot tds in this study and 3.0 log scot tds in Thomas et al (2004) study.*

Table 4.1 E*xperimental differences between studies.*

	This Study (2011)	**Thomas et al. (2004)**
Stimulus Size (In Periphery):	4.0-deg	0.6, 2.0, and 7.4 deg
Retinal Location:	10-deg Temporal	7-deg Nasal
Retinal Illuminances:	1.0 and 3.0 Log Scot Td, 0.3 and 2.3 Log Phot Td	1.0 and 3.0 Log Scot Td

Thomas and colleagues (2004) have also compared unique hues obtained in a bleach condition to those obtained in a no-bleach condition. These unique hue loci are compared with unique hue loci from this study. Table 4.1 highlights the experimental differences between this study and Thomas et al. (2004). Both 2.0 and 7.4 deg stimuli from Thomas et al. (2004) were plotted with the 4.0 deg stimuli from the present study. In figures 4.1 - 4.4, the unique hue bleach data from both studies are plotted against the unique hue no-bleach data from both studies. The solid diagonal line indicates bleach and no-bleach unique hue loci are the same, suggesting little or no rod influence on the unique hue locus. The dotted lines represent the ±3 nm criteria, where any data points falling outside of the lines suggest a shift in the locus of the unique hue. The closed triangle symbols represent data from this study, while the open squares represent data measured with the 2-deg stimuli from Thomas et al. (2004) and the open circles represent data measured with their 7.4-deg stimuli. Figure 4.1 compares 1.0 log scotopic td unique hue loci obtained in this study with the 1.0 log scotopic td loci from Thomas et al. (2004). Figure 4.2 is the same comparison, only at 3.0 log scot tds. Figure 4.3 compares unique hue loci obtained in this study at 0.3 log phot tds with those obtained at 1.0 log scot td in the Thomas et al. (2004) study. Likewise, Figure 4.4 presents unique hue loci measured

in this study at 2.3 log phot tds with those obtained at 3.0 log scot tds in the Thomas et al. (2004) study.

At the low retinal illuminances (Figures 4.1 and 4.3), all three unique hue loci (blue, green, and yellow) at both stimulus sizes from the Thomas et al. (2004) study shift to longer wavelengths in the no-bleach condition compared to the bleach condition. A similar shift is observed with unique blue and unique green loci for two of four observers from this study, while there were no differences between bleach and no-bleach unique yellow loci for observers from this study. At high retinal illuminances (Figure 4.2), the only difference between the bleach and no-bleach loci from this study and Thomas et al. (2004) is seen when comparing this study's unique green scotopic loci (one observer shifted to shorter wavelengths in the bleach condition compared to the no-bleach condition and the remaining observers showed now shifts) to Thomas et al.'s (2004) unique green loci (all observers shifted to longer wavelengths in the no-bleach condition compared to the bleach condition). All remaining high retinal illuminance data is similar between the two studies. Different conclusions are drawn from this study and Thomas et al. (2004) regarding rod effects on unique yellow loci at low retinal illuminances; Thomas et al. (2004) showed all observers shifting to longer wavelengths in the no-bleach condition compared to the bleach condition while none of the observers in this study showed differences between bleach and no-bleach.

Some possible reasons why the data from this study do not correspond with the respective data from Thomas et al. (2004) is that there are many procedural differences between the studies. Stimuli in this study were 4-deg in size, and placed at 10 deg in the temporal retina for the bleach and no-bleach conditions. In the Thomas et al. (2004)

study, their data were collected with 0.6, 2.0, and 7.4 deg stimuli located in the nasal retina at 7 deg. Curcio et al. (1990) has shown that the distribution of cones can vary between the nasal and temporal retina. Furthermore, perceptive field sizes for the four elemental hues vary depending on the retinal location (Volbrecht et al., 2009) and stimulus intensity (Troup et al., 2005). A perceptive field is defined as the stimulus size where color appearance stabilizes and further increases in size do not produce changes in the amount of hue perceived (Troup et al., 2005). Researchers have shown that the perceptive field sizes from the bleach condition are smaller than their no-bleach counterparts (Troup et al., 2005; Volbrecht et al., 2009), and perceptive field sizes in the temporal retina are smaller than perceptive field sizes in the nasal retina (Volbrecht et al., 2009). The 2.4 deg stimuli used by Thomas et al. (2004) may not have filled the perceptive fields for the four elemental hues in the no-bleach condition, while stimuli larger than 4 deg would have filled the perceptive fields for all four elemental hues. Despite these perceptive field size differences, the 2.4 deg stimuli shifted in the same manner as the 7.4 deg stimuli across both high and low retinal illuminances.

Nerger et al. (1998), who equated stimuli photopically, found in general that no-bleach loci were at longer wavelengths than bleach loci for unique blue and unique yellow; however, upon imposing a 3 nm criterion, only 25% of the no-bleach loci were at longer wavelengths than bleach loci for unique blue at both test sizes and for unique yellow loci at the smaller stimulus size. Volbrecht et al. (2000), who also equated stimuli photopically, found that unique green loci did not differ depending on whether they were obtained in a bleach or no-bleach condition. In general, the unique hue loci from this

study correspond with the unique hue loci trends reported by Nerger et al. (1998) and Volbrecht et al. (2000).

Individual Differences

In this study, unique hue loci varied among the four observers. This is not unusual and has been cited in previous unique hue research. For example, Kuehni (2004) noted that there is a high degree of variability in unique hue loci among observers. What appears unique blue for some observers may appear reddish blue or greenish blue for other observers. The same can be said for unique green and unique yellow stimuli. None-the-less, it is important to examine the individual variability in more detail.

The only male in this study, ND, has been a type 1 diabetic for the last 23 years; studies (Adams et al., 1987; Bresnick et al., 1985; Volbrecht et al., 1994) have shown that diabetics can have a decrease in S-cone sensitivity, especially with fluctuations in blood sugar levels and diabetes duration. It was for this reason, ND monitored blood sugar levels and kept them consistent on data collection days. Also, the battery of color vision tests showed that ND was color normal; and recent fundal photos indicated he was free of ocular disease, such as retinopathy, neovascularization, and macular edema. Following from the models of Volbrecht et al. (2000) and Nerger et al. (1998), a decrease in S cone input to the opponent processes mediating color perception would result in a shift of unique blue and unique green loci to shorter wavelengths. Models proposed by Schefrin et al. (1991) also predict that unique green loci should be shorter for diabetics compared to non-diabetic individuals. ND, however, shows unique blue loci at similar values as the other three observers, and his unique green are at longer wavelengths than the other three

observers. Volbrecht et al. (1997) has shown that unique green loci measured in males are often at longer wavelengths than those obtained from females.

The remaining observers were female. Two of those observers were in their early 20's, and the other observer was in her early 50's. Werner (1996) has reported that age can affect color perception, possibly due to the loss of photoreceptors. Studies have shown that photoreceptor loss is not specific to one cone type but evenly distributed across all cone types (Curcio et al., 1993; Gao and Hollyfield, 1992) and is restricted to the peripheral retina (Curcio et al., 1993). As a result, it is possible that there would be no noticeable effects of receptor loss on unique hue loci due to the ratio of the three types remaining constant.

Also, with age, the number of rods declines, with a 30% decrease by age 90 in the central 28.5 deg of the retina (Curcio et al., 1993). A decrease in the number of rods would only be problematic if the total rod count was responsible for differences seen between bleach and no-bleach conditions; there were no notable patterns between bleach and no-bleach for VV or the other female observers. Curcio et al. (1993) did note that as rods die, the remaining rods change in size to fill the gaps left by the previous rods. Werner and Steele (1988) found sensitivity losses for hue perception with age for each cone mechanism, while Schefrin and Werner (1990) showed that unique green loci shifted to shorter wavelengths with age; but unique blue and unique yellow loci did not shift with age. As far as the results of the current study are concerned, VV did not show results that were representative of the older eyes seen by Schefrin et al. (1990), as her unique green loci (bleach and no-bleach) were very similar to AM (see Figures 3.1 and 3.4). Conversely, results from Volbrecht et al. (1997) showing that females have unique

green loci at shorter wavelengths than males, may mask any signs of aging associated with unique green loci.

Lastly, one observer was a synesthese. KG's unique green loci were at longer wavelengths than the other two female observers, while her unique blue and unique yellow loci were in the same ranges as AM and VV. By the battery of color vision tests given, she appeared color normal. Results from Gimmestad (2006) suggest that individuals with synesthesia perform no differently than non-synesthetics on the FM-100 hue color vision test. Whether the condition of synesthesia alters color perception has yet to be determined.

Expected Differences between Photopic and Scotopic Stimuli

Converting photopic trolands to scotopic trolands is a simple, linear conversion. If the location of particular unique hue loci were simply attributed to changes in luminosity, and assuming there is a linear relationship between unique hue loci and retinal illuminance, a linear line should fit data points from both photopic and scotopic conditions (i.e.,when scot td is converted to phot td, the scotopically equated unique hue loci fall on the same continuum as the photopically equated unique hue loci). One way to determine if unique hue loci from the photopically and scotopically equated conditions fall on the same continuum is to fit one line through all four loci obtained under a particular experimental condition (fovea, bleach, no-bleach). Figures 4.5 – 4.7 show linear fits to the unique blue, green, and yellow loci, respectively. Unique hue loci obtained with photopic (circles) and scotopic (squares) retinal illuminances are plotted for each observer (columns) and each condition [fovea (top panel), bleach (middle panel),

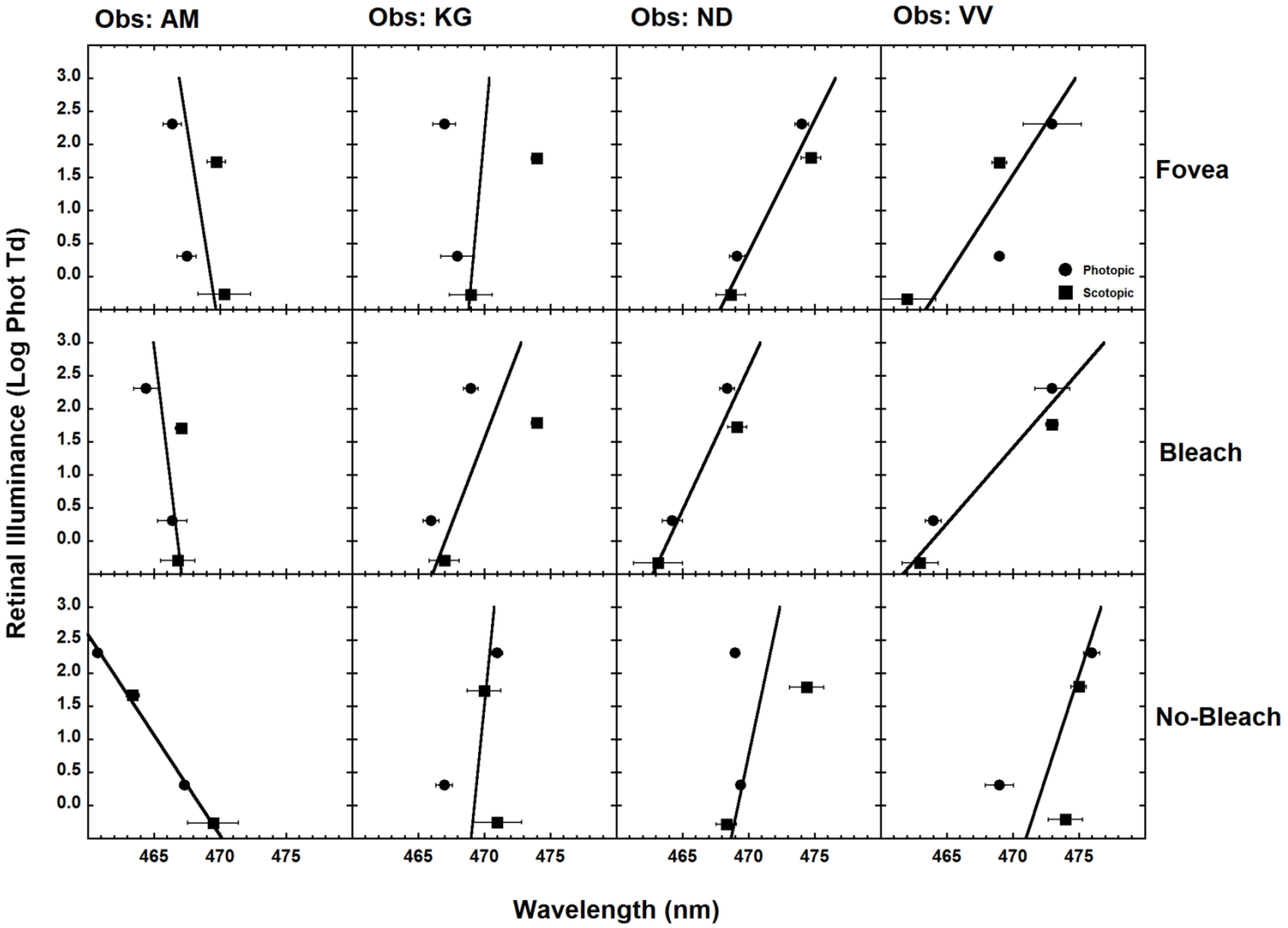

Figure 4.5. *Linear fits to scotopic and photopic unique blue loci.*

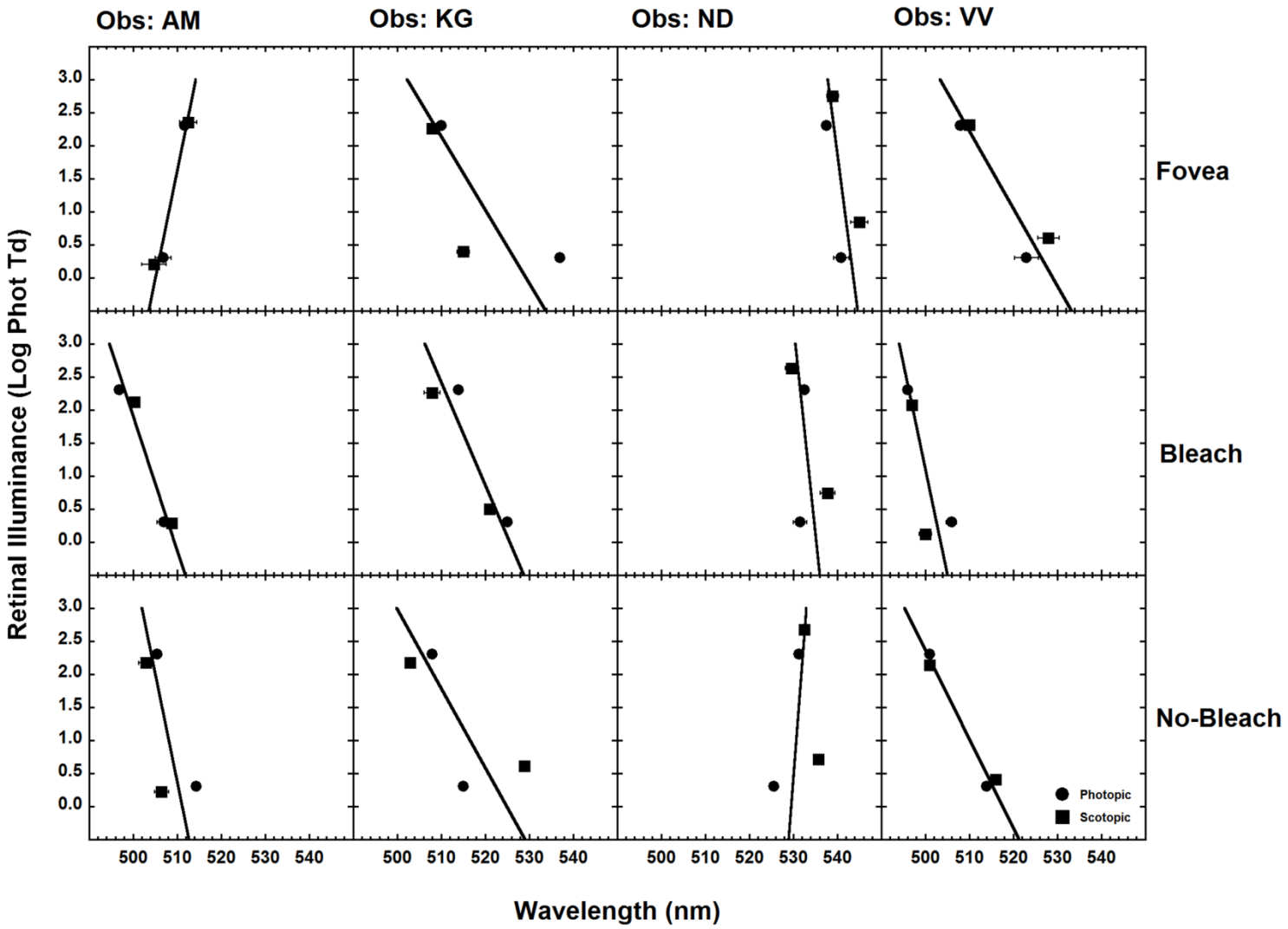

Figure 4.6. *Linear fits to scotopic and photopic unique green loci.*

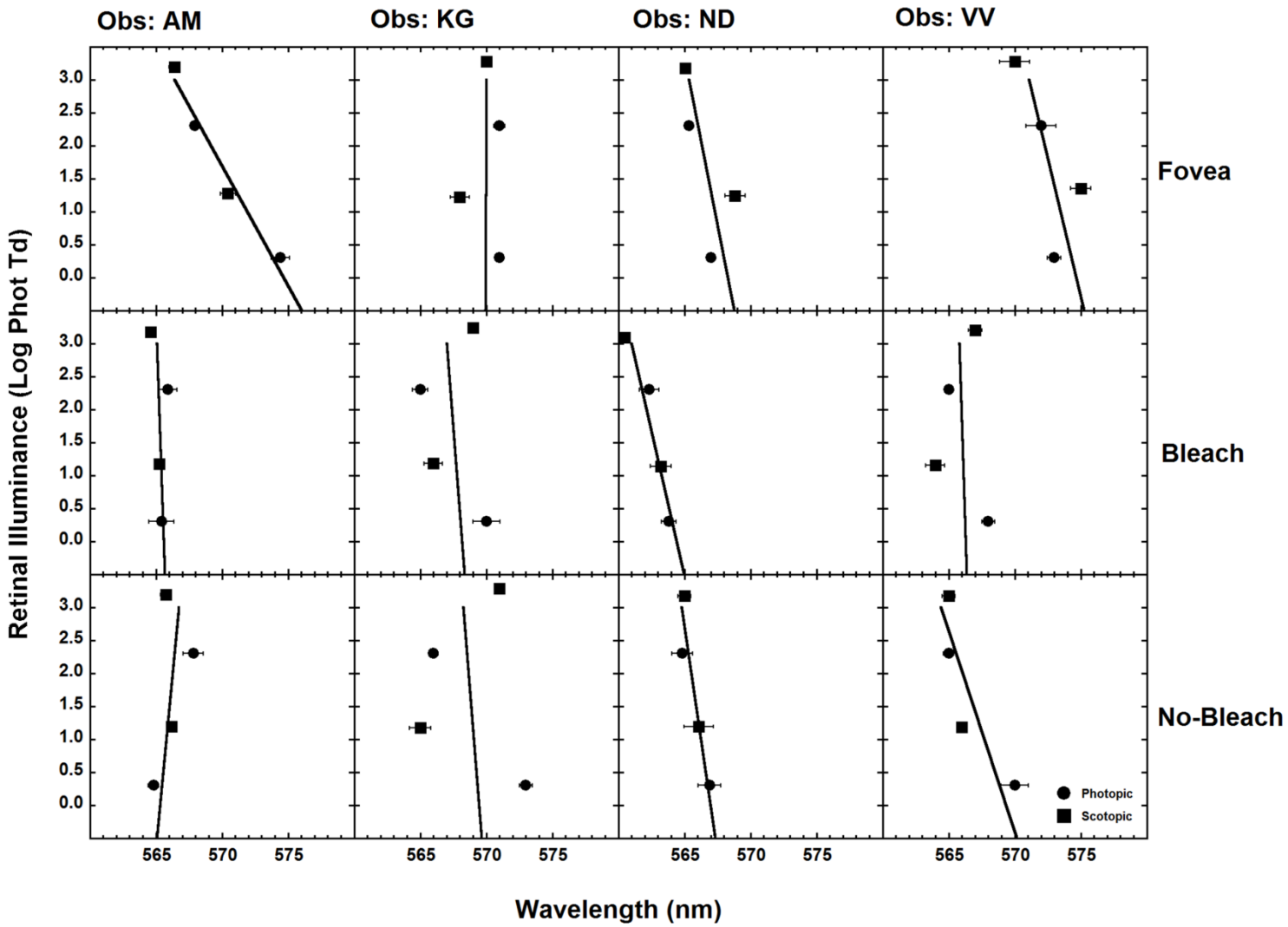

Figure 4.7. *Linear fits to scotopic and photopic unique yellow loci.*

Table 4.2: *Slope, χ^2, and R^2 values for linear fits.*

Unique Blue				Unique Green				Unique Yellow			
Fovea	**χ^2**	**Slope**	**R^2**	**Fovea**	**χ^2**	**Slope**	**R^2**	**Fovea**	**χ^2**	**Slope**	**R^2**
AM	7.55	-0.79	0.26	AM	1.66	3.08	0.96	AM	1.26	-2.74	0.96
KG	*28.14**	0.44	0.03	KG	*227.46**	-9.03	0.57	KG	5.99	0.03	0
ND	2.57	2.5	0.91	ND	*16.86**	-1.92	0.47	ND	4.59	-0.98	0.49
VV	*15.42**	3.24	0.75	VV	*31.20**	-8.56	0.89	VV	6.08	-1.19	0.53
Bleach				**Bleach**				**Bleach**			
AM	2.77	-0.61	0.37	AM	4.81	-4.92	0.95	AM	0.77	-0.17	0.15
KG	*21.48**	1.92	0.43	KG	*23.27**	-6.42	0.86	KG	*16.26**	-0.39	0.04
ND	2.42	2.33	0.91	ND	*27.43**	-1.57	0.26	ND	0.51	-1.13	0.92
VV	4.69	4.35	0.95	VV	*21.68**	-3.15	0.64	VV	*9.87**	-0.16	0.01
No Bleach				**No Bleach**				**No Bleach**			
AM	0.22	-3.29	0.99	AM	*37.31**	-3.03	0.49	AM	3.68	0.47	0.22
KG	*9.67**	0.5	0.1	KG	*158.78**	-8.33	0.58	KG	*43.92**	-0.4	0.02
ND	*18.38**	1.05	0.21	ND	*48.47**	1.17	0.1	ND	0.36	-0.73	0.87
VV	*17.65**	1.63	0.39	VV	4.48	-7.42	0.98	VV	4.36	-1.63	0.74

** Denotes statistically significant χ^2 values* ($\chi^2 = 7.815$, df = 3, $p<.05$).

and no-bleach (bottom panel)]. Error bars represent ±1 SEM between experimental sessions. The solid line represents the linear fit to the data points. The χ^2 and R^2 values for each fit are presented in Table 4.2. The higher the R^2 value, the more variance accounted for by the linear fit, which suggests scotopic and photopic unique hue loci fall along the same line. The χ^2 values indicate the fit of the line to the data: large χ^2 values indicate the data do not fit the line and smaller values suggest the line is a good fit for the data.

The results show that in many conditions and with multiple observers, both photopic and scotopic data from the same condition are well accounted for with a single

linear line (e.g., AM, no-bleach unique blue) and may explain the lack of differences seen between methods of equating stimuli. On the other hand, there are conditions where the lines do not fit the data (e.g., KG, foveal and no-bleach unique green). One reason why the method of equating stimuli may contribute to these differences is because of the differential activity between rods and cones throughout the visible spectrum. Even though stimuli have been equated to one system, both systems are operating simultaneously and differentially. By equating photopically, the retinal activity in the M and L cones is equated for all light throughout the visible spectrum. When stimuli are photopically equated, rods in the scotopic system are affected by light differently at each wavelength throughout the visible spectrum, i.e., wavelengths near the peak sensitivity for rods (approximately 500 nm, Dartnall et al., 1983) may appear brighter than wavelengths farther away from 500 nm. For example, a 620 nm (yellowish-red), 2.3 log phot td stimulus has a scotopic retinal illuminance of 0.98 log scot td (much dimmer to the scotopic system). A 620 nm, 3.0 log scot td stimulus has a photopic retinal illuminance of 4.32 log phot tds (much brighter with the photopic system). By that same token, a 430 nm (reddish-blue) 2.3 log photopic stimulus would appear much brighter to the scotopic system, at 3.93 log scot tds. These brightness differences due to the method of equating stimuli may explain why unique hues from scotopically equated stimuli do not fall on the same line as unique hues from photopically equated stimuli. When selecting an arbitrary R^2 criterion of 0.80, only 36% (13 of the 36) of the lines are considered a good fit for both photopic and scotopic data. The remaining 64% of lines are not considered a good fit for the data. The χ^2 values show that 50% (18 of the 36) of the unique hue loci are significantly ($\chi^2 = 7.815$, df = 3, $p<.05$) different from the best fit line, with most of the

poor fits from unique blue and unique green data. Lastly, it could also be that a line does not define the relationship between unique hues and retinal illuminance.

Conclusion

The method of equating stimuli yielded differences in very specific conditions, but with no clear patterns. It has been noted throughout the literature that stimulus size, stimulus intensity, adaptation, bleaching procedures, and location in the retina all play a role in hue perception. It could be possible that there are too many variables which play a role in color perception and clear distinctions between photopically and scotopically equated stimuli may not be apparent with the specific stimulus constraints used in this study. Conversely, the results of this study may very well suggest that there are no discernable differences between previous studies solely based on the method of equating stimuli used.

APPENDIX

Unique hue loci and SEMs for all observers for each experimental condition (fovea, temporal bleach, and temporal no-bleach), and retinal illuminance.

Unique Blue	**AM**	**AM**	**KG**	**KG**	**ND**	**ND**	**VV**	**VV**
Retinal Illuminance: 1 log scot td	**Means**	**SEM**	**Means**	**SEM**	**Means**	**SEM**	**Means**	**SEM**
Fovea	470.33	1.99	469.48	1.61	468.67	1.11	461.73	2.18
10° T-Bleach	466.83	1.30	467.45	1.14	463.16	1.84	462.99	1.36
10°T-No Bleach	469.50	1.92	470.95	1.86	468.33	0.77	473.80	1.27
Retinal Illuminance: 3 log scot td								
Fovea	469.75	0.68	473.98	0.43	474.75	0.73	469.31	0.55
10° T-Bleach	467.08	0.46	474.15	0.42	469.17	0.73	473.16	0.47
10°T-No Bleach	463.42	0.49	469.80	1.28	474.42	1.30	475.21	0.57
Retinal Illuminance: 0.3 log td								
Fovea	467.50	0.71	468.48	1.26	469.17	0.57	469.21	0.36
10° T-Bleach	466.42	1.12	465.65	0.61	464.25	0.76	464.39	0.58
10°T-No Bleach	467.33	0.36	466.63	0.62	469.42	0.31	469.15	1.05
Retinal Illuminance: 2.3 log td								
Fovea	466.42	0.68	466.98	0.86	474.04	0.52	473.33	2.19
10° T-Bleach	464.42	0.94	469.48	0.57	468.42	0.56	472.71	1.31
10°T-No Bleach	460.75	0.38	470.63	0.43	469.00	0.25	475.89	0.60

Unique Green	**AM**	**AM**	**KG**	**KG**	**ND**	**ND**	**VV**	**VV**
Retinal Illuminance: 1 log scot td	**Means**	**SEM**	**Means**	**SEM**	**Means**	**SEM**	**Means**	**SEM**
Fovea	504.84	2.78	515.13	1.38	545.08	1.97	528.05	2.43
10° T-Bleach	508.82	0.96	521.30	1.00	537.88	1.70	500.43	1.38
10°T-No Bleach	506.50	1.58	529.10	0.96	535.75	1.08	515.85	1.06
Retinal Illuminance: 3 log scot td								
Fovea	512.58	1.96	508.48	0.34	539.00	1.28	510.08	0.55
10° T-Bleach	500.33	0.44	508.15	1.84	529.67	1.40	496.98	0.56
10°T-No Bleach	503.00	1.68	502.80	0.58	532.54	0.64	500.58	0.28

Retinal Illuminance: 0.3 log td								
Fovea	506.83	1.82	537.48	0.73	540.96	1.71	523.28	2.70
10° T-Bleach	507.00	1.59	525.33	1.00	531.58	1.54	505.98	1.15
10°T-No Bleach	514.42	0.61	515.30	0.43	525.58	0.74	513.90	0.80
Retinal Illuminance: 2.3 log td								
Fovea	511.75	0.55	510.48	1.10	537.58	0.92	508.08	0.33
10° T-Bleach	496.87	0.80	513.63	0.73	532.50	0.61	496.23	0.41
10°T-No Bleach	505.42	0.82	507.95	0.69	531.25	0.83	500.99	0.50

Unique Yellow	**AM**	**AM**	**KG**	**KG**	**ND**	**ND**	**VV**	**VV**
Retinal Illuminance: 1 log scot td	**Means**	**SEM**	**Means**	**SEM**	**Means**	**SEM**	**Means**	**SEM**
Fovea	570.46	0.56	568.30	0.72	568.83	0.76	575.16	0.74
10° T-Bleach	565.25	0.25	565.63	0.71	563.21	0.79	563.74	0.72
10°T-No Bleach	566.17	0.33	564.63	0.79	566.08	1.10	566.40	0.30
Retinal Illuminance: 3 log scot td								
Fovea	566.42	0.41	570.30	0.29	565.08	0.39	570.15	1.14
10° T-Bleach	564.58	0.18	568.83	0.18	560.50	0.24	567.24	0.50
10°T-No Bleach	565.75	0.39	570.98	0.27	565.00	0.50	565.40	0.49
Retinal Illuminance: 0.3 log td								
Fovea	574.42	0.71	570.83	0.18	567.00	0.25	573.40	0.51
10° T-Bleach	565.42	0.96	569.80	1.02	563.83	0.56	567.65	0.47
10°T-No Bleach	564.83	0.39	572.50	0.50	566.92	0.86	569.89	1.03
Retinal Illuminance: 2.3 log td								
Fovea	567.96	0.36	570.80	0.42	565.33	0.18	571.99	1.15
10° T-Bleach	565.92	0.68	564.65	0.57	562.33	0.76	565.39	0.28
10°T-No Bleach	567.83	0.76	566.48	0.34	564.83	0.80	565.40	0.40

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