THE EFFECT OF WAVELENGTH ON 2-POINT LIGHT THRESHOLDS

by

YAW B BUABENG

(Under the Direction of Billy R. Hammond Jr.)

ABSTRACT

Intraocular scatter significantly impairs visual performance and is a critical factor in limiting the ability to perform vision-dependent tasks, such as safe driving. Visual stimuli—ranging from lighting and road signs to lenses and ocular implants—can be optimized to minimize the detrimental effects of scatter. The success of such optimizations relies on accurate data concerning the behavioral effect of light spread across different wavelengths within the eye. This study aims to provide foundational data to inform and enhance the design of visual aids and stimuli for improved visual performance. Additionally, we investigated how ocular chromophores, such as iris and macula pigmentations, contribute to variations in intraocular scatter.

INDEX WORDS: light scatter, wavelengths, action spectrum, macula pigment, iris

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DEDICATION

I dedicate this thesis to the memory of my late mother, Mrs. Georgina Buabeng, and my late father, Mr. Stephen Nkansah Buabeng. Your unwavering love, guidance, and sacrifices continue to inspire me every day, and this achievement is a testament to the values you instilled in me.

To my brothers—Stephen, Andrew, and Charles—thank you for your steadfast support and belief in me. Your encouragement has been a pillar of strength throughout this journey.

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To all my friends who have stood by me with unwavering encouragement and kindness, your presence has made this journey more meaningful.

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Background

Action spectra are commonly defined as a measure of how different wavelengths of light elicit biological responses (e.g.,Coohill, 1991). The exploration of wavelength efficacy began with investigations into the light sensitivity of plants. Engelmann (1883) discovered that the rate of photosynthesis peaked in the red and blue regions of the spectrum and inferred that the plant pigment chlorophyll was involved in photosynthesis (Drews, 2005). Since then, studies have been done across many species, including humans, to ascertain their biological responses to different wavelengths of light. For instance, (Tan et al., 1970) observed that the waveband from 254nm to 300nm effectively induced damage to the DNA in cell nuclei within the skin of hairless mice. At a wavelength of 310nm, however, about four times more energy was required to induce the same level of photochemical damage to nuclear DNA (Tan et al., 1970). Stringham et al., 2003, focusing on action spectrum for photophobia in humans, showed that individuals exhibited greater sensitivity to shorter wavelengths and argued that photophobia may function as a natural protective mechanism against these harmful short wavelengths. Light is comprised of different wavelengths that can have positive or negative biological responses in organisms. These responses can be influenced by factors that include the amount of energy exposed, duration of exposure, and so on. Action spectra isolate the effect of wavelength by keeping all the other aspects of the stimulus (energy, size, behavioral response, etc.) constant.

The effects of wavelength on human biology are widespread, influencing various factors that, initially, may appear unrelated. Brainard et al., 2001, for instance, showed that wavelengths within the range of 446 nm to 477 nm have a regulatory effect on melatonin secretion in humans and drive circadian rhythms. These internal clocks use light as the major input for regulating physiology (e.g., sleep) to align with diurnal and seasonal changes. Golmohammadi et al., 2021, showed that strategic exposure to short wavelengths (SW) improve cognitive function. Specifically, short wavelengths (SW) increase reaction time and attention, particularly when exposed in the mornings. Taken together, research on action spectra have emphasized the ubiquitous effects that light has on human biology.

Given these pervasive effects, scientific investigation turned to the question of how specific wavelengths of light could be used for therapeutic purposes, an area often called Photobiomodulation (PBM) or Low-level Laser therapy (LLLT). A foundational study on this topic was done (Mester et al., 1968) on using light to treat cancer tumors. Mester et al., 1968, using a mouse model, showed that low-level laser treatment stimulated tissue regeneration and enhanced wound healing. Following this, other studies have shown (see the review by (Buch & Hammond, 2020)) that PBM can promote hair growth, reduce inflammation, enhance mitochondrial function, or even influence neural function (Huang, 2022).

Effects of Wavelengths on the Visual System

The human eye is sensitive to a relatively small range of wavelengths within the electromagnetic spectrum. This range extends from about 380 nm to about 720 nm but, under certain circumstances can be as low as 315 nm (essentially UVB; Hammond & Renzi-Hammond, 2018) and as high as 1050 nm (infrared; Palczewska et al., 2014). It is clear, however, that individuals are not equally sensitive to this band of visible wavelengths. Understanding the exact form of the photopic and scotopic spectral sensitivity functions has allowed the development of lighting and visual displays that are optimized to that sensitivity. Given these kinds of obvious applications, it is surprising that action spectra have not been measured for many aspects of vision. One conspicuous category is vision under bright light or aversive/deleterious conditions. For example, no study has measured how wavelength predicts dysphotopsias (halos and spokes, a common consequence of cataract and multifocal implants, and laser correction of myopia; (Masket et al., 2020). There is considerable data on the wavelength dependence of intraocular scatter, but it is contradictory: some data suggest wavelength independence (H. S. Ginis et al., 2013a; Wooten & Geri, 1987a) whereas other data suggest relations that scatter within the eye is Rayleigh-dependent (Coppens et al., 2006; Whitaker et al., 1993). There is no data on the actual behavioral effects of wavelength-based scatter on visual resolution. That is the purpose of the present study.

One simple method for determining the behavioral effects of intraocular scatter is to use a resolution method based on separating two distinct points of light (illustrated in an ecological setting in Figure 1). This was originally done by Ogle (1962) but more recently by Renzi-Hammond et al. (2022). In the latter study, the visual performance of high-energy visible (HEV)-filtering contact lenses was tested, and the results indicated that individuals wearing these contact lenses showed enhanced ability to resolve two light points (by filtering the highly scattering portion of the broad-band energy used in the experiment).

The underlying basis for the two-point method is based on simple optics. Visual performance is influenced by the quality of the retinal image (Artal et al., 2001). One way to characterize that image is the point spread function (PSF). The PSF is influenced by elements such as aberrations, pupil characteristics, and scatter (H. Ginis et al., 2012). As these factors worsen, the PSF of a single point widens. The wider the PSF, the more distance is needed before the PSF from two distinct points is completely separated. This is shown in Figure 2.

The data that exists using the two-point method, however, is based on broad-band (xenon-white) and violet light (with no attempt at equalizing energy to isolate wavelength effects). No data exists on how wavelength affects two-point light spread. What might we expect? Data from Coppens et al. (2006) suggest that there is Rayleigh dependence (λ^{-4}) within the eye, but that dependence is most notable in young individuals with dark irises. Ginis et al. (2013) also showed that the PSF changes with wavelength. In contrast, Wooten & Geri (1987) and Whitaker et al. (1993) using psychophysical methods, found no relation between wavelength and intraocular scatter. In all these studies, however, the only consideration was the proximal stimulus (the physical quality of the image falling on the retina). Visual performance is a function of not just the proximal, but also the distal, stimulus and the visual task. In our study, the visual task represents a functional measure (resolution), and the distal stimulus is four feet distant from the subject (as shown in Figure 1, a more ecologically valid method of measuring the behavioral effects of light scatter).

Intraocular scatter is generally pernicious. It is one of the more significant limiters, for example, in the ability to perform vision-dependent tasks safely (like driving, especially for older subjects at night; Ortiz-Peregrina et al., 2020). Fortunately, however, visual stimuli (from lighting to road signs to lenses and implants) can be designed to minimize the effects of scatter. Optimal design, however, depends on basic data on the action spectra of behaviorally relevant scatter. This study will provide that data.

The major goal of this project is simply descriptive (describe the average behavioral scatter when wavelength is isolated across the visible spectrum). An ancillary goal, however, is to explore individual differences (Hammond et al, 2020) in this average curve and factors that might drive those differences. We hypothesize that the largest differences in the curve will be in the short-wave region (400-500 nm). Hence, we plan to measure ocular pigmentation (the short-wave absorbing macular pigments and iris color) to determine whether covariation explains some of these differences.

CHAPTER 2

METHODS

Subjects

A total of sixty (60) subjects were tested. The target population consisted of young adults (age range, 18-30) with normal or corrected vision. Normal vision, for the purposes of subject inclusion criteria, was defined as 20/40 or better visual acuity (VA) in each eye – this was determined by using a wall-mounted chart. Dominant eye was also identified using the Snellen's VA chart. No subject wore glasses or contact lenses during the testing. Ocular-health/history was obtained through self-report. Additional inclusion criteria included fluency in English and sufficient literacy to understand the consent document. Exclusion criteria, broadly, included subjects with ocular conditions or abnormalities such as corneal infections, stye, or any conditions that could directly interfere with the measurements. Participants were recruited primarily from the UGA student population as well as some community volunteers. This study was approved by the University of Georgia institutional review board (PROJECT00009383). Experimental procedures were conducted in accordance with Good Clinical Practice Guidelines and the ethical principles of the Declaration of Helsinki.

Design

This study implemented a within-person, cross-sectional design. Measurements from two different tasks were recorded. Demographic information (e.g., age, gender, ethnicity, race) was collected via a self-report questionnaire. In addition, glasses and contact lens use information was also recorded via questionnaire. Iris color (see figure 3) – both hue and lightness – was also assessed and recorded (based on the classification scheme from Mackey et al., 2011). Visual acuity was measured at 20 feet using a Snellen Eye Chart. Ocular dominance was determined by asking participants to form a triangle with their hands and center the big “E” (20/200 line) on the Snellen chart. Participants were then instructed to close their left eye, followed by their right eye, and report which eye kept the "E" centered. The eye that maintained the "E" closest to the center was identified as the dominant eye.

Measurement of MPOD

A macula densitometer was used to measure the Macular Pigment Optical Density (MPOD) based on the principles of heterochromatic flicker photometry (for details see Wooten et al., 1999). Participants were instructed to look through an adjustable eyepiece that presents a flickering target disk. The target disk (one degree in diameter) is composed of two monochromatic lights – a 460nm light, strongly absorbed by MP and a 570nm light, not absorbed by MP – presented in counter-phase. This stimulus is presented with central fixation and while the subject is fixating a peripheral point seven degrees in their periphery. This latter stimulus, like the 570nm light, is used as a reference since MP density is minimal at this eccentricity (for this condition the stimulus is increased to two-degrees visual angle). The subject’s task is to minimize flicker in both locations (using an automated bracketing procedure). The underlying assumption of the method is that higher MPOD requires more 460nm energy to reach a flicker null (that energy being a direct reflection of MP density).

Principles Behind Measuring Action Spectra

The measure of visual response to specific wavelengths can be achieved by employing either a criterion response or an equal energy approach(Flannagan et al., 1990; Stringham et al., 2003).

Stringham et al. (2003) employed the criterion response approach to assess photophobia over a range of wavelengths from 440nm to 640nm in steps of 20nm. Photophobia was defined as squinting in response to exposure to specific wavelengths. The intensity of the light (five-second exposures) was increased until the exposure elicited a predefined level of squint. Electromyography was used to measure the degree of squint. The degree of squint was the criterion response while the intensity of each wavelength was varied. Thus, the energy/wavelength was varied while the criterion visual response remained constant.

An alternative approach involves keeping the energy of the stimulus constant while assessing variability in the visual response. Flannagan et al. (1990) utilized this approach to measure glare discomfort as a function of wavelength. He used a subjective rating scale, specifically the DeBoer scale, to assess the discomfort experienced by subjects while maintaining constant energy levels across the different wavelengths. By keeping either the visual response or the energy constant, the effect of wavelength is isolated.

Measuring Action Spectra

In this research study, the equal energy approach was utilized to measure the action spectra of 2-point light thresholds (for details see Hammond et al., 2020). The light source was a 1000-Watt Xenon arc lamp. A collimating lens (L_C) was positioned in front of the light source, followed by another lens (L_F) that focused the light through a circular neutral density wedge (used for linear attenuation of light energy). This wedge was used to adjust the energy for each wavelength condition so that each wavelength was presented at the same energy. The wedge preceded a circular filter holder containing narrowband (20nm half bandpass) interference filters for each peak wavelength of 420nm, 460nm, 500nm, 540nm, 580nm, 620nm, and 660nm and a broad-band xenon white. The monochromatic light (and the white light condition) was then projected onto a light shield with two small (2mm) apertures (creating a homogeneous field about 6 degrees in diameter on the back of the shield). These apertures could either be adjoining (so that the stimulus appeared as a single point of light) or slowly moved apart until they appeared as two points. The light shield contained a collapsible baffle that blocked light between the apertures as the two apertures moved apart. A built-in micrometer recorded the separation between the two points. Extensive baffling throughout the system ensured minimal straylight. An adjustable chin-and- forehead rest assembly was positioned 67mm away from the light aperture shield (see figure 4).

Before data collection, the total light energy in the system was confirmed. For each waveband, the experimenter adjusted the wedge to maintain a constant energy (628 uW). This value was verified by a radiometer (photodetector head abutting the apertures; UDT model S370). Since the energy at 660nm was the maximum available with our conditions, this maximum was used for all the wavelengths, all procedures were conducted in a darkened room.

Participants were briefed on the clinical protocol, shown a depiction of point separation (see figure 5), and instructed to cover their nondominant eye with a patch while resting their chin on an adjustable chin-and-forehead rest. Alignment with the stimulus was achieved by using a post with a small hole that was precisely positioned along the optic axis (this post was removed before data collection). Wavelengths were presented in random order. Testing began with the micrometer at zero and the aperture closed. Participants signaled when the light appeared as two points, and this separation value was recorded. After closing the aperture and resetting the micrometer to zero, this process was repeated for all trials. Each waveband was tested three times (averages were then used in data analyses). The estimated duration for each session was approximately one hour.

CHAPTER 3

RESULTS

Descriptive statistics

A total of 60 healthy subjects were assessed of which 60% were female and 40% were male. The mean age of the participants was 22.73 years (SD = 3.33). A summary of additional descriptive statistics, including other relevant demographic and variables, is provided in Table 1.

Between-groups Analyses

A one-way ANOVA was conducted to determine the effect of wavelength on the two-point separation task. The results indicated that wavelength had a statistically significant effect on task performance, $F(6,413) = 13.52$, $p<0.001$, showing that there were significant differences in performance across the seven (7) wavelengths (420 nm, 460 nm, 500 nm, 540 nm, 580 nm, 620 nm, and 660 nm). A graphical representation of these results is provided in Figure 6. Table 2 shows the average and the standard error of the mean across wavelengths for the performance task.

Main Effect of Iris Pigmentation

To assess whether iris pigmentation (light and dark) affects the ability to discriminate between two points across different wavelengths, a two-way analysis of variance (ANOVA) was conducted. The ANOVA examined the effects of both wavelength and lightness on performance in the two-point separation task. However, the primary focus of this analysis was on the effect of iris pigmentation on task performance.

The results indicated a significant main effect of iris pigmentation on task performance, $F(1, 406) = 17.80$, $p < .001$. Participants with lighter irises had greater two-point separation than those with darker irises. As seen in Figure 7, values across all wavelengths were consistently higher for participants with lighter iris pigmentation, suggesting higher effective scatter in that group.

The interaction between wavelength and iris pigmentation was not statistically significant, $F(6, 406) = 0.20$, $p = .978$, indicating that the effect of wavelength on task performance was independent of the iris pigmentation.

Correlations: MPOD vs 2-Point Light Thresholds

Bivariate Pearson correlations were conducted to examine the relationships between macular pigment optical density (MPOD) and two-point thresholds across wavelengths. The mean MPOD was 0.41 ($SD = 0.15$). The analysis revealed that MPOD was moderately related to 2-point thresholds at the shorter wavelengths (based on a one-tailed criterion) but not related to wavelengths that are not absorbed by the macula pigments (longer wavelengths). Table 3 presents the correlation coefficients and corresponding p-values for each wavelength.

Table 1

Descriptive statistics (n = 60)

Variable	Average	SD	Range	n Analyzable
Age	22.73	3.33	18 to 29	60
MPOD	0.41	0.15	0.08 to 0.85	60
Race	13% Asian 32% Black/African American 3% Latinx 52% White/Caucasian	N/A	N/A	60
Gender	40% male 60% female	N/A	N/A	60
Ethnicity	3% Hispanic 97% non-Hispanic	N/A	N/A	60
Iris Color (Hue)	15% Blue 62% Brown 12% Green 12% Hazel	N/A	N/A	60
Iris Color (lightness)	45% Dark 55% Light	N/A	N/A	60

Table 2

Average & Standard Error of the Mean Across the Wavelengths

Wavelengths (nm)	Average	SEM	n
420	4.39	0.44	60
460	3.43	0.39	60
500	2.69	0.34	60
540	1.90	0.21	60
580	1.53	0.19	60
620	1.75	0.24	60
660	1.51	0.16	60

Table 3

Between-group Analyses: Pearson's Correlations

Variables	N	Correlation	Significance
MPOD & 420nm	60	-0.22	0.05
MPOD & 460nm	60	-0.21	0.05
MPOD & 500nm	60	-0.18	0.09
MPOD & 540nm	60	-0.15	0.12
MPOD & 580nm	60	0.01	0.46
MPOD & 620nm	60	-0.05	0.36
MPOD & 660nm	60	0.10	0.22

Figure 1. An ecological example of the two-point light separation task. The two headlights in the distant vehicle are fused and separate as the vehicle becomes closer to the observer. (Renzi-Hammond et al., 2022a)

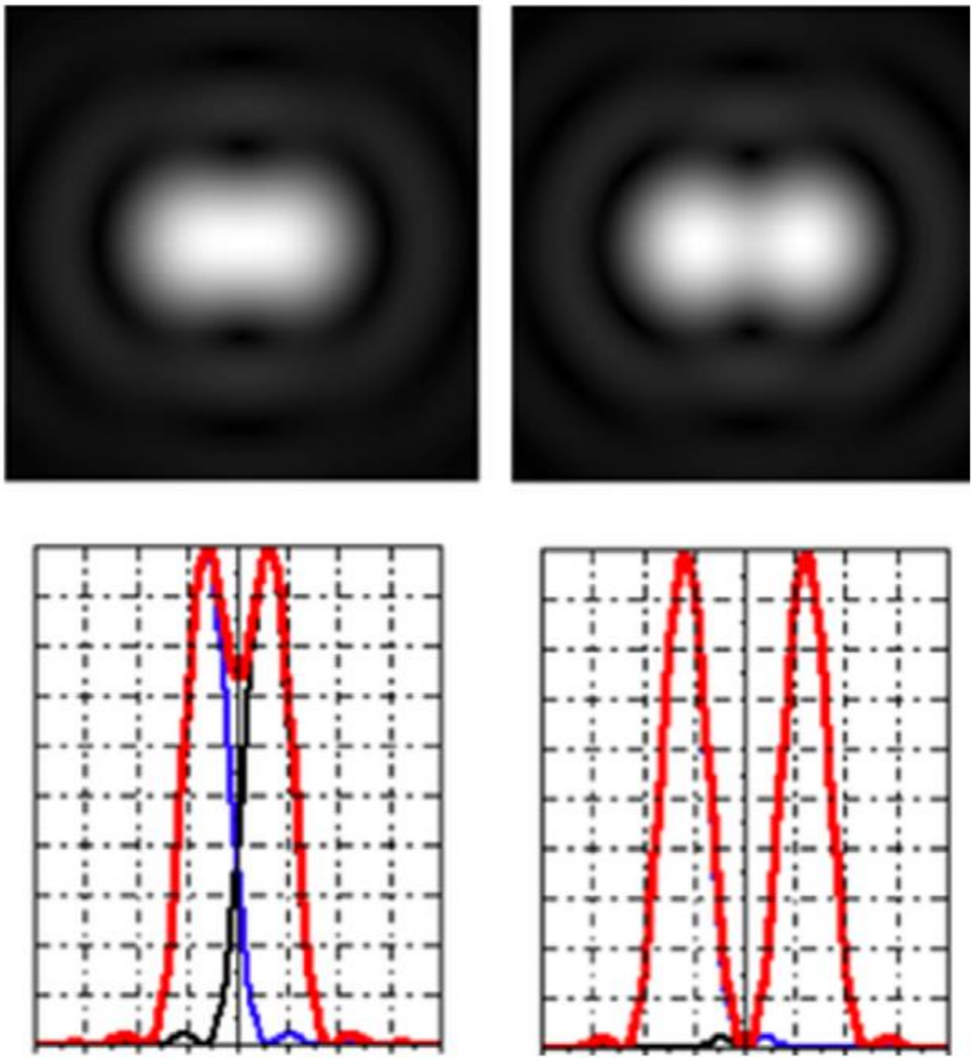

Figure 2. Two points (with their associated PSF) at varying distance. The wider the PSF, the more disparate the two points will need to be in order to be seen as completely distinct (from Fig 4 of Hammond, Perez-Vives and Alba, Bueno, 2023 whitepaper from https://us.alconscience.com/).

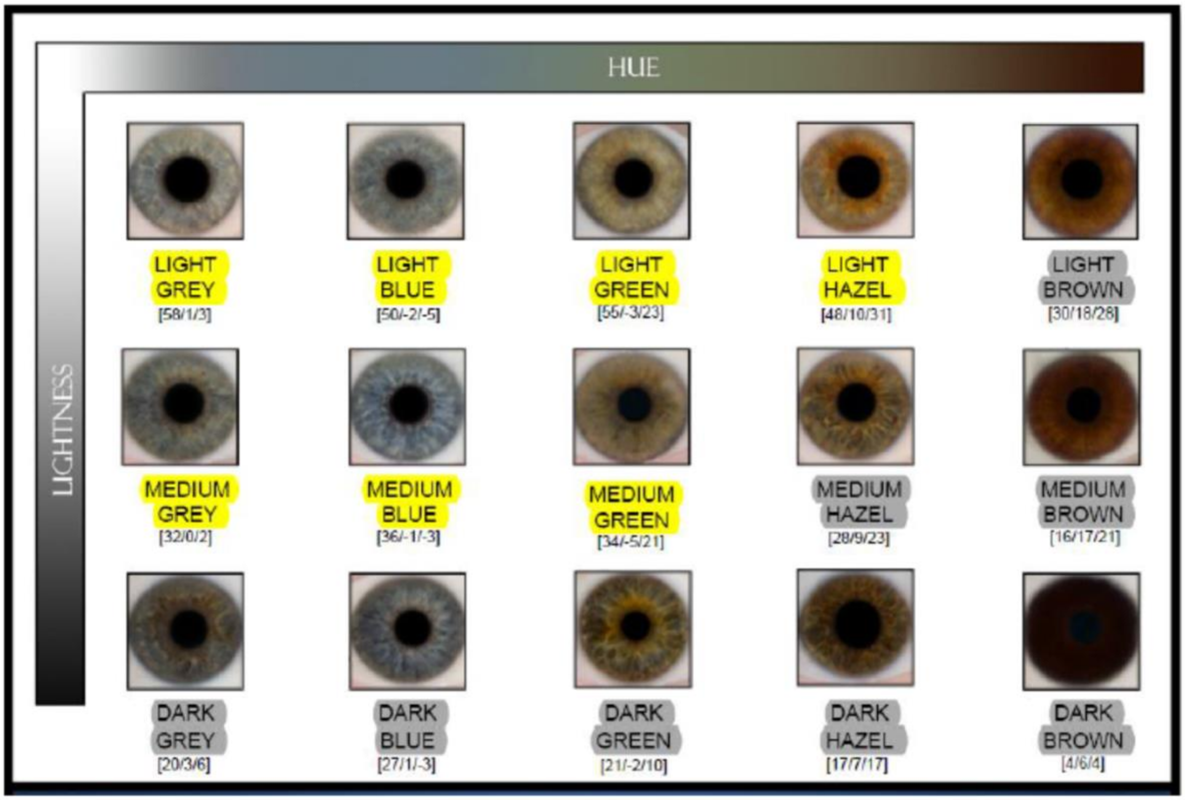

Figure 3. Iris Color scale

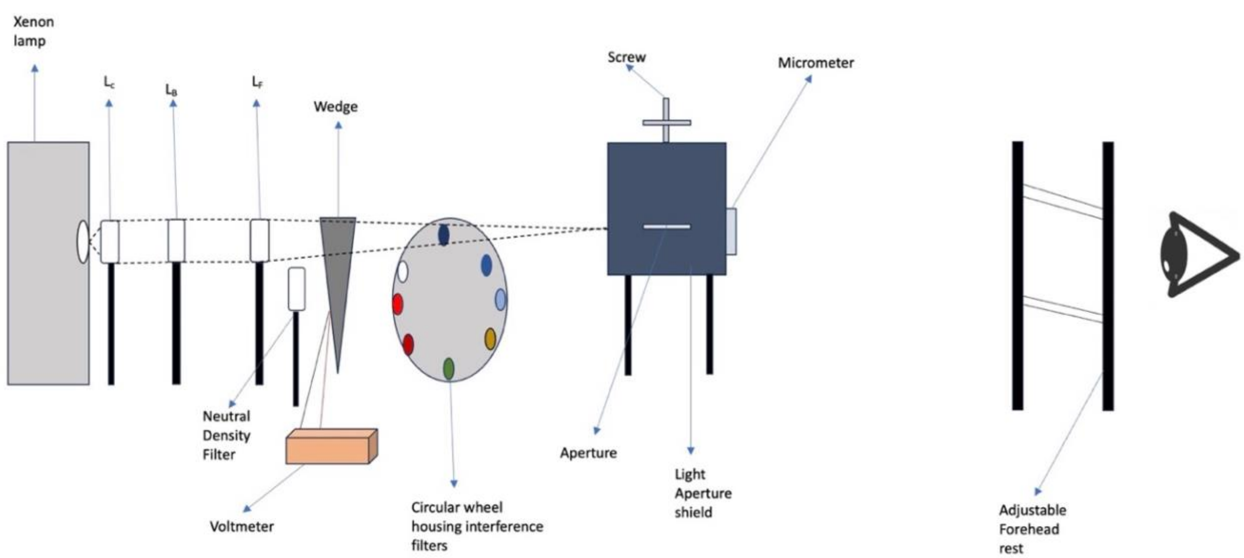

Figure 4. Schematic diagram of the optical system

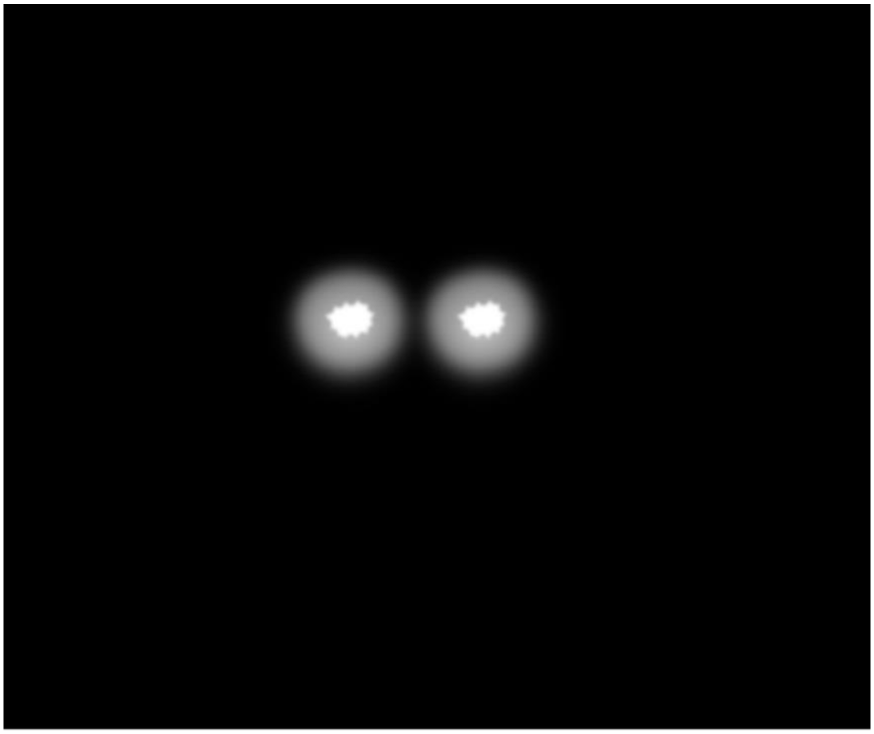

Figure 5. Illustration of two separated light points as they would appear to a participant

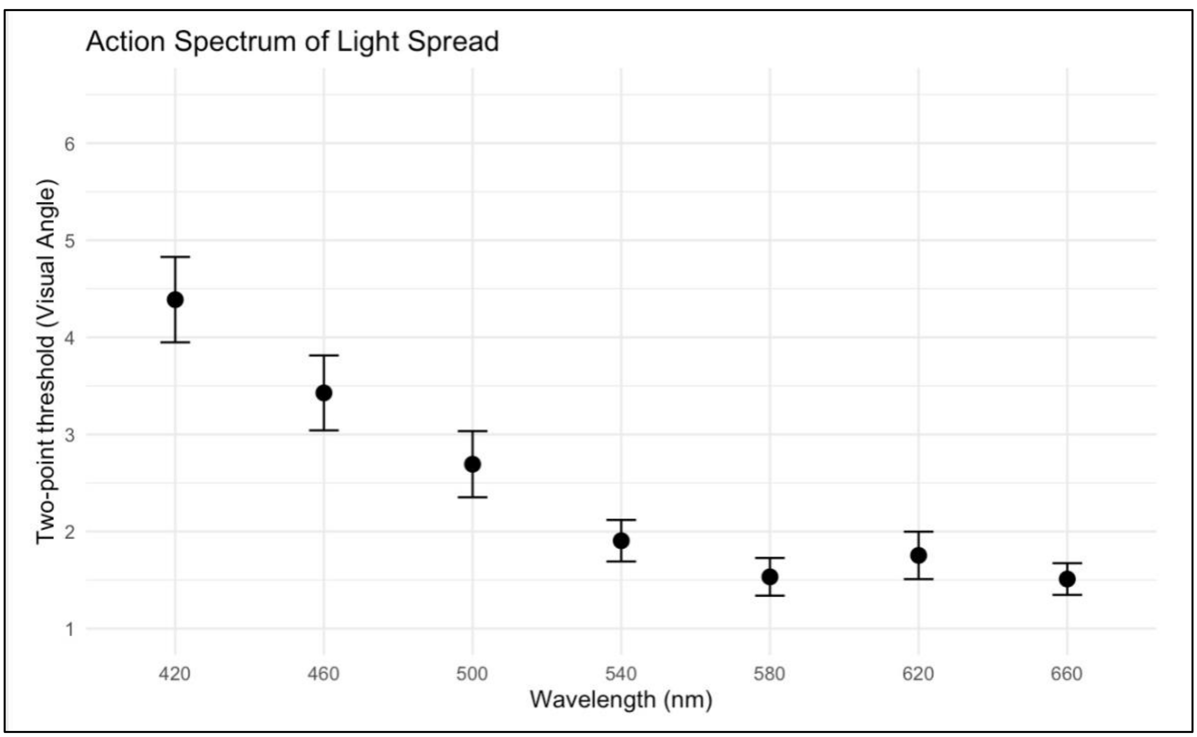

Figure 6. Two-point thresholds across wavelength (average, standard error of mean)

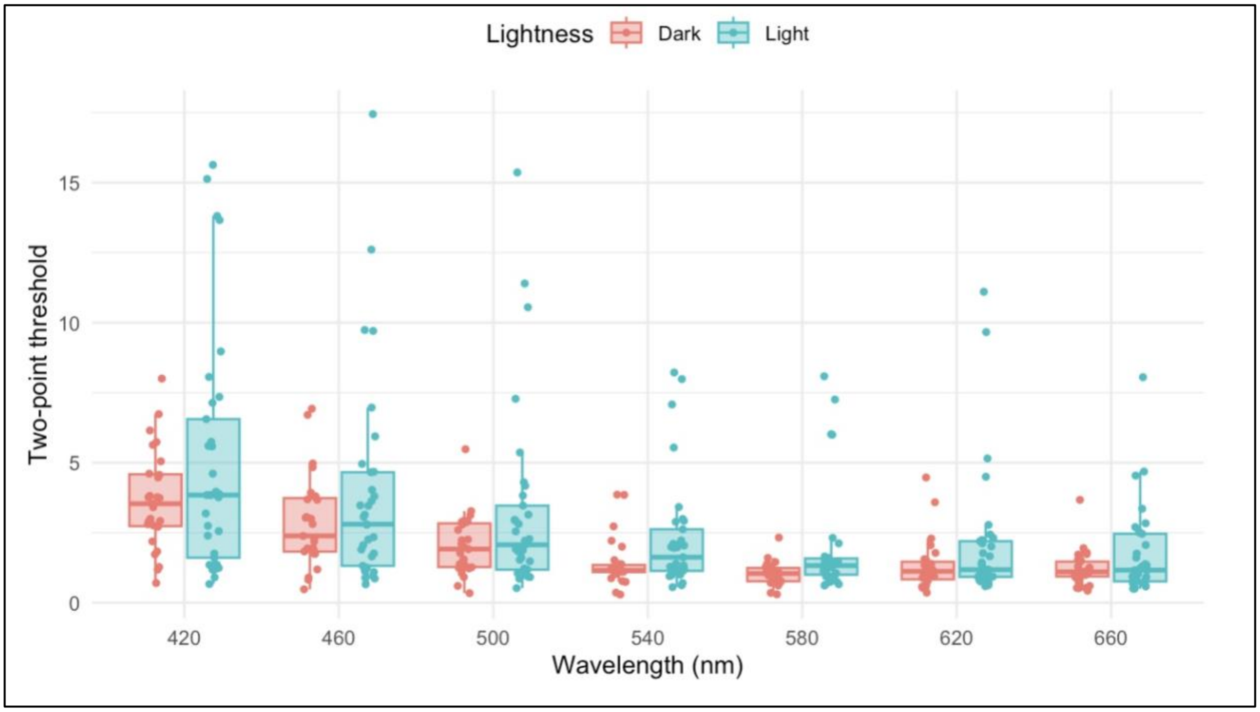

Figure 7. Effect of Wavelength and Iris Pigmentation on Two-point thresholds

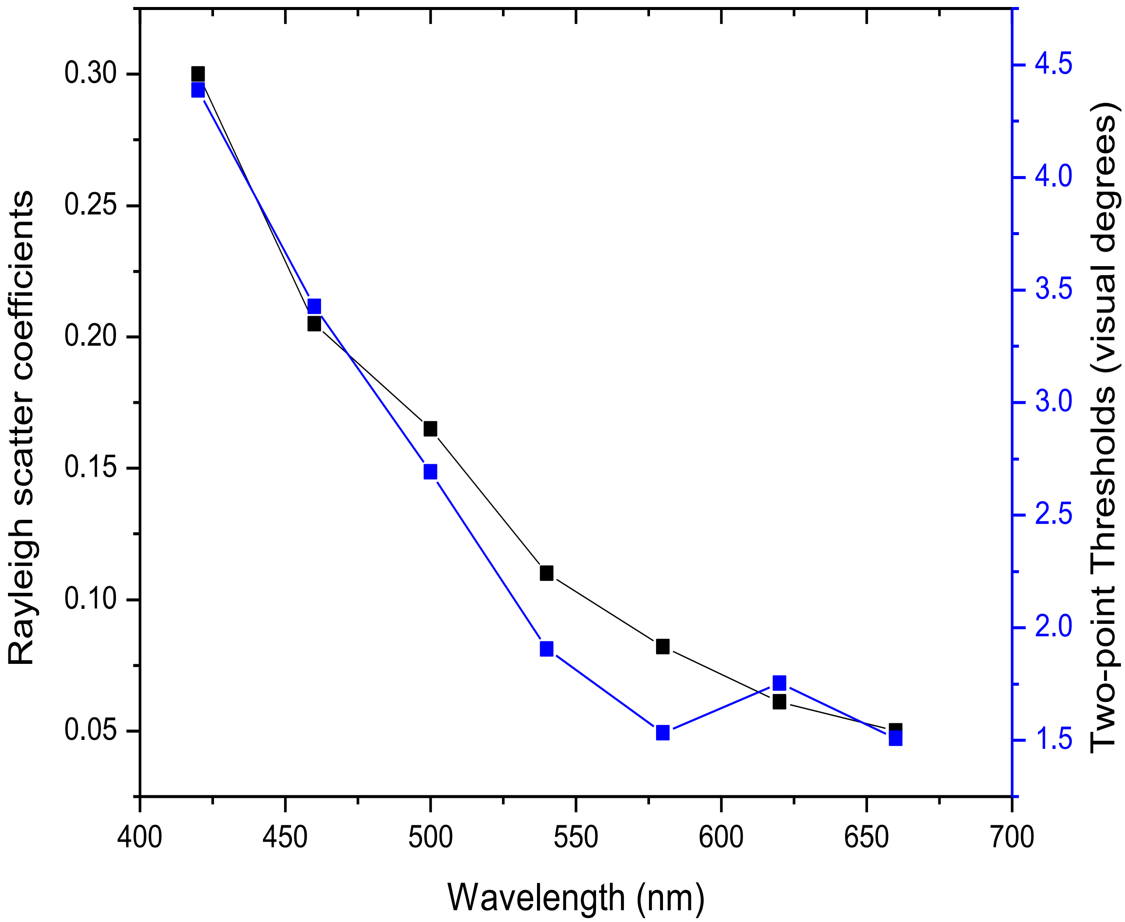

Figure 8. Comparison between Rayleigh Scatter Coefficients and Two-Point Thresholds

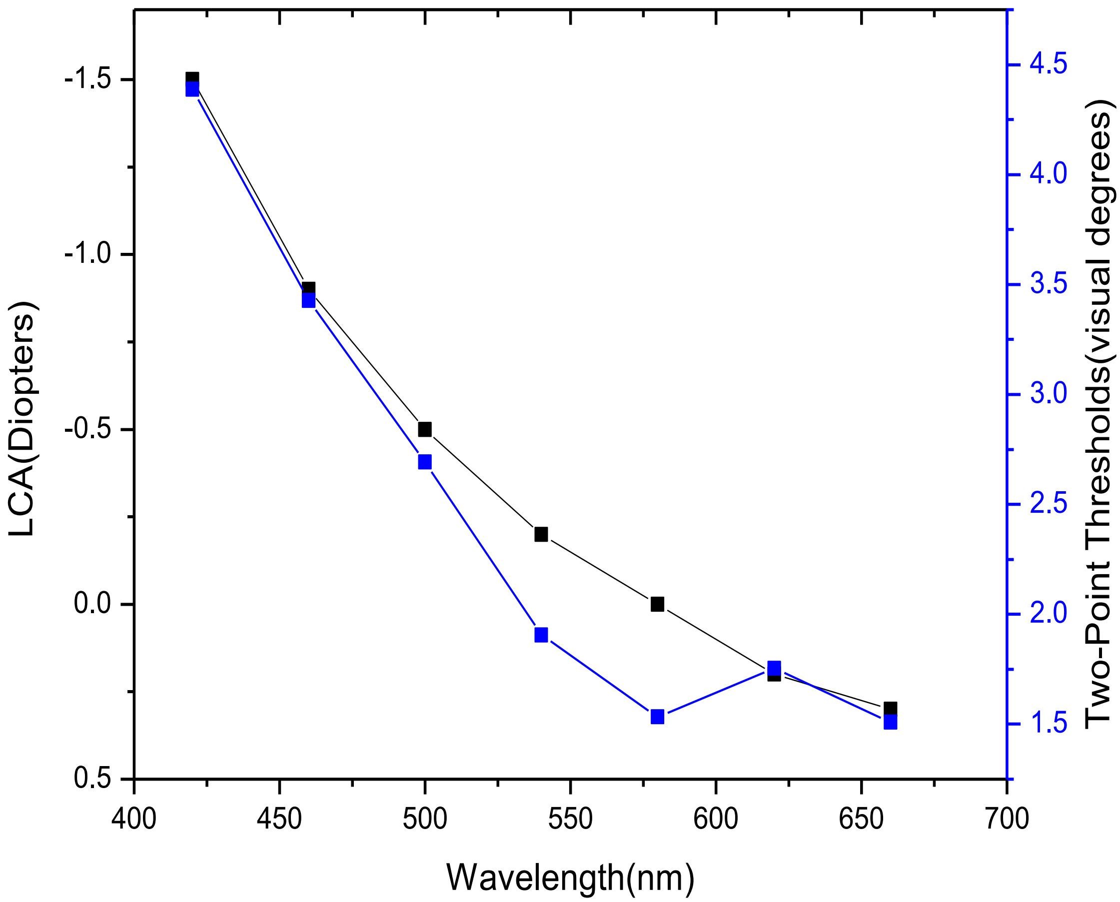

Figure 9. Comparison between Longitudinal Chromatic Aberration (LCA) and Two-Point Thresholds

CHAPTER 4

DISCUSSION AND CONCLUSION

Light scattering within the eye is typically detrimental, acting as a substantial limiting factor in the safe execution of vision-dependent tasks (Ortiz-Peregrina et al., 2020). The question of whether intraocular light scattering is wavelength-dependent remains unresolved in the scientific literature. Some studies, such as Ginis et al., (2013b) and Wooten & Geri, (1987b) argue against wavelength dependence in intraocular scatter, while others, including Coppens et al., (2006) and Whitaker et al., (1993) suggest that Rayleigh scattering within the eye introduces wavelength-dependent effects. This discrepancy in the literature formed the basis for this study, aimed at clarifying the wavelength dependence of intraocular scatter.

To date, no studies have investigated the behavioral effects of intraocular scatter across different wavelengths. This study addressed this gap using a two-point light separation task to assess the impact of scatter on visual resolution. Sixty (60) subjects were tested under controlled conditions to provide insight into the behavioral implications of wavelength-dependent scattering.

The findings of this study indicate that intraocular scatter exhibits a significant wavelength dependence, as subjects demonstrated varying levels of two-point light resolution across different wavelengths. Specifically, resolution thresholds were lower at shorter wavelengths, suggesting increased scatter and reduced clarity compared to longer wavelengths. These results align with the findings of Coppens et al., (2006) and Whitaker et al., (1993) who reported wavelength-dependent scatter; those authors described this pattern as, potentially, due to Rayleigh scattering effects within the eye.

Rayleigh scatter describes the interaction between light and particles that scatter that light. This relation is quantified mathematically by a simple power exponent(λ^{-4}) (Young, 1981). This physical constant, however, is foundational to understanding light behavior in atmospheres where particle sizes are smaller than the wavelength of light. In this study, the data were also well-described by Rayleigh's constant (see Figure 8). It seems unlikely, however, that the eye contains particles small enough to be based on the same principles as those manifest in atmosphere. Most intraocular (forward) light scatter within the eye arises from the interaction of light with the major focusing elements, the cornea and crystalline lens (Leopoldo Spadea et al., 2016; T. J. van den Berg, 1996). These tissues are composed of relatively large molecules (like crystallin proteins) set within the solid matrix of the lens;Delaye & Tardieu, 1983). Unlike atmospheric scattering where the air molecules (i.e., gasses) are significantly smaller than the wavelength of light, the eye (i.e., liquids and solids) lacks particles of this scale (originally argued by Barbur et al., 1993). If, however, the actual mechanism of scatter is not based on Raleigh principles as commonly argued (e.g., van den Berg, 2018; Yaroslavsky et al., 1994) what then could explain the Rayleigh-type scatter patterns within the eye?

One possibility is Tyndall scatter which has a similar mathematical expression to Rayleigh but admits scatter from larger particles (e.g., colloidal proteins within the lens, Bassnett & Costello, 2017). Another possibility is defocus caused from the effects of longitudinal chromatic aberration (LCA). LCA arises because different wavelengths of light focus at different planes orthogonal to the optical axis of the eye. Like our two-point threshold data, short-wave light is particularly out of focus. Past data (e.g., Gawne & Banks, 2024) has shown that, when presented in isolation, the young lens can accommodate to narrow-band wavelength, particularly at the edges of the visible spectrum (short and long wavelengths), where focal alignment with the retina becomes challenging. Our stimuli, however, were characterized by light scatter/spread which may not have provided a sufficient cue for effective accommodation to specific wavebands. Hence, the effects of LCA may have driven some of the differences in our two-point thresholds across wavelengths (see the comparison in Figure 9, LCA data taken from Barkan & Spitzer, 2018).

What does seem clear is that action spectra (differences in the biological effectiveness of wavelength) are more the rule than the exception when it comes to human visual function. A number of studies have shown that, when all else is equal, the response of the visual system to wavelength is decidedly not equal. Probably the most obvious is simply spectral sensitivity across all adaptive states (photopic, mesopic and scotopic): at equal energy, these sensitivity curves peak around the middle of the visible spectrum. Other variables, however, driven largely by light scatter, also have shown differential response to wavelength. These include photostress recovery (Stringham & Hammond, 2007), glare discomfort (Bullough, 2009) and photophobia (Stringham et al., 2003), all of which show an inverse and monotonic relation to wavelength (i.e., the largest response to the shortest wavelengths). In fact, even retinal damage due to wavelength follows this inverse pattern (van Norren & Gorgels, 2011).

These findings suggest that intraocular scatter, particularly at shorter wavelengths, may pose specific limitations in tasks requiring high-resolution visual discrimination. Visual stimuli—ranging from lighting to road signs—can be optimized to minimize the detrimental effects of scatter and thereby lead to enhanced visual performance. Lenses have been specifically designed (IOLs, Renzi-Hammond & Hammond, 2022a, contact lenses, Renzi-Hammond et al., 2022b) with short-wave absorbing chromophores to improve wavelength-dependent scatter.

The fact that artificial filters can improve wavelength-dependent scatter suggests that natural chromophores may serve this function as well. To this end, we also explored the potential effects of iris pigmentation and macular pigment density on intraocular scatter. Both factors have been hypothesized to influence scatter due to their roles in light absorption and filtering within the eye.

The analysis revealed a significant association between darker iris pigmentation and reduced intraocular scatter, suggesting that pigmentation may mitigate the effects of light scattering within the eye. Similarly, higher macular pigment density was associated with lower scatter levels specifically at the short-wave regions, supporting the role of macular pigments as optical filters that reduce the effects of light scatter.

These findings are consistent with previous research suggesting that both iris pigmentation (Nischler et al., 2013) and macular pigments (Putnam et al., 2017; Wooten & Hammond, 2002) may contribute to reducing the effects of intraocular scatter, enhancing visual clarity.

In conclusion, this study advances our understanding of intraocular scatter by demonstrating that light scattering within the eye is indeed wavelength-dependent, with shorter wavelengths exhibiting higher scatter as expressed by reduced visual resolution (wider spaced two-point thresholds). One caveat is simply that these results are specific to the task used in this study. We used a resolution task at relatively low energy. The question of whether other tasks, known to be impacted by light scatter, are influenced similarly cannot be inferred from these data. In fact, glare disability and photostress recovery (scatter at high energy levels) display action spectra that are substantively different (Stingham et al, 2007).

The wavelength-dependent scattering effects in this study likely arise from factors beyond Rayleigh scatter, possibly influenced by longitudinal chromatic aberration, anatomical structures

(Tyndall effects), and retinal sensitivity. Our findings highlight the potential benefits of considering wavelength effects in visual tasks that require high resolution, as well as the value of optical filters and lens designs that target short-wave light. Furthermore, the association between darker iris pigmentation, higher macular pigment density, and reduced intraocular scatter suggests that natural chromophores play an important role in mitigating the impact of scatter under these conditions. These insights may inform strategies for optimizing visual performance in both natural and artificial environments, ultimately contributing to safer and more effective visual experiences across a range of conditions.

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