DETECTION OF ULTRAVIOLET LIGHT BY HUMANS AS A FUNCTION OF AGE

by

LAURA MICHELLE FLETCHER

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

ABSTRACT

It has long been thought that the yellow color of the crystalline lens is what prevents us from being able to see light in the ultraviolet; it has been hypothesized that young children, whose lenses have not yet yellowed, may be able to detect these wavelengths. Studies on *ex vivo* anterior media transmission characteristics which have included the eyes of infants and young children have noted a small transmission “window” in the lens centered at approximately 320 nm. Additionally, aphakics have been shown to be able to respond to ultraviolet light. Therefore, it seems that when this light reaches the retina, we can indeed detect and respond to it. This study is the first to assess detection of ultraviolet light (315 nm) in phakic children and adults. As the S-cones are the most likely to mediate this ability, S-cone sensitivity was also assessed. There was a very clear relationship between the ability to detect the ultraviolet stimulus and the age of the subject. All subjects under the age of 30 could reliably detect the stimulus. Between the ages of 30 and 40, 38 percent of subjects could detect it; for the remainder, detection was essentially nonexistent. Detection ability was not related to S-cone sensitivity, as assessed by threshold for a 405 nm stimulus. It seems definitive that a visually significant amount of ultraviolet radiation does reach the retina of children and young adults, at least under present testing conditions. Further characterization of the true visual range of humans is needed.

INDEX WORDS: Ultraviolet light, Visual range, Lens transmission

DETECTION OF ULTRAVIOLET LIGHT BY HUMANS AS A FUNCTION OF AGE

by

LAURA MICHELLE FLETCHER

M.S., The University of Georgia, 2013

A Dissertation Submitted to the Graduate Faculty of The University of Georgia in Partial Fulfillment of the Requirements for the Degree

DOCTOR OF PHILOSOPHY

ATHENS, GEORGIA

2016

DETECTION OF ULTRAVIOLET LIGHT BY HUMANS AS A FUNCTION OF AGE

by

LAURA MICHELLE FLETCHER

Major Professor:	Billy R. Hammond, Jr.
Committee:	James M. Brown Janet E. Frick

Electronic Version Approved:

Suzanne Barbour
Dean of the Graduate School
The University of Georgia
March 2016

DEDICATION

For my husband and my parents, whose unconditional support has made this possible.

ACKNOWLEDGEMENTS

I would like to express my gratitude to my major professor, Randy Hammond, for his guidance throughout my graduate career. I would also like to thank the members of my committee, James Brown and Janet Frick, for their helpful suggestions which contributed to the integrity of this report. Special acknowledgements to Kevin O'Brien, for his construction of the device used in the study, as well as his friendship and general intellectual contributions, and Emily Bovier, for her unwavering support in both my academic and personal life.

TABLE OF CONTENTS

Page

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

INTRODUCTION

The solar irradiance reaching the Earth’s surface is broadband, extending from approximately 260 to 2500 nm (Mecherikunnel & Richmond, 1980; Hammond, Johnson, & George, 2014). This portion of the electromagnetic spectrum can be broken into subcategories including ultraviolet (approximately 200 – 400 nm); “visible” (approximately 400 – 700 nm); through infrared, radio wave, and microwave (though the exact break points vary a bit from discipline to discipline, and many of the categories have several subcategories). Despite the broad range of electromagnetic energy available in the environment, most species possessing any form of vision have evolved to primarily utilize only a narrow band, typically the wavelengths between approximately 400 and 700 nm (Jacobs, 1992). Despite similarities in sensitivity across many species, some species have adaptations allowing them to utilize even shorter wavelengths, extending into the ultraviolet (UV). Within the UV portion of the spectrum (approximately 200 – 400 nm), there are three subdivisions: UVC from 200 – 290 nm, (the majority of which is prevented from reaching the Earth’s surface by our magnetic field and the ozone layer; Diffey, 1991; Norval, et al, 2007); UVB from 290 – 320 nm; and UVA from 320 – 400 nm. Because many biological molecules (e.g., proteins and the nucleotide bases of DNA; Diffey, 1991) very strongly absorb light shorter than approximately 310 nm, species which can detect UV light are typically only sensitive to UVA and the very longest portion of UVB. Thus, a species’ visible range is really determined by several factors, including: the radiation within its environment; the transmittance of its ocular media; and the properties of the visual pigments within the animal's photoreceptors (Douglas & Jeffery, 2014).

The ability to respond visually to UV light was first demonstrated in invertebrates such as ants (e.g., Lubbock, 1882 as cited in Stark & Tan, 1982), bees (e.g., Bertholf, 1931), flies (Bertholf, 1932), and other insects. It has also been shown to be utilized by many species of birds (e.g., hummingbirds – Goldsmith, 1980; zebra finches – Bennett, Cuthill, Partridge, & Maier, 1996; pigeons – Emmerton, 1983), some shallow-water fish (e.g., brown trout and goldfish – Douglas, 1989), and possibly a narrow selection of amphibians (e.g., axolotl – Deutschlander & Phillips, 1995) and reptiles (e.g., turtles – Ventura, Zana, de Souza, & DeVoe, 2001). Many animals have not explicitly tested been tested for the ability to detect UV or had the transmittance of their anterior media measured, yet features of their anatomy suggest that UV light may indeed be reaching the retina. For example, several species of deep water fish (e.g., the long horned sculpin) have extraordinarily clear corneas in their natural habitat; however, upon approaching the surface, or when exposed to bright lights, the cornea becomes colored a deep orange (Sivak 1979). Although one likely purpose of this transformation is to maintain retinal adaptation levels, it may also serve to protect the retina from damaging short wave light.

Mammalian Sensitivity to Ultraviolet Light

The ability of mammals to detect UV light has only relatively recently begun to be studied. While most mammals do not possess a photopigment with peak sensitivity in the UV, some degree of UV sensitivity is more widespread among mammals than previously thought (Douglas & Jeffery, 2014). As early as 1969, it was determined that several mammalian species possess lenses that readily transmit UVA light (Cooper & Robson, 1969a). Some rodents appear to possess a photopigment with peak absorbance in the UV (typically at approximately 360 nm; Jacobs, Neitz, & Deegan, 1991), but it is unclear how common this is throughout the class Mammalia. More recently, Tsukahara, Tani, Kikuchi, and Sugita (2014) investigated the separate transmission spectra for all anterior media in several species of birds and mammals. Although the avian ocular media had the greatest UV transmission, the total transmission spectra for rats, pigs, and rabbits were found to remain above 50% until approximately 390 nm. Additionally, the transmission of the lens of the rat and rabbit remained around 20% or higher for wavelengths as short as approximately 325 nm. Similarly, Dillon, Zhen, Merriam, and Galliard (2000) found that the anterior segment of the rat transmits nearly the entire UVA portion of the spectrum, whereas rabbits transmit out to approximately 350 nm. Fruit bats, though not possessing a photopigment with a peak in the UV, are still able to respond behaviorally to light as low as 310 nm (Winter, López, & von Helversen, 2003). Thus, UV light is, at the very least, reaching the retina of many mammals. It also seems likely that such light is capable of influencing perception.

Mammals with Yellow Lenses

Two mammalian orders are known to consistently have yellow-appearing lenses; the primates and the sciurids (Walls, 1942). How this might affect the spectrum of light reaching the retina has been of interest for over a century (e.g., Hess, 1909, cited in Norren & Vos, 1974; Ludvigh & McCarthy, 1938; Wald, 1945; Kinsey, 1948), and it has long been suspected that the yellow color of the human lens is the reason for our inability to detect UV light (e.g., Brücke, 1845, as cited in Boettner & Wolter, 1962). Although most of this previous work has focused primarily on humans, Cooper and Robson (1969b) compared human lens transmission to several other primate and sciurid species and found that for all the species examined, an absorption maximum existed in the UVA portion of the spectrum (specifically, somewhere between 365 and 368 nm), and that this peak was consistent across species. It was later determined that, in humans and other primates, but not lower animals, the yellow color of the lens is primarily caused by the compound 3-hydroxykyneurenine glucoside (3-HKG), which has an absorption maximum at 365 nm (van Heyningen, 1971; Wood & Truscott, 1993; Dillon, et al., 2000). This molecule is thought to be responsible for preventing nearly all UVA light from reaching the retina.

Cooper and Robson (1969b) also noted that the infant lenses of all the species examined were much less yellow than the adults, with the most dramatic change in optical density occurring before eight years of age. In fact, many researchers studying the crystalline lens have noted that it becomes more optically dense with age. The change in density with increasing age has been investigated using both psychophysical methods (e.g., Wald, 1945; Tan, 1971; Wooten, Hammond, & Renzi, 2007) and physical methods (e.g., Ludvigh & McCarthy, 1938; Said & Weale, 1959; Boettner & Wolter, 1962; Mellerio, 1971). Part of the reason for the change has to do with levels of glutathione, one of the most important molecules for maintaining lens transparency; this molecule actively scavenges oxidant molecules in the crystalline lens (Cheng & Chylack, 1980). The levels of glutathione in the lens decreases with increasing age, and its oxidized version appears to increase in concentration until approximately the age of forty, after which it levels off (Kamei, 1993). Additionally, the amount of 3-HKG in the lens actually appears to decrease with age, with a concomitant rise in the yellowing of other lens proteins (Bando, Nakajima, & Satoh, 1981). The increased pigmentation and scattering nuclei are also not uniform throughout the lens. It seems that the nuclear portion of the lens becomes more pigmented, while the cortical regions actually increase in path length (Mellerio, 1987).

Primate Ex Vivo Lens Transmission and the Transmission Window

Studies on anterior media transmission characteristics which have included the eyes of infants and young children have frequently noted a small transmission “window” in the lens centered at approximately 320 nm (see Figure 1). However, inclusion of UV wavelengths in examinations of human lens transmission is not common, and conclusions about the existence of a transmission window are usually based on very small numbers of subjects (see Table 1 for a summary of the existing studies which include lens transmissivity measurements for wavelengths below 380 nm). Boettner and Woltner (1962) examined three eyes from young humans (4 weeks, 2 years, and 4.5 years) and found a transmission window centered at 320 nm which transmits approximately eight percent of incident 320 nm light. They estimated that by the early twenties this transmission window has largely closed, with less than one tenth of a percent being transmitted. However, their study included no eyes between the ages of 5 and 22 so this conclusion as to when the window closes may not be correct. Cooper and Robson (1969b) had lens sections from six human perinates (two stillborn, two 1-day-old, 6 months, and 8 months) and also found an absorption minimum for UV centered at approximately 320 nm. However, the reported optical density at the absorption minimum is approximately 1.5, which is quite high; it is possible that this was due to the fact that their lenses were in stacked slices (see Weale, 1988). Lerman and Borkman (1976) measured the percent transmission of the *ex vivo* human lens from 200 to 800 nm. Their sample included lenses from a six-month-old and an eight-year-old for which they found transmission for the range between 300 to 400 nm to be 85% and 75%, respectively, though subsequent studies have not confirmed transmission values to be this high. Lerman (data reported in Lerman, 1986) reports transmission data for a three-day-old, six-month-old, eight-year-old, and two teenagers (13 years and 17 years), and shows UV transmission remaining above twenty percent for all with no real variation in transmission amongst the young sample. He demonstrates a dramatic reduction in UV transmission occurring at 25 years of age and beyond. Weale (1988) measured lens transmission from 327 to 700 nm for 24 *ex vivo* lenses between the ages of zero and 85 years. Contrary to Lerman, he found that transmission in the UVA does vary with age, and his total percent transmission for UVA falls between that of Cooper and Robson (1969b) and Lerman (1976; 1986). He also notes a transmission window occurring at approximately 330 nm, though the extent of the transmission was variable even amongst young lenses. Additionally, he finds a 25-year-old lens that shows very little transmittance at 330 nm (specific data not reported), and an older lens from a 63-year-old man that does show the classic dip in absorption like those seen in younger subjects.

A small number of studies have examined the *ex vivo* transmission of UV light for the young non-human primate lens. For example, Galliard, Merriam, Zheng, and Dillon (2011) examined the transmission properties of the anterior segment as a whole using macaque eyes. They note that because 3-HKG is not synthesized until the last trimester of pregnancy, neonatal eyes are largely transparent to UV down to approximately 300 nm. For the slightly older monkeys used (e.g., two years of age), they found a transmission window centered at 320 nm, which begins to flatten out around eight years of age, and which was completely closed by the second decade of life. Galliard, Zheng, Meriam, and Dillon (2000) examined age-related changes in transmission of the lens for human and non-human primates (though their only human lenses were from a 48-year-old and a 78-year-old). For the young macaque lens (two years of age), they found that at 320 nm, approximately ten percent of the light is transmitted to the center of the lens, and one percent of that light makes it to the retina.

It is known that the spectral transmissivity of the human lens after death (at least down to 381 nm) is largely unchanged, even after a considerable length of time, provided that the lenses are properly treated and stored (Weale, 1985). It seems reasonable to assume that this relationship holds for shorter wavelengths as well, especially when the lenses are tested soon after death. Thus, when taken as a whole, the *ex vivo* data for lens transmission of human and non-human primates for UV light indicates that, at the very least, some UVA light is making it to the young retina.

Studies with aphakics

Studies from aphakic observers suggest that humans are able to respond behaviorally to this range of light when it does reach the retina. There are, however, few empirical studies on this topic, and those that exist can be divided into those that measure scotopic sensitivity (the majority), and those that measure either photopic sensitivity as a whole or the spectral sensitivity of the individuals cones. In addition, a few anecdotal reports exist from aphakics describing their visual perceptions. The first to report the ability of aphakics to perceive ultraviolet light was Gaydon (1938) who lost the lens of one eye due to a laboratory accident. He reported being able to perceive low intensity light at wavelengths as short as 310 nm, and that the light appeared blue, not violet. Interestingly, after this report was published, many other scientists of the time wrote letters to the editor of the journal in which it was published detailing similar experiences, or the experiences of acquaintances. None, however, seem to have been examined empirically other than Gaydon. Not long after this, Goodeve, Lythgoe, and Schneider (1942) used Gaydon as a subject in their experiment on scotopic sensitivity in the UV. They found his sensitivity at 365 nm to be approximately four times that of the normal subjects. Additionally they found his sensitivity at 365 nm to be not much reduced from its sensitivity at 546 nm (though this flattening out of sensitivity has been contradicted by later studies).

Scotopic Sensitivity in Aphakics

Wald (1945) was the first to study scotopic sensitivity in more than one aphakic observer (39 eyes in 24 observers) and demonstrated that their sensitivity at 365 nm is approximately 1000 times that of normal observers (though sensitivity at 365 nm is about 1/30 of what is seen at the rod peak in contradiction to the findings of Goodeve, et al). He reports that the aphakic observers “see very well in the ultra-violet”, and that their perceptions of stimuli illuminated by UV light are not distorted in any way.

Wolf (1946) measured dark adaptation curves for normal and aphakic observers after exposure to light between 290 – 365 nm. He found that rod sensitivity was considerably lower for the aphakic observers than the normal observers, indicating that substantially more light was reaching the retina and partially bleaching the rhodopsin photopigment. Wald (1952) repeated this experiment, and found no effect on rod vision, but that cone sensitivity was severely depressed for aphakic observers compared to normal observers. Interestingly, the aphakic observers also reported that the stimulus which included the UV wavelengths appeared much brighter than the UV-free stimulus; to normal observers these stimuli appeared the same.

Wright (1949) described an experiment he conducted in 1944 after reading Gaydon’s report of his own experience. He measured sensitivity to 365 nm, 404.7 nm, 435.8 nm, and 546.1 nm in several aphakic and normal observers. He found that for the 365 nm task, the aphakics were approximately 2.35 log units more sensitive than the normal observers. This relationship was reversed for the longest wavelength, with the normal observers outperforming the aphakics by 0.80 log units. This rules out the possibility that the aphakic observers are somehow more sensitive overall than the normal subjects.

Tan (1971) measured the optical density of the lens by comparing the scotopic spectral sensitivity curve for aphakic observers to that of normal observers. He only measured down to 350 nm, but found that the aphakic curve still reached the appropriate maximum at the peak rod sensitivity of 505 nm. Sensitivity remained high throughout the UV portion tested.

Williams (1982) measured absolute thresholds for the wavelengths between 300 and 700 nm in two aphakic subjects. He found that their sensitivity matched that of normal observers for wavelengths longer than 500 nm, but was dramatically different for shorter wavelengths, with sensitivity in the ultraviolet estimated as 300 times that of normal observers.

Anderson (1983), an ophthalmologic surgeon who was himself aphakic in one eye, reported on some of his post-surgery experiences. While visiting an exhibit in a museum, he was largely unimpressed until he covered his aphakic eye and viewed through his normal lens; at that point the rocks in the exhibit appeared phosphorescent as they were “supposed” to appear. He also describes the experience of his brown dress socks appearing a brilliant purple (and having a disagreement with his wife about it). Self-testing with various UV filters confirmed his ability to perceive the entire UVA spectrum.

Photopic and Spectral Sensitivity in Aphakics

Griswold and Stark (1992) measured the scotopic spectral sensitivity for aphakic and phakic observers from 314.5 to 650 nm. They followed the procedure of Tan (1971), and like him found the normal rod peak, and that the sensitivity remained high even down to 314.5, nearly the shortwave limit of the light that makes it through the cornea. In comparison to phakic observers, aphakics were four log units more sensitive at 350 nm. They, like Stark and Tan (1982), attribute this secondary peak in sensitivity in the UV to rhodopsin's *cis*-peak (also sometimes called a *β*-band), and not to some special mechanism for UV sensitization.

Studies of photopic spectral sensitivity to UV light in aphakics are much rarer. Although, notes of normal observers being able to see the line at 365 nm of the mercury spectrum are relatively common throughout the literature (e.g., de Groot, 1934, who tested 21 observers with positive results as low as 313 nm; Goodeve, 1934 – who also claims to be able to see the lines in his monochromator at approximately 312 nm). Wald (1945) measured cone sensitivity in six aphakics and found that the subjects could read an entire Snellen chart when illuminated by 365 nm light, when he himself could not even see the chart. Tan (1971) used an increment threshold technique to separate out the three cone spectra; he found normal peaks for L and M cones (with *cis*-peaks occurring in the UV), but found S-cone sensitivity to continue to increase into the UV (measured to 350 nm as described above).

Stark (1987) examined aphakic photopic sensitivity with corrections for the macular pigment in four subjects, but did not examine the individual cone spectral sensitivities. For foveal measurements, he found the standard photopic peak at approximately 555 nm, and a secondary peak near 380 nm which was about 0.7 log units lower in sensitivity. For measurements made 5.5 degrees outside the fovea (the correction for the macular pigment) he found a broad area of sensitivity from 330 to 560 nm with no distinct peaks and a rapid drop off in sensitivity above 560 nm. This contradicts the findings by Tan (1971) that S-cone sensitivity rises in the UV and cannot be accounted for by a *cis*-peak in the absorption spectrum.

Stark, Wagner, and Gillespie (1994) also used the increment threshold technique to determine cone sensitivity curves for three aphakic observers. Like Tan (1971), they found that the S-cone peak does not occur in the visible portion of the spectrum, but instead continues to climb throughout the UV portion tested (down to 315 nm). They claim that measured S-cone sensitivity exceeds what would be expected by the cone opsin *cis*-peak, and thus the true S-cone peak sensitivity may really occur in the UV portion of the spectrum. They make no note that this work contradicts the earlier work by Stark (1987), but the fact that Stark measured the photopic sensitivity as an average of all three cone types may have muted the S-cone contribution to the curve and underestimated its sensitivity in the UV.

Summary and Purpose

The data on scotopic and photopic sensitivity of aphakic observers, taken together with the various anecdotal reports from aphakics of being able to see UV light, are convincing enough that it is generally well accepted that aphakics can detect and respond to UV light down to approximately 310 nm. The other groups for whom significant amounts of UV light may reach the retina – the human infant and child– have largely been ignored. The question of whether or not human infants and children can detect UV light is currently entirely theoretical; to date, there have been no studies assessing whether the *in vivo* human infant and child lens transmits UV light, nor whether she can make a behavioral response to said light[1]. Hallaeur (1909) suggested that UV absorbance of the lens after birth is quite low and increases with age (cited in Weale, 2009), but this has never been empirically demonstrated in living children. The present study will

---

[1] Saidman (1933) claims to have tested 102 individuals for visibility of the 313 nm mercury line. His subjects were children and adults from a nearby hospital, but no description of the sample is included in the study, so it is unclear what ages were tested other than that some of them were younger than 33 years old.

assess detection of UV light (peak =315 nm) in children and adults[2]. Additionally, the time course for the closing of the lenticular UV transmission window, should it exist, will be estimated. While the majority of previous studies have included small numbers of subjects, the present study will include enough children to determine if the ability to detect UV light is common, or whether lens transmission for these wavelengths is as variable amongst young lenses as some of the *ex vivo* transmission studies would suggest (e.g., Weale, 1988).

Specific hypotheses

Ultraviolet detection in children. The majority of children between the ages of four and approximately sixteen will be able to reliably detect the presence of a UV light source (peak wavelength = 315 nm) in a two-alternative forced-choice experiment. Performance for the UV stimulus will not significantly differ from that measured in detection of a 405 nm light at an easily visible intensity.

Ultraviolet detection in adults. With increasing age, the likelihood of detection of UV light will decrease, with a notable drop-off in performance occurring sometime in the late teenage years or early twenties (the approximate average of the human *ex vivo* lens transmission studies discussed above). Correct identification of the UV source will be approximately chance after this point, while detection of the 405 nm light (at its most intense setting) will be at or near 100 percent.

Relationship between UV detection and threshold for 405 nm stimulus. Because the ability to detect UV light is likely to be mediated by the S cones, detection may be related to

---

[2] Originally this study proposed testing infants, children, and adults. After data collection began, it became clear that the transmission window closed much later than previously thought and the age range to be tested was adjusted accordingly.

sensitivity to the shortwave visible stimulus (i.e., those who can detect UV light may have lower thresholds for the 405 nm light).

CHAPTER 2

METHOD

Subjects

Subjects were children and adults recruited from throughout the state of Georgia. A total of 40 subjects were included: 20 children (ages 4 – 17 years); and 20 adults (19 – 57 years). See Table 2 for full demographics information. Exclusion criteria included: failure to provide informed consent, age younger than four years or greater than 60 years, and a history of relevant ocular disease (e.g., cataract), or history of epilepsy and/or seizure in response to flashing lights. The children recruited spanned the age range, but a special focus was initially given to children aged 10 to 14, as that was the proposed time for the closing of the transmission window. As data collection proceeded, it became clear that the closing of the transmission window actually occurred much later, and a subsequent focus was given to recruitment of subjects between 25 and 40 years of age. All subjects enrolled in the experiment completed all components, and none were excluded from analyses.

A Novel Apparatus

A novel tabletop device was created for this experiment in collaboration with Kevin O'Brien (See Figure 2 for a schematic). The stimuli consisted of two sets of light-emitting diodes (LEDs), which could be controlled separately. One set, the UV stimulus, has a peak of 315 nm (half bandwidth = 10.7 nm; QPhotonics, LLC); the other set consists of visible short wavelength LEDs (peak = 405 nm; half bandwidth = 5 nm; Bivar, Inc.). For spectra, see Figures

3 and 4 respectively. This UV wavelength was chosen to maximize the likelihood of detection if a transmission window at 320 nm did indeed exist. Importantly, the spectrum does not extend into the visible region, allowing for isolation of the UV. After initial testing of the UV stimulus with a spectroradiometer (Photo Research, Inc. SpectraScan PR-655) it was determined that a small amount of visible light was present in the stimulus. A bandpass filter with a peak transmission at 313 nm and bandwidth of 10 nm was added in front of the LEDs (Omega Optical, Inc. 313BP10). Further testing with the same spectroradiometer confirmed that no visible light was detectable.

Intensity for both sets of LEDs was controlled by high frequency pulse-width modulation. The intensity of the UV LEDs remained constant throughout the experiment (0.512 $\mu W/cm^2$ at the source), as the only goal was to assess detection ability; the intensity was confirmed before each subject using a UV power meter (General Tools & Instruments, LLC. UVA-UVC Light Meter UV254SD). The intensity of the visible short wavelength LEDs was altered from trial to trial. This had two purposes: 1) to make the task somewhat more interesting, and maintain subject motivation; and 2) intensity at threshold for the detection of the visible short wavelength LED may be related to the ability to detect the UV stimulus, particularly for those subjects at the “transition” point of losing that ability. The LED array was seen in free view with no intervening filters or diffusers.

Procedure

All procedures were approved by the University of Georgia’s Institutional Review Board. Assessment required one visit which took approximately 30 minutes. Subjects had the option of being tested in their own home (n = 1), or in any other suitable location (n = 3). All other subjects (n = 36) were tested in the same location. Detection of ultraviolet light was assessed using a two-alternative forced choice method. Both children and adults indicated verbally which of a pair of LEDs were flickering. Sensitivity to a 405 nm light was also assessed using a two-alternative forced-choice method. Approximately 15 trials each were conducted for the ultraviolet and the visible stimuli.

For all testing sights, a darkened, windowless room was used. A standard 70 lumen LED desk lamp paired with a neutral density filter (1.0) was used for the ambient illumination; average total illumination (lamp and computer screen) at the position of the subject chair was 1.10 (± 0.07) cd/m^2 (see Figure 5 for a photograph of a testing session) This was confirmed daily (or any time equipment was moved) before data collection began by a spectroradiometer (Photo Research, Inc. SpectraScan PR-655).

While subjects adjusted to the dimmer lighting of the experiment room, they completed the informed consent/assent process and filled out a brief demographics questionnaire to confirm eligibility to participate. Before testing, children and adults were seated in an adjustable chair 127 cm from the device. The device was also adjustable in height and was placed approximately at eye level for the subject. This distance was necessary given the very narrow beam angle of both sets of LEDs; closer viewing made it impossible for both LEDs within a set to be seen at once, which is important for a two-alternative forced choice task. A narrow beam angle was chosen to allow for the majority of the light to reach the subject, which is important as the stimulus is in free view and sensitivity to both light sources was anticipated to be quite low. For the UV LEDs the beam angle was 6 degrees ($2\theta_{½} = 12°$), and the 405 nm LED beam angle was 7.5 degrees ($2\theta_{½} = 15°$).

Before the first trial, a central red fixation light was used to orient the subjects to midline and to confirm that the equipment was correctly receiving input from the control computer. For each trial, one LED out of the pair being tested was made to flicker at 10 Hz, approximately the peak of the temporal contrast sensitivity function for both children and adults (e.g., Hartman & Banks, 1992). The other LED of the pair was set above flicker fusion threshold (75 Hz) and thus appeared stable. The LED pair not being tested was turned off during all trials and between trials.

Testing began with the 405 nm stimuli as it was assumed to be the easier of the two and the majority of the subjects were naïve to psychophysical experiments and thus needed time to become accustomed to the task. For both sets of stimuli, the target of interest was varied randomly between the two sides. It was explained to subjects before testing began that due to the random nature, the flickering stimulus could appear on the same side many times in a row. For younger subjects the presentation was changed to semi-random; the number of same-side presentations was limited to no more than four in a row to avoid biasing them or creating confusion (Saint, unpublished Thesis).

Assessment of Threshold for 405 nm and UV Detection

For the visible (405 nm) stimulus, the first trial was conducted at maximum intensity (0.23 μW/cm^2) for all subjects. Each time the subject correctly identified the location of the flickering target the intensity was halved until the subject's first miss. The next trial returned to the lowest previous intensity with a correct response. If the subject got that trial correct, the halved intensity was attempted again; if missed, the same intensity was attempted again; if missed a second time, the next lowest intensity with a correct response was tested. Once an approximate threshold was determined in this way, intermediate values were tested until the value for which the subject achieved approximately a 70% correct response rate was determined. This value was then taken as the subject's threshold. For some subjects, the stimulus could still reliably been seen at the lowest possible setting. This was taken to be their threshold, despite the fact that the percent correct was sometimes as high as 100 percent.

For the ultraviolet stimulus, the intensity was kept at the maximum for all trials. For subjects who had a 90 percent or higher correct response rate after ten trials, the study was concluded at that point. If percent correct was lower than 90 percent after ten trials, an average of ten additional trials were conducted.

Statistical Analyses

Data were analyzed with Microsoft Excel and SPSS 23.0. The relationship between age and ability to detect UV is best represented graphically (see Figure 6), but a binary logistic regression was also performed. A Pearson product-moment correlation was performed between age and threshold for the 405 nm stimulus, as well as for that threshold with the room illumination. A comparison of means for threshold for the 405 nm stimulus was done between the child and adult subjects, as well as between those who could and could not detect the UV stimulus. Finally, a Pearson chi-square analysis of UV detection and sex was performed.

CHAPTER 3

RESULTS

Ultraviolet Detection

There was a very clear relationship between the ability to detect the UV stimulus and age of the subject (see Figures 6 and 7). One hundred percent of subjects under the age of 30 years (N = 28) could reliably detect the stimulus. Between the ages of 30 and 40 (N = 8), 38 percent of subjects could reliably detect the UV, though most commented that it was very difficult to see and often remarked that they felt they were “guessing”.[3] For the remainder of the subjects (N = 4; 41 – 57 years of age) UV detection was nonexistent (with the exception of the oldest subject; see discussion for more about this individual case). The binary logistic regression of age as a predictor for ability to detect UV was statistically significant ($\chi^2 = 18.04$, $p < 0.001$).

There is no obvious reason to expect that sex should be a factor in ability to detect the stimulus; however, a Pearson chi-square test was conducted to be sure that it was not, particularly for those subjects at the transition point. The relationship between subject sex and the ability to detect the UV stimulus was nonsignificant ($\chi^2 = 2.03$; $p = 0.154$). Though, it should be noted that for two of the bins there were fewer than 5 subjects, which limits the validity of the test.

The 405 nm Stimulus and UV Detection

---

[3] This experimenter was not an official test subject, but also falls into the 30 – 40 age range and could relatively easily see the UV stimulus.

Threshold for the 405 nm stimulus was not related to age (*r* = -0.121; *p* = 0.458; see Figure 8); nor did the children have significantly lower thresholds than the adults (*t* = -1.036; *p* = 0.307). Because there were several outliers in the threshold data, particularly for the children, a Levene's test of homogeneity of variance was conducted for the two groups; it was nonsignificant (*F* = 3.85; *p* = .057). A means comparison for the 405 nm threshold was also conducted for those individuals who could detect UV light versus those who could not; it was also nonsignificant (*t* = -0.234; *p* = 0.816).

Due to the fact that the data were collected in multiple locations, a Pearson product-moment correlation was run for room illumination and threshold for the 405 nm stimulus to rule it out as a contributing factor. There was not a statistically significant relationship (*r* = 0.099; *p* = 0.545).

CHAPTER 4

DISCUSSION

Summary and Interpretation

Overall, it seems definitive that not only does a significant amount of ultraviolet radiation reach the retina of children and young adults, they are indeed able to respond behaviorally to that light, at least under the present testing conditions. For those who could detect the UV, all had a 100 percent correct response rate for that stimulus, implying that it was not only possible, but relatively easy to detect. Using age as a predictor variable in a binary logistic regression model for UV detection, there was a good fit and the model was statistically significant. Interestingly, the age at which the transmission window for UVA begins to close was much later than hypothesized. The present data suggest that the closing of this window is more likely to be in the early- to mid-thirties. Additionally, because every subject under the age of 30 was able to detect the UV light, this may be a relatively universal property of the young lens, which is more similar to the findings of Lerman and Borkman (1976) than those of Weale (1988).

Of additional interest was the observation that the oldest subject in the sample (57 years of age) was able to reliably detect the UV stimulus, and was the only subject over the age of 34 years to do so. The subject maintained that he could not see any sort of light during the trials, but that he was merely “looking for change” when making his judgments; however, over the course of 20 trials, he had an 83 percent correct response rate so presumably he could detect something. It is unknown whether he is simply an excellent psychophysical observer, and that other observers of a similar age may also have been able to detect the light had they been as careful, or if he is unique amongst older observers. As noted previously, Weale (1988) did observe what appeared to be a small transmission window at 330 nm in the lens of a 63-year-old subject, so it is possible that the present subject could be a similar example. It is worth noting that one 35-year-old subject is a highly experienced psychophysical observer, and also attempted to use a "change detection" criterion for detecting the UV. Despite conducting approximately 30 trials with this subject, he remained at a chance level of detection. This lends additional support to the idea that the 57-year-old observer was, in fact, unique in his ability to detect the UV light amongst older subjects. It has been demonstrated that while lens density does generally increase with age, this is highly variable amongst individuals, and occasionally the lens essentially collapses in on itself, rendering it as transparent to short wavelengths as a young lens (Sample, Esterson, Weinreb, & Boynton, 1988; see Figure 9). This could help explain the present findings, and suggests that a measure of lens optical density should be included in any future study evaluating UV detection.

The relationship between the ability to detect UV light and the sensitivity of the S-cones (as measured by the threshold for the 405 nm stimulus) was nonsignificant. However, there are several important factors which may have contributed to this null finding. First, while the visible stimulus was adjustable in intensity (from approximately 0.23 $\mu W/cm^2$ to 0.08 nW/cm^2 based on the manufacturer's specifications), the lowest value was not dim enough for some subjects to fully lose sight of the target. Thus there was a floor effect for a large number of subjects ($n = 9$), which may have muted any existing relationship. Second, because the threshold was assessed by the method of constant stimuli rather than the method of limits, a larger number of trials were likely needed for a truly accurate threshold estimate. The inclusion of children in the present study precluded this from happening. The threshold value obtained is therefore likely only an approximate estimate of a subject’s true threshold. If a more lengthy and accurate evaluation of threshold for the 405 stimulus were conducted, perhaps a relationship to ability to detect UV would emerge. This is most likely to be the case for subjects who are at the precipice of losing the ability.

Most of the subjects who could see the UV stimulus commented that it was, in fact, much easier to detect than the 405 nm stimulus, which was initially very surprising. They also tended to describe it as blue, not violet, which is consistent with Gaydon’s (1938) description. Younger subjects frequently had very creative descriptions for the appearance of the UV including that it looked “sparkly”, or like: “fireworks”; “the deepest blue I’ve ever seen, but not dark”; “a black light in a dark room”; and “a bubble shining in the sun”. By contrast, the adult subjects who could reliably detect the UV described it in terms like: “a very dim light”; “a tiny speck of something”; and “completely invisible”. This certainly suggests that the stimulus was far more visible to the younger subjects than those near the transition point of losing the ability, but this should be examined in the future by finding the threshold for the UV stimulus and its relation to age.

Can This Be True: Device Validation and the Issue of Fluorescence

Given the novelty of the present study and the implications of its outcome, the device validation will now be discussed in greater detail. As mentioned previously, the published spectra for the UV LEDs and the bandpass filters indicate that no visible light (greater than 400 nm) should be present in the stimulus. The filters were secured in specialized holders which were painted black and wrapped in black electrical tape to prevent the possibility of any light leakage from the LED behind the filter. After this, the spectroradiometer indicated no detectable radiation.

As I could easily see UV stimulus, this allowed for a few subjective methods of validation as well. When a piece of normal glass was placed in front of the eye, the stimulus disappeared entirely. This was also true for every subject who wore glasses, including the children. It is well established that glass absorbs nearly all UV radiation (see Siegel, 1974 for a review) while being largely transparent to wavelengths longer than 400 (modern eyeglasses are also often coated with a substance that entirely absorbs UV for the patient's protection when outdoors), so it should not have been visible through eyeglasses. I also attempted to take a picture of the UV stimulus while it was at maximum intensity (Nikon Corp., Coolpix S6300); while it looked very bright to me, every picture turned out completely black.

Finally, a spectroradiometer which measures from 250 to 1000 nm was used to measure the stimulus directly (International Light Technologies, Inc. Spectralight ILT950). This confirmed that the peak of the stimulus was 315.22 nm (energy at peak was 0.56 $\mu W/cm^2$ at the source – which matches well with the General Tools light meter used for daily calibration checks). More importantly, there was no measurable light with a wavelength longer than 332.39 nm.

Once the presence of visible light in the stimulus is ruled out, there is one remaining possibility which could explain the results. This second possibility is that subjects are not detecting UV light at all, but merely the fluorescence of one or more of the anterior ocular media and/or the retina. Meaning, the incoming UV light interacts with a structure in the eye in such a way that the UV light is reemitted in the "visible" spectrum and subsequently detected by the cells of the retina. This has been a common assumption for previous reports of an ability to detect UV or infrared light sources (e.g., Helmholtz's claim in 1855 that he could detect both under the right conditions).

If fluorescence is the explanatory factor for this phenomenon, the lens would be the most likely culprit. It has been known for over a century that the lens fluoresces in the presence of UV light (e.g., Hess, 1911 cited in Weale, 1985), and the majority of the studies on fluorescence of ocular media have been on the lens (e.g., Bando, Ishi, & Nakajima, 1976; Weale, 1985; Lerman, 1986). Fortunately, we can rule out fluorescence of the lens as the sole factor for detection by the simple fact that the ability to detect UV has repeatedly been demonstrated in aphakics.

Helmholtz (1855) subjected an excised retina to UV light and noted that it fluoresced with a greenish-white light (Bachem, 1953). The retinal pigment epithelium (particularly the lipofuscin therein) is well known to fluoresce in the presence of many wavelengths including UV. The emission spectra of this fluorescence was a matter of debate for some time, but it now seems that fluorescence under UV light peaks at approximately 580 nm, and appears yellow (Eldred, Miller, Stark, & Feeny-Burns, 1982). A more recent study of the *in vivo* fundus fluorescence showed that while many of the structures do fluoresce, the emission spectra are generally in the green and yellow portions of the spectrum (Delori, et al., 1995). As all subjects in the present study who could see the UV stimulus described it as blue or violet, it is unlikely that ocular fundus fluorescence is the cause. Wyszecki and Stiles (1982) also note that the retina fluoresces in the presence of UV light. They theorize that the reports from aphakics that UV looks blue instead of violet is due to a mixture of the fluorescence with the true sensation of the UV (p. 116). This is essentially the same as the idea put forth by Helmholtz (1855): the final experience of seeing UV light is a mixture of fluorescence and true detection. This, however, is controversial and has been criticized by others (e.g., Fechner, 1859 cited in Bachem, 1953).

There is a dearth of information on the fluorescence of other ocular structures under UV light; however, there is another reason to think that fluorescence does not explain the present results. This is the fact that the UV stimulus does not appear as a formless blob or veiling light to those who can see it, which is what one would expect when detecting fluorescence. Instead, it appears as a sharply defined blue/violet point of light surrounded by a large blue/violet ring. This ring is almost certainly due to chromatic aberration, which would be extreme for wavelengths in this range. The hypothesis that the subjects are detecting some mixture of UV light combined with fluorescence of one or more structures cannot be ruled out at this point.

Why Are We Learning This Now: Maybe We Aren't

Having ruled out the dual possibilities of there being visible light contaminating the UV source, and that subjects are detecting solely fluorescence of the ocular media, the remaining explanation must be that, under the right circumstances, phakic humans can detect and respond to an ultraviolet stimulus. This then prompts one to ask how it is possible that we did not know this before (i.e., why has the lower limit of the visible portion of the spectrum always been defined as 400 nm). Although there has been some acknowledging of the fact that individuals can see below 400 nm in some circumstances, the untested assumption seems to be that our sensitivity is so low that it is effectively irrelevant. An examination of the classic studies on spectral sensitivity, the photopic luminosity function, and spectral transmission of ocular media shows that essentially all measure the range from 400 to 700 nm. Occasionally, data will be extrapolated into the UV (e.g., the CIE 1931 ideal observer data), but even this is uncommon. How this came to be is not particularly relevant here, but it is likely some combination of convention, the fact that the majority of vision scientists have been outside the age range able to see UV, and the difficulty in finding suitable light sources with energy in the UV for much of scientific history.

What is fascinating is that there are actually quite a few reports of normal observers being able to detect UV throughout the early literature. As discussed previously, Helmholtz reported being able to see the wavelengths between approximately 300 and 800 nm. Herschel (1840) wrote that he and a friend created a monochromator using sunlight as a light source combined with a flint glass prism (which was a personal gift from Fraunhofer and so of "faultless purity" p. 20). When they stretched out the colors on an opposite wall, they could see far beyond where the violet ended and experienced a sort of lavender-grey sensation which was he described as almost annoyingly persistent. Inspired by Herschel, Stokes (1852) conducted a similar experiment in which a solution of sulphate of quinine in a makeshift monochromator powered by sunlight showed a strange blue light beyond the violet portion which could not be further refracted. Some, including Stokes, took this to be a perception of ultraviolet, but it is more likely to be fluorescence in this case. It is now known that quinine fluoresces heavily in UV light (in fact, this was one of the very early checks used on the LEDs purchased for the present study to confirm their UV output). When he repeated the experiment with only water in the glass, he noted that he could only see as far into the violet as usual.

There are numerous other examples similar to these two, and it is something of a mystery as to why they did not make more of a lasting impression on vision science. It is difficult to determine the validity of these early experiments as many important details are missing from the reports, but they interesting nonetheless. The knowledge of them must not have disappeared entirely because, in 1912, Nutting wrote in his book on applied optics: "If sufficiently intense, radiation as far out as wavelength 0.32 [320 nm] (ultra violet) or 1.0μ (infra-red) may be perceived.” (p. 120); and later in the same chapter: “At about 320 in the ultra violet the eye media become opaque and shorter waves may affect the cornea or even the pupil, but cannot reach the retina.” (p. 137). He did not feel the need to cite either of these statements, but seems to have taken them as well-accepted fact.

What is truly surprising is that there are actually several experiments which have been conducted on the visibility of the ultraviolet on normal observers prior to the present one (see Table 3 for a comprehensive list). By the early twentieth century, the emission spectrum for mercury was well described, and this element was commonly used for arc or vapor lamps manufactured for scientific use. These lamps have about a third to a half of their energy in the visible short wavelengths (Luckiesh & Moss, 1937), which was uncommon for lighting sources of the time. Furthermore, there are additional peaks at 365, 334, 313, and 302 nm (Hulbert, 1928). It is these wavelengths of the mercury emission spectrum that were used in the very early experiments on ultraviolet visibility.

The first of these (Saidman, 1933) is also arguably the most thorough. He tested 102 subjects whom he described as sick children and the doctors and medical students who treated them. He tested visibility for the 313 nm line of the mercury spectrum and found, almost identically to the present study, that visibility for that wavelength disappears sometime between the ages of 34 and 43. He does not describe the sample of children in his study, and reports results for all the subjects under the age of 33 together (all of them could successfully see it). The following year, both Goodeve and de Groot performed similar studies, though on much smaller groups of subjects. It is unknown whether they were influenced by Said’s study, though as that one seems to have never been translated out of French, and neither of them cites it, it is unlikely. Goodeve (1934) tested nine subjects of undisclosed age for visibility of all the emission lines of the mercury spectrum between 253.6 to 404.7 nm. He also found that the 312.5 nm line was visible to all subjects (suggesting they were probably at least younger than 40 years of age), and commented that it creates a similar color sensation as the 404.7 nm line. This is also what was found in the present study: the UV stimulus appears as blue, not violet, to the majority of subjects. de Groot (1934) tested visibility for the same wavelengths on 21 subjects between the ages of 25 and 50 years of age. He does not break down the results by age, but merely states that one subject could not see the 365 nm line; 3 could not see it at 313 nm; and none could sense anything at 307.6 nm.

This area of research seems to have then been forgotten for two decades until Bachem picked it up in 1953. He begins his report seemingly very frustrated by the fact that vision in the ultraviolet was known in the mid-nineteenth century, rediscovered later, and then promptly forgotten again. He sets out to explain the color appearance of UV light, noting that Helmholtz and Herschel both describe it as a lavender-grey, but a mechanism by which this sensation might arise is missing. He either is unaware of the studies by de Groot and Goodeve, or chooses to disregard them, as the color sensation described in those studies is not mentioned in his. No mention is made of the study by Saidmann either. He does not say how many subjects were tested, nor what their ages were, only that some were younger (in their twenties), and some were older and aphakic. He found that all subjects could detect wavelengths down to 312.5 nm, and all described it as a desaturated blue.

Again, it is hard to draw conclusions from these studies because many important details are missing from the reports (most notably subject descriptions and the intensities of the wavelengths tested). However, there are certainly common outcomes amongst them which are also consistent with the findings of the present study. It seems fairly well established that subjects younger than approximately 30 years of age can consistently see wavelengths down to somewhere between 315 nm (present study) to 312 nm (the four described above). Furthermore, the sensation caused by these wavelengths of light does seem to be blue and not violet.

The Biological Utility of Seeing UV

Once we accept that young, phakic observers can detect UV light, the question arises as to what (if any) purpose this may serve. This is reasonably well understood for animals such as bees, which seem to use their ultraviolet vision to discriminate between flowers (e.g., von Frisch, 1967) or for navigation (e.g., Edrich, 1979); other pollinating insects that possess ultraviolet vision likely use it for similar purposes (Klugh, 1925). For birds, UV vision is also likely to be used for discriminating nectar sources (e.g., hummingbirds – Goldsmith, 1980); it has also been demonstrated to be used for mate selection (e.g., zebra finches – Bennet, et al, 1996), and prey detection from the air (e.g., kestrels - Viitala, Korpimäk, Palokangas, & Koivul, 1995).

Mammals with UV sensitivity include the pigmented house mouse, and the Mongolian gerbil, which are known to have photoreceptors with peaks in the UV (Jacobs & Degan, 1994), and animals which have lenses which transmit well into the UV (e.g., rats, pigs, rabbits, etc. - Tsukahara, et al., 2014; bats – Winter, et al., 2003). Bats are known to utilize sensitivity to UV much like the pollinating insects; what is less clear is what UV sensitivity might be used for in the other mammals. One of the only hypotheses put forward to date is for the regulation of circadian rhythms (e.g., Brainard, et al., 1994), and little definitive work has been done so far.

While it is tempting to try to find an adaptive reason for the existence of sensitivity to UV light in humans, it may be the case that it is simply a vestigial trait or even entirely coincidental. Walls (1942) and others have cautioned against searching for an adaptive purpose to all the features and anomalies of the eye and its function. One must remember that evolution is not a goal-directed process, and as long as a trait is not explicitly harmful, it will often be conserved in a species even if it serves no current purpose. That being said, some speculation may be worthwhile. If it turns out that other primate species can also detect UV light when young, it may be worth exploring whether the ability contributes in any way to foraging behavior. It has been hypothesized that trichromacy developed in Old World primates to enhance detection of ripened fruit against dark foliage (e.g., Mollon, 1989). Something that has not often been considered is that that this scene is illuminated by a source with a significant amount of energy in the UV (see Figure 10). If the ratio of reflectance between fruits and leaves is enhanced by inclusion of the ultraviolet wavelengths, then perhaps it is useful in that context. UV detection could also be used for breaking camouflage: many objects which are highly reflective to "visible" light absorb significant amounts of UVA (e.g., Richards, 2001). This has been demonstrated to work particularly well in Arctic conditions, where white animals photographed in UV light are easily visible and appear dark against the snow which strongly reflects UV light. This camouflage-breaking advantage may apply to the sun-dappled forests of our early evolutionary history as well.

Unanswered Questions & Future Directions

The present study, while definitively answering the question of whether or not phakic humans can detect and behaviorally respond to ultraviolet radiation under the right conditions, raises many more questions than it answers. The most pressing is a reexamination of the "visible" spectrum. While the present study was conducted with the idea that there may be a specific transmission window centered at 320 nm, it seems more likely that there is good transmission across all the wavelengths down to approximately 310 nm. The previous studies which measured the visibility of lines in the mercury spectrum seem to confirm this. These studies should be repeated with modern equipment to determine whether there are specific windows of transmission in the UV which happen to coincide with the mercury spectrum, which seems unlikely, or if there is simply a gradual tapering off of transmission throughout the UVA.

The next project in the reexamination of the wavelengths considered visible should also examine the reports of ability to see infrared (IR) and x-rays. As mentioned above, Helmholtz reported an ability to detect an IR source. While some have considered this to be merely the detection of heat by the cornea, there have been other reports of being able to detect light as far out as 900 nm (e.g., Goodeve, 1936); Nutting (1912) also wrote that wavelengths out to 1000 nm may be seen if they are sufficiently intense. van den Berg and Spekreijse (1997) examined the transmission of the ocular media for the wavelengths between 700 and 2500 nm. They found that for the purposes of calculating total light loss, considering the eye’s water components is likely adequate; this leads to light losses of approximately 4.5 percent at 810 nm and 25 percent at 1064 nm. Thus, it seems reasonable that detection may be possible for these wavelengths Sliney, Wangemann, Franks, and Wolbarscht (1976) measured the visual sensitivity to an IR laser (1064 nm) and found that it appeared red to observers. Regardless, most studies of human cone spectral sensitivities report little to no sensitivity beyond approximately 750 nm. Further studies should aim to clarify the true upper limit.

Of additional interest are the reports x-rays eliciting a sensation of light. The first to successfully demonstrate this were Brandes and Dorn in 1897 (cited in Lipetz, 1955). They found that both aphakic and normal observers could detect an x-ray source while blindfolded. In the subsequent decade, these experiments were repeated and confirmed by many other researchers. It was described in most of the reports as homogenous luminous glow across the entire visual field, with its color being described as everything between desaturated blue to clear green, making it seem likely that observers are actually detecting fluorescence of one or more structures of the eye (descriptions cited in Lipetz, 1955). However, Rushton (1938) found that x-rays could be used to measure the axial length of the eye in living subjects, and this procedure was commonly used in clinics for quite some time. This requires the subject to report when the light appears only as a point (i.e., it is in focus on the retina), which calls into question whether or not fluorescence is the only contributor to the detection of these wavelengths (see Deller, O'Connor & Sorsby, 1947 for a detailed description of the procedure). Clearly, more research is needed into the true lower limit of visual sensitivity as well. It may be that x-rays are merely destroying photopigment molecules rather than isomerizing them (much like the phosphenes seen by astronauts when exposed to cosmic rays; Pinsky, Osborne, Hoffman, & Bailey, 1975), but this has not yet been explored. Because biological molecules absorb light shorter than 310 nm (and many of the studies discussed above demonstrated an inability to detect light shorter than this), it seems unlikely that x-rays are being "seen" in the traditional sense of the word.

Future studies should also attempt to further characterize the visibility of ultraviolet in human observers. Determining how variable this ability is for older observers (i.e., what percentage of adults in their 50s and 60s can also detect UV), is an important next step. If it turns out that some minority of adults retain the transmission window throughout their lives, it would be interesting to know if these patients are at an increased risk for macular degeneration (or if they have some built in protection against developing cataract). The 57-year-old subject in the present study grew up in Miami, Florida and spent a great deal of time outside as a child and young adult. It seems unlikely that a lack of environmental exposure is what is keeping his lens less optically dense for these wavelengths than would be expected for his age. Future studies should include measures of lens optical density to determine if the collapse of the lens is what is allowing older subjects to detect UV.

Additionally, a follow up study should be done with greater numbers of subjects between the ages of 25 and 40 years of age to gain a more complete understanding of when the transmission window closes for the average observer. If we treat the graph in Figure 6 like a psychometric function and look at the 0.5 probability of seeing, we can see that the approximate age of closure is 34 years for the present study (this is also approximately what was found by Saidmann, 1933). Future studies should also make the UV stimulus variable in intensity, because it is likely that threshold for the UV stimulus will be much more tightly related to age and give a clearer picture of the phenomenon.

It would also be interesting to re-measure the spectral sensitivity of the S cones and include wavelengths in the UV. Tan (1971) and Stark, et al (1994) have done this with aphakic observers using an increment threshold technique, and both found that the S cone peak sensitivity continues to rise into the UV. If this is true, it would be a fascinating change to our current understanding of cone sensitivities; however, because S cone sensitivity is known to decrease with age (Haegerstrom-Portnoy, 1988) it would be wise to repeat these experiments using younger subjects who can also easily see in the UV. Similarly, absolute sensitivity to UV after dark adaptation should be explored with younger observers.

Finally, the contribution of fluorescence by one or more of the ocular media should be more carefully addressed. There is one simple way of examining this with the current equipment. Viewed peripherally, does the penumbra around the point of light stay with the source, or stay on the optical axis? If it stays with the source, this would imply that it is truly caused by chromatic aberration; if it appears to stay on the optical axis then it may well be fluorescence. This was performed with one subject who saw that the penumbra stayed with the stimulus (i.e., both were visible with peripheral vision). There was no sensation of light where the subject was looking (approximately 10° to the right of the stimulus). This obviously does not answer the question entirely, but does suggest that fluorescence is likely not the cause of the penumbra appearing around the UV stimulus.

REFERENCES

Anderson, R. M. (1983). Visual perceptions and observations of an aphakic surgeon. *Percept Motor Skills, 57*(3f), 1211-1218.

Bachem, A. (1953). The Color of Ultraviolet Light. *Amer J of Psych, 66*(2), 251-260.

Bando, M., Ishii, Y., & Nakajima, A. (1976). Changes in blue fluorescence intensity and coloration of human lens protein with normal lens aging and nuclear cataract. *Ophthal Res, 8*(6), 456-463.

Bando, M., Nakajima, A., & Satoh, K. (1981) Spectrophotometric estimation of 3-OH L-Kynurenin O-β-Glucoside in the human lens. *J Biochem, 89*(1), 103-109.

Bennett, A. T. D., Cuthill, I.C., Partridge, J.C., & Maier, E.J. (1996). Ultraviolet vision and mate choice in zebra finches. *Nature, 380*, 433-435.

Bertholf, L. M. (1931). The distribution of stimulative efficiency in the ultraviolet spectrum for the honeybee. *J Agricult Res, 43*, 703-713.

Bertholf, L. M. (1932). The extent of the spectrum for Drosophila and the distribution of stimulative efficiency in it. *Zeitschrift für vergleichende Physiologie, 18*(1), 32-64.

Boettner, E. A. & Wolter, J. R. (1962). Transmission of the ocular media. *Invest Ophthalmol Vis Sci, 1*(6), 776-783.

Brainard, G. C., Barker, F. M., Hoffman, R. J., Stetson, M. H., Hanifin, J. P., Podolin, P. L., & Rollag, M. D. (1994). Ultraviolet regulation of neuroendocrine and circadian physiology in rodents. *Vis Res, 34*(11), 1521-1533.

Cheng, H.-M. & Chylack, L. T. (1980). Thiol oxidation in the crystalline lens. 1. The rate-limiting role of hexokinase in aging rat and human lenses. *Invest Ophthalmol Vis Sci, 19*(5), 522-528.

Cooper, G. F. & Robson, J. G. (1969a). The yellow colour of the lens of the grey squirrel (*Sciurus Carolinensis leucotis*). *J Physiol, 203,* 403-410.

Cooper, G. F. & Robson, J. G. (1969b). The yellow color of the lens of man and other primates. *J Physiol, 203*, 411-417.

de Groot, W. (1934). Seeing in the ultra-violet. *Nature Letters, 134*(3387), 494.

Deller, J. F. P., O'connor, A. D., & Sorsby, A. (1947). X-ray measurement of the diameters of the living eye. *Proc Royal Soc London. Series B, Biological Sciences*, 456-467.

Delori, F. C., Dorey, C. K., Staurenghi, G., Arend, O., Goger, D. G., & Weiter, J. J. (1995). In vivo fluorescence of the ocular fundus exhibits retinal pigment epithelium lipofuscin characteristics. *IOVS, 36*(3), 718-729.

Deutschlander, M. E. & Phillips, J. B. (1995). Characterization of an ultraviolet photoreception mechanism in the retina of an amphibian, the axolotl (*Ambystoma mexicanum*). *Neurosci Let, 197*(2), 93-96.

Diffey, B. L. (1991). Solar ultraviolet radiation effects on biological systems. *Phys Med Biol, 36*(3), 299-328.

Dillon, J., Zheng, L., Merriam, J. C., & Galliard, E. R. (2000). Transmission spectra of light to the mammalian retina. *Photochem Photobiol, 71*(2), 225-229.

Douglas, R. H. (1989). The spectral transmission of the lens and cornea of the brown trout (*Salmo trutta*) and goldfish (*Carassius aurataus*) – effect of age and implications for ultraviolet vision. *Vis Res, 29*(7), 861-869.

Douglas, R. H. & Jeffery, G. (2014). The spectral transmission of ocular media suggests ultraviolet sensitivity is widespread among mammals. *Proc R Soc B: Bio Sci, 281*(1780), 20132995.

Edrich, W. (1979). Honey bees: Photoreceptors participating in orientation behaviour to light and gravity. *J Comp Phys, 133*(2), 111-116.

Eldred, G. E., Miller, G. V., Stark, W. S., & Feeney-Burns, L. (1982). Lipofuscin: resolution of discrepant fluorescence data. *Science, 216*(4547), 757-759.

Emmerton, J. (1983). Pattern discrimination in the ultraviolet by pigeons. *Percept Psychophys, 34*(6), 555-559.

Gaillard, E. R., Merriam, J., Zeng, L., & Dillon, J. (2011). Transmission of light to the young primate retina: possible implications for the formation of lipofuscin. *Photochem Photobio, 87*, 18-21.

Gaillard, E. R., Zheng, L., Merriam, J. C., & Dillon, J. (2000). Age-related changes in the absorption characteristics of the primate lens. *Invest Ophthalmol Vis Sci, 41*(6), 1454-1459.

Gaydon, A. G. (1938). Color sensations produced by ultra-violet light. *Proc Phys Soc, 50*(5), 714.

Goldsmith, T. H. (1980). Hummingbirds see near ultraviolet light. *Science, 207*(4432), 786-788.

Goodeve, C. F. (1934). Vision in the ultra-violet. *Nature Letters, 134*, 416-417.

Goodeve, C. F. (1936). Relative luminosity in the extreme red. *Proc Royal Soc London A: Math, Phys, Eng Sci, 155*(886), 664-683.

Goodeve, C. F., Lythgoe, R. J., & Schneider, E. E. (1942). The photosensitivity of visual purple solutions and the scotopic sensitivity of the eye in the ultra-violet. *Proc R Soc Lon. S B-Biol Sci,130*(861), 380-395.

Graham, W. P. (1922). The absorption of the eye for ultraviolet radiation. *JOSA*, *6*(6), 605-609.

Griswold, M. S. & Stark, W. S. (1992). Scotopic sensitivity of phakic and aphakic observers extending into the near ultraviolet. *Vis Res, 32*(9), 1739-1743.

Haegerstrom-Portnoy, G. (1988). Short-wavelength-sensitive-cone sensitivity loss with aging: a protective role for macular pigment?. *JOSA A*, *5*(12), 2140-2144.

Hammond, B. R., Johnson, B. A., & George, E. R. (2014). Oxidative photodegradation of ocular tissues: beneficial effects of filtering and exogenous antioxidants. *Exp Eye Res, 129*, 135-150.

Hartman, E. E. & Banks, M. S. (1992). Temporal contrast sensitivity in human infants. *Vis Res,32*(6), 1163-1168.

Herschel, J. F. (1840). On the chemical action of the rays of the solar spectrum on preparations of silver and other substances, both metallic and non-metallic, and on some photographic processes. *Philosophical Transactions of the Royal Society of London*, 1-59.

Hulburt, E. O. (1928). The Intensities of the Lines in the Spectrum of Mercury. *Physical Review, 32*(4), 593-600.

Jacobs, G. H. (1992). Ultraviolet vision in vertebrates. *Amer Zool, 32*, 544-554.

Jacobs, G. H., & Deegan, J. F. (1994). Sensitivity to ultraviolet light in the gerbil (Meriones unguiculatus): characteristics and mechanisms. *Vis Res, 34*(11), 1433-1441.

Jacobs, G. H., Neitz, J., & Deegan, J.F. (1991). Retinal receptors in rodents maximally sensitive to ultraviolet light. *Nature Letters, 353*, 655-656.

Kamei, A. (1993). Glutathione levels of the human crystalline lens in aging and its antioxidant effect against the oxidation of lens proteins. *Biol Pharm Bull*, *16*(9), 870-875.

Kinsey, V. E. (1948). Spectral transmission of the eye to ultraviolet radiations. *Arch Ophthalmol, 39*(4), 508-513.

Klugh, A. B. (1925). Review: Flower-visiting insects and the reflection of ultraviolet by flowers. *Ecol Soc Amer*, *6*(2), 179-181.

Lerman, S. (1984). Biophysical aspects of corneal and lenticular transparency. *Curr Eye Res, 3*(1), 3-14.

Lerman, S. (1986). In vivo and in vitro biophysical studies on human cataractogenesis. *Lens Res, 3*(1-2), 137-160.

Lerman, S. & Borkman, R. (1976). Spectroscopic evaluation and classification of the normal, aging, and cataractous lens. *Ophthalmol Res, 8*, 335-353.

Lipetz, L. E. (1955). The x ray and radium phosphenes. *British J Ophthal, 39*(10), 577.

Luckiesh, M., & Moss, F. K. (1937). science of seeing. New York, NY: D. Van Nostrand Company, Inc.

Ludvigh, E. & McCarthy, E. F. (1938). Absorption of the visible light by the refractive media of the human eye. *Arch Ophthalmol, 20*(1), 37-51.

Mecherikunnel, A. T. & Richmond, J. (1980). Spectral distribution of solar radiation. (NASA Technical Memorandum No. 82021). Greenbelt, MD: US.

Mellerio, J. (1971). Light absorption and scatter in the human lens. *Vis Res, 11*, 129-141.

Mellerio. J. (1987). Yellowing of the human lens: nuclear and cortical contributions. *Vis Res, 27*(9), 1581-1587.

Mollon, J. D. (1989). "Tho’ she kneel’d in that place where they grew...”: The uses and origins of primate color vision. *J Exp Bio, 146*, 21-38.

Norren, D. V. & Vos, J. J. (1974). Spectral transmission of the human ocular media. *Vis Res, 14,* 1237-1244.

Norval, M. Cullen, A. P., de Gruijl, F. R., Longstreth, J., Takizawa, Y., Lucas, R. M., Noonan, F. P., & van der Leun, J. C. (2007). The effects on human health from stratospheric ozone depletion and its interactions with climate change. *Photochem Photobiol Sci, 6*, 232-251.

Nutting, P. G. (1912). Outlines of applied optics. P. Blakiston's son & Company.

Pinksy, L. S., Osborne, W. Z., Hoffman, R. A., & Bailey, J.V. (1975). Light flashes observed by astronauts on Skylab 4, *Science,188,* 928-930.

Richards, A. A. (2001). Alien Vision: Exploring the Electromagnetic Spectrum with Imaging Technology. SPIE Press Monograph Vol. PM104.

Rushton, R. H. (1938). The clinical measurement of the axial length of the living eye. *Trans Ophthalmol Soc UK, 58*(1), 36-142.

Said, F. S. & Weale, R. A. (1959). The variation with age of the spectral transmissivity of the living human crystalline lens. *Gerontologica, 3*, 213-231.

Sample, P. A., Esterson, F. D., Weinreb, R. N., & Boynton, R. M. (1988). The aging lens: in vivo assessment of light absorption in 84 human eyes. *IOVS, 29*(8), 1306-1311.

Saidman, J. (1933). Sur la visibilité de l’ultraviolet jusqu’à la longuer de l’onde 3130 A [313 nm]. *CR Hebd Séances Acad Sci, 196*, 1537-1539.

Saint, S. H. (2014). Investigating the development of infant temporal processing speed via critical flicker fusion. (Master’s thesis, University of Georgia).

Siegel, G. H. (1974). Ultraviolet spectra of silicate glasses: a review of some experimental evidence. *J Non-Crystalline Solids, 13*(3), 372-398.

Sivak, J.G. (1979). Accommodation in vertebrates: a contemporary survey. *Curr Top in Eye Res, 3,* 281-330.

Sliney, D. H., Wangemann, R. T., Franks, J. K., & Wolbarsht, M. L. (1976). Visual sensitivity of the eye to infrared laser radiation. *JOSA, 66*(4), 339-341.

Stark, W. S. (1987). Photopic sensitivities to ultraviolet and visible wavelengths and the effects of the macular pigments in human aphakic observers. *Curr Eye Res, 6*(4), 631-638.

Stark, W. S. & Tan, K. E. W. P. (1982). Ultraviolet light: photosensitivity and other effects on the visual system. *Photochem Photobiol, 36*(3), 371-380.

Stark, W. S., Wagner, R. H., Gillespie, C. M. (1994). Ultraviolet sensitivity of three cone types in the aphakic observer determined by chromatic adaptation. *Vis Res, 34*(11), 1457-1459.

Stokes, G. G. (1852). On the change of refrangibility of light. *Philosophical Transactions of the Royal Society of London, 142,* 463-562.

Tan, K. E. W. P. (1971). *Vision in the ultraviolet*. Drukkerij, Elinkwijk.

Tsukahara, N., Tani, Y., Kikuchi, H., & Sugita, S. (2014). Light transmission of the ocular media in birds and mammals. *J Vet Med Sci, 76*(1), 93-95.

van den Berg, T. J. & Spekreijse, H. (1997) Near infrared light absorption in the human eye media. *Vis Res, 37*(2), 249-253.

van Heyningen, R. (1971). Fluorescent glucoside in the human lens. *Nature Letters, 230,* 393-394.

Ventura, D. F., Zana, Y., de Souza, J. M., & DeVoe, R. D. (2001).Ultraviolet colour opponency in the turtle retina. *J Exp Bio, 204,* 2527-2534.

Viitala, J., Korpimäki, E., Palokangas, P., & Koivula, M. (1995). Attraction of kestrels to vole scent marks visible in ultraviolet light. *Nature*, *373*(6513), 425-427.

von Frisch, K. (1967). The dance language and orientation of bees. Cambridge, MA: Harvard University Press.

von Helmholtz, H. (1855). Über die zusammensetzung von spectralfarben. *Annalen der Physik, 170*(1), 1-28.

Wald, G. (1945). Human vision and the spectrum. *Science, 101*(2635), 653-658.

Wald, G. (1952). Alleged effects of the near ultraviolet on human vision. *J Opt Soc Am, 42*(3), 171-177.

Walls, G. L. (1942). *The vertebrate eye and its adaptive radiation.* Oxford, England: Cranbrook Institute of Science.

Weale, R. A. (1985). The post-mortem preservation of the transmissivity of the human crystalline lens. *Exp Eye Res, 41*(5), 655-659.

Weale, R. A. (1988). Age and the transmittance of the human crystalline lens. *J Physiol, 395*, 577-587.

Weale, R. A. (2009). The effects of the ageing lens on vision. In The Human Lens—in Relation to Cataract, Ciba Foundation Symposium (Vol. 19, pp. 5-24).

Williams, T. T. (1982). Ultraviolet sensitivity in aphakia and pseudoaphakia. (Doctoral dissertation, Concordia University).

Winter, Y., López, J., & von Helversen, O. (2003). Ultraviolet vision in a bat. *Nature Letters, 425*, 612-615.

Wolf, E. (1946). Effects of exposure to ultra-violet light on human dark adaptation. *Physiol,32,* 219-226.

Wood, A. M. & Truscott, R. J. W. (1993). UV filters in human lenses: tryptophan catabolism. *Exp Eye Res, 56,* 317-325.

Wooten, B. R., Hammond, B. R., & Renzi, L. M. (2007). Using scotopic and photopic flicker to measure lens optical density. *Opthal Physiol Opt, 27*, 321-328.

Wright, W. (1949). VII.-The visual sensitivity of normal and aphakic observers in the ultra-violet. *L'année psychologique*, *50*(1), 169-177.

Wyszecki, G., & Stiles, W. S. (1982). Color science: Concepts and methods, quantitative data and formulae. (2nd ed.). New York, NY: John Wiley & Sons.

Table 1. Studies reporting primate *ex vivo* lens transmission in the UV (380 nm and below)

Study	**Subjects**		**Wavelengths Tested (nm)**	**Transmission Window or Peak**	**Percent Transmission at Peak**	
	N	Age				
Boettner & Wolter, 1962	9 humans	4 wks – 75 years	200 – 2000	Centered at 320 nm	Under 5 years: 8%	
					22 years: 0.1%	
Cooper & Robson, 1969	21 humans	Stillborn – 87 years	300 – 600	Absorption minimum at ~320 nm	Neonate: 2%*	
					18 years: 0.5%*	
Galliard, et al (2000)	2 rhesus macaques	2 years & 12 years	200 – 700	Absorption minimum at ~320 nm	2 years: 1%	
					12 years: 0.5%	
	2 humans	48 years and 78 years			Not reported	
Gaillard, et al (2011)	2 rhesus macaques	128 days gestation & 160 days gestation	300 – 600	Band from 320 – 330 nm	3%*	
	4 rhesus macaques	5 – 20 years	310 – 340	Centered at 320 nm	5 years: 2.75%*	
					8 years: 0.6%*	
					12 years: 0.3%*	
					20 years: 0.0%*	
Graham, 1922	4 humans	4 months, 20 years†, and 2 unspecified cataract patients	Absorption and emission spectra for a cadmium spark	Infant lens transmits down to approximately 313.4 nm	Unknown	
				Adult lenses transmit to 340.4 nm and 441.5 nm		
Lerman & Borkman, 1976	6 humans	6 months – 82 years	200 – 800	Report cumulative transmission values from 300 – 400 nm	6 months: 85%	
					8 years: 75%	
					25-82 years: 20%	
cited in Lerman, 1986	9 humans	3 days – 82 years	275 – 750	Not mentioned	At ~325 nm	3 days: 82%*
						6 months: 77.5%*
						8 years: 75%*
						13 years: 38%*

						17 years: 25%*
						25+ years: 2%*
Schanz, 1913 (cited in Graham, 1922)	3 humans	"Child", 28 years, and 40 years	300 to at least 360	Unknown	Complete absorption for wavelengths shorter than 350 nm	
Weale, 1988	24 humans	0 – 85 years	327 – 700	330 nm	13-year-old: 63%*	
					63-year-old: 0.63%*	

*Percentages are approximate and are derived from published graphs

†Subject not included in analysis due to abnormalities in the eye

Table 2. Subject demographics split by decade of life.

Age Range	**Mean Age (SD)**	**Number**	**Females**
4-10	7.5 (2.3)	6	3
11-20	14.2 (2.5)	15	6
21-30	25.9 (3.2)	8	6
31-40	35 (2.9)	7	4
41-50	43.5 (0.7)	2	1
51-60	54.0 (4.2)	2	1

Table 3. Studies which have tested UV detection in phakic human observers.

Study	**Subjects**		**Stimulus Generation**	**Wavelengths Tested (nm)***	**Results**
	N	**Age Range**			
Bachem, 1953	Unknown	“Approximately 20 years” and aphakics of “advanced age”	Quartz mercury arc lamp filtered through a noviol glass	302 – 405	All subjects could detect down to 312.5 and described it as a desaturated blue
de Groot, 1934	21	25 – 50 years	Quartz discharge tubes containing either high-pressure mercury or low-pressure cadmium and zinc	307.6 – 404.7	1 subject couldn’t see line at 365 nm
					3 subjects couldn’t see line at 313 nm
					No subjects could see line at 307.6 nm
Goodeve, 1934	9	Unknown	Müller-Hillger universal monochromator with a mercury light source	253.6 – 404.7	312.5 seen by all and produced a similar sensation as 404.7
Saidman, 1933	102	“Sick children”, doctors, and medical students	Mercury vapor lamp with a specialized container with various metal oxides	302 – 365	All subjects younger than 33 saw the 313 nm line
					Visibility for the 313 nm line disappears between the ages of 34 – 43
					No subject between 43 and 73 saw the 313 nm line

*Most of these were tested in discrete steps determined by the emission spectra of the element used; for the present purposes, a range is sufficient

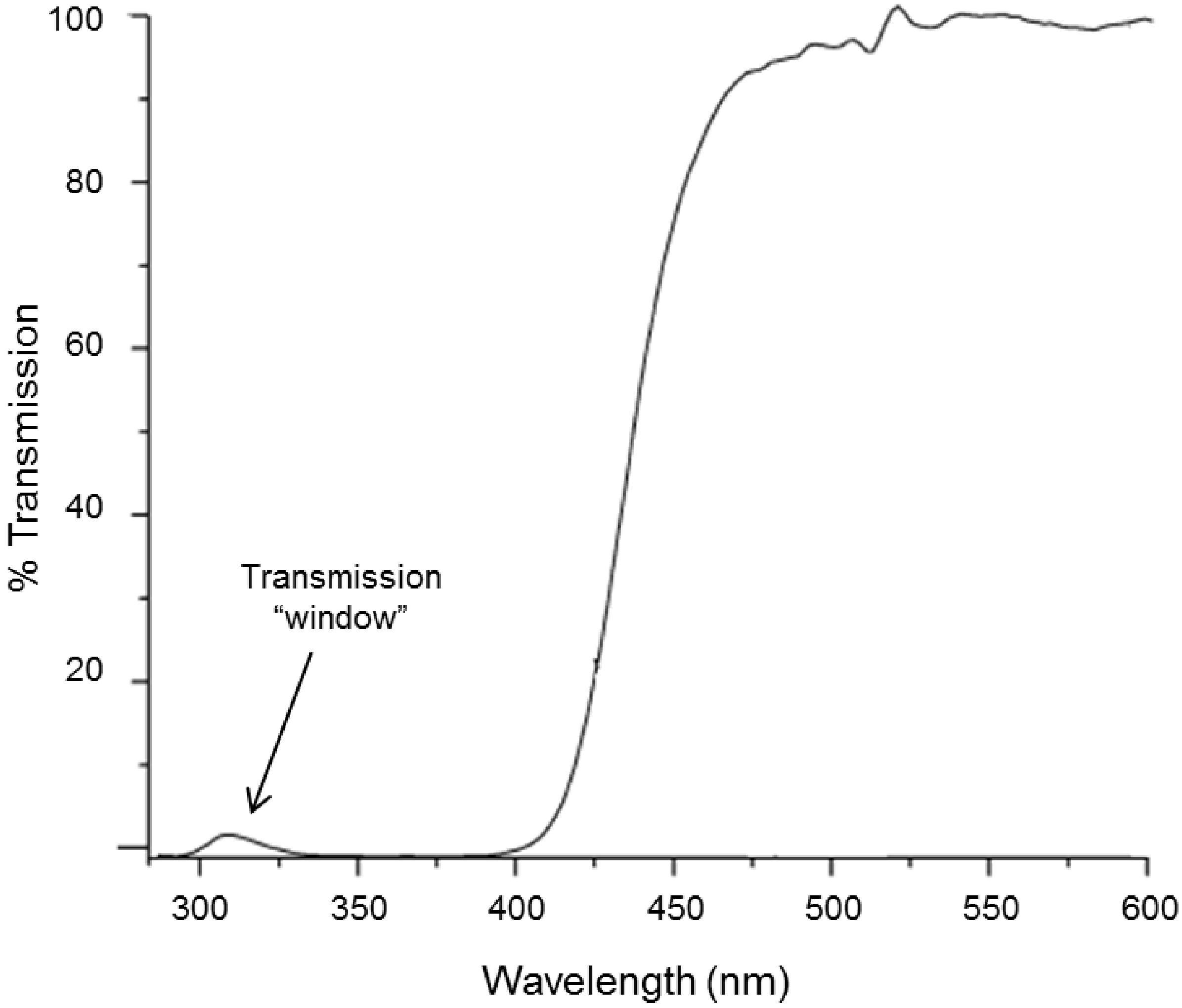

Figure 1. The *ex vivo* transmission spectrum of the neonatal primate lens, including the transmission window at 320 nm (derived from Galliard, et al 2011).

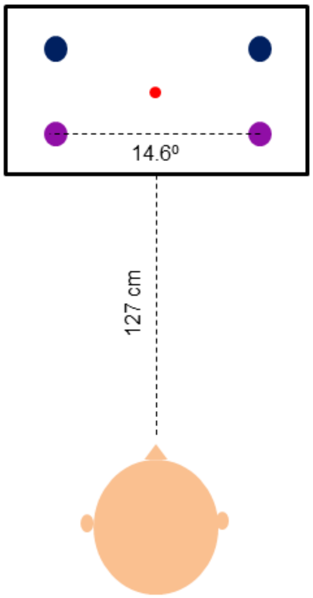

Figure 2. Schematic of novel tabletop device to assess UV detection.

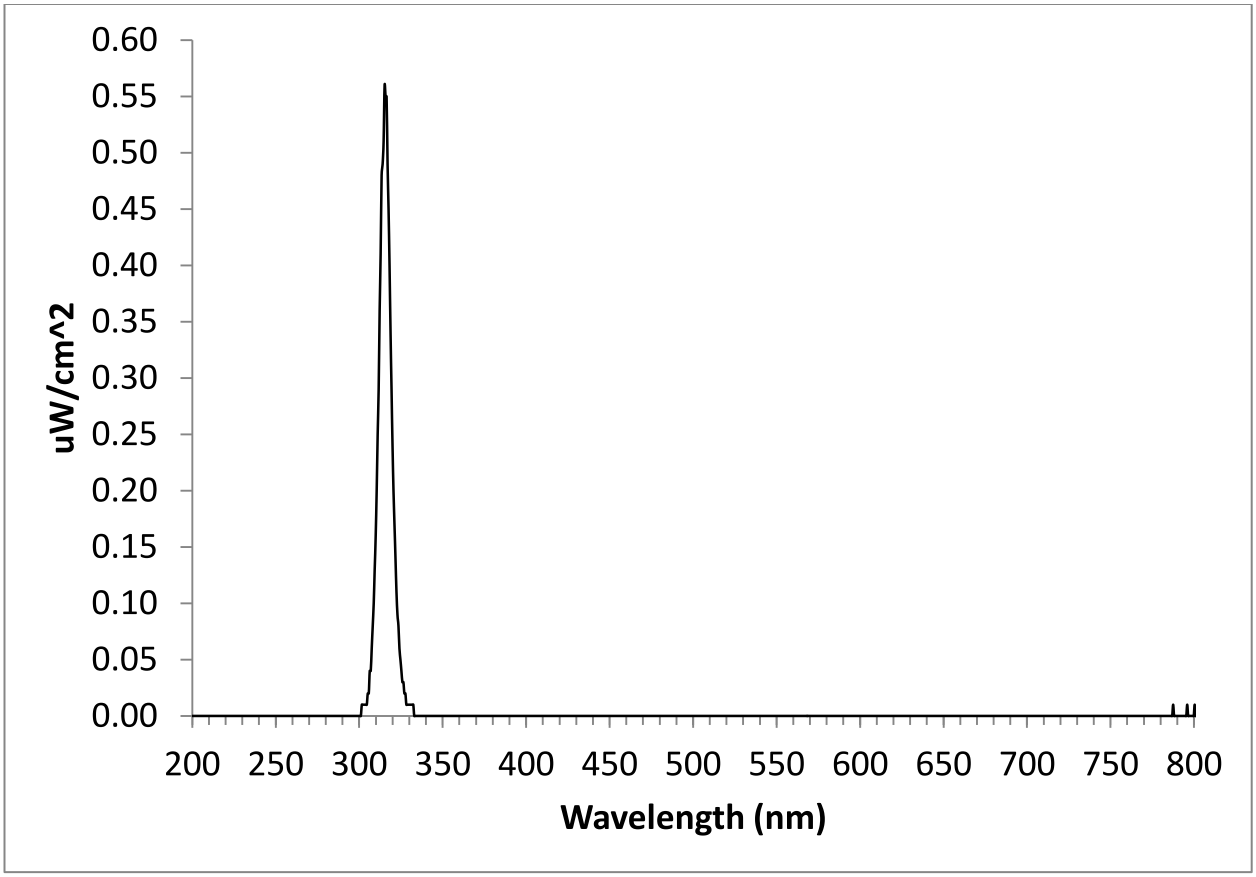

Figure 3. The emittance spectrum of the ultraviolet LEDs with 310 nm bandpass filter.

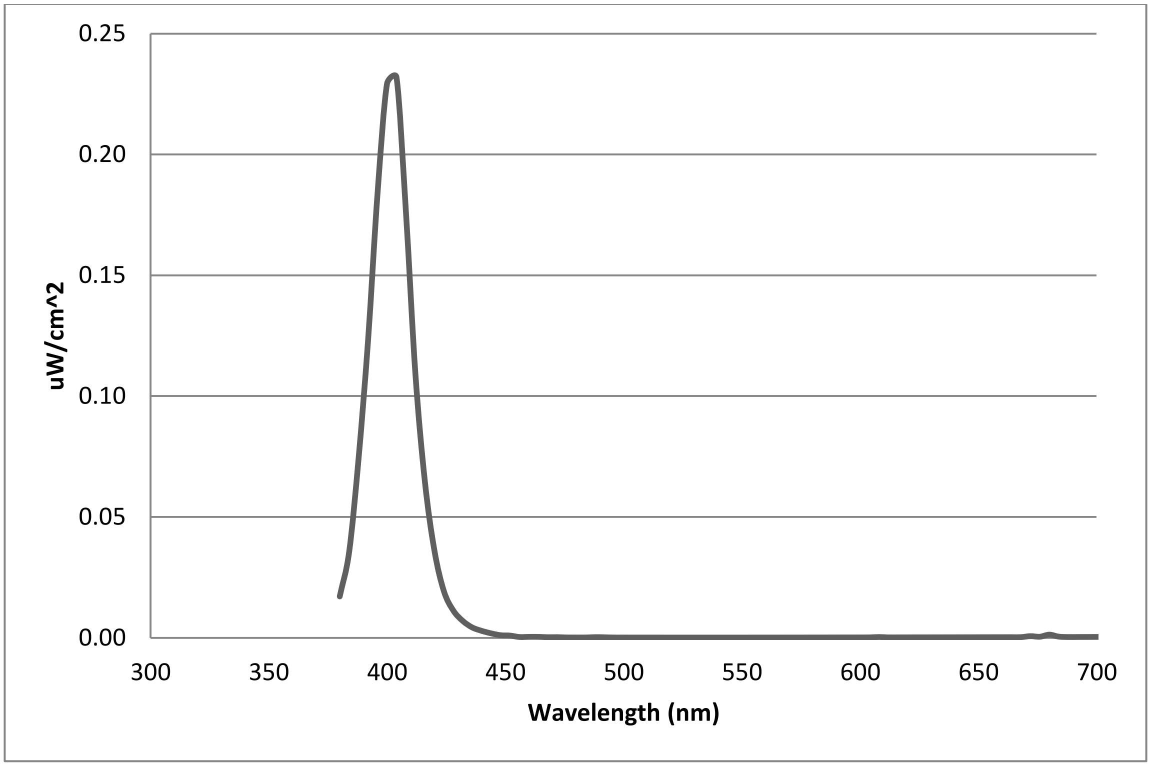

Figure 4. The emittance spectrum of the visible short wavelength LEDs.

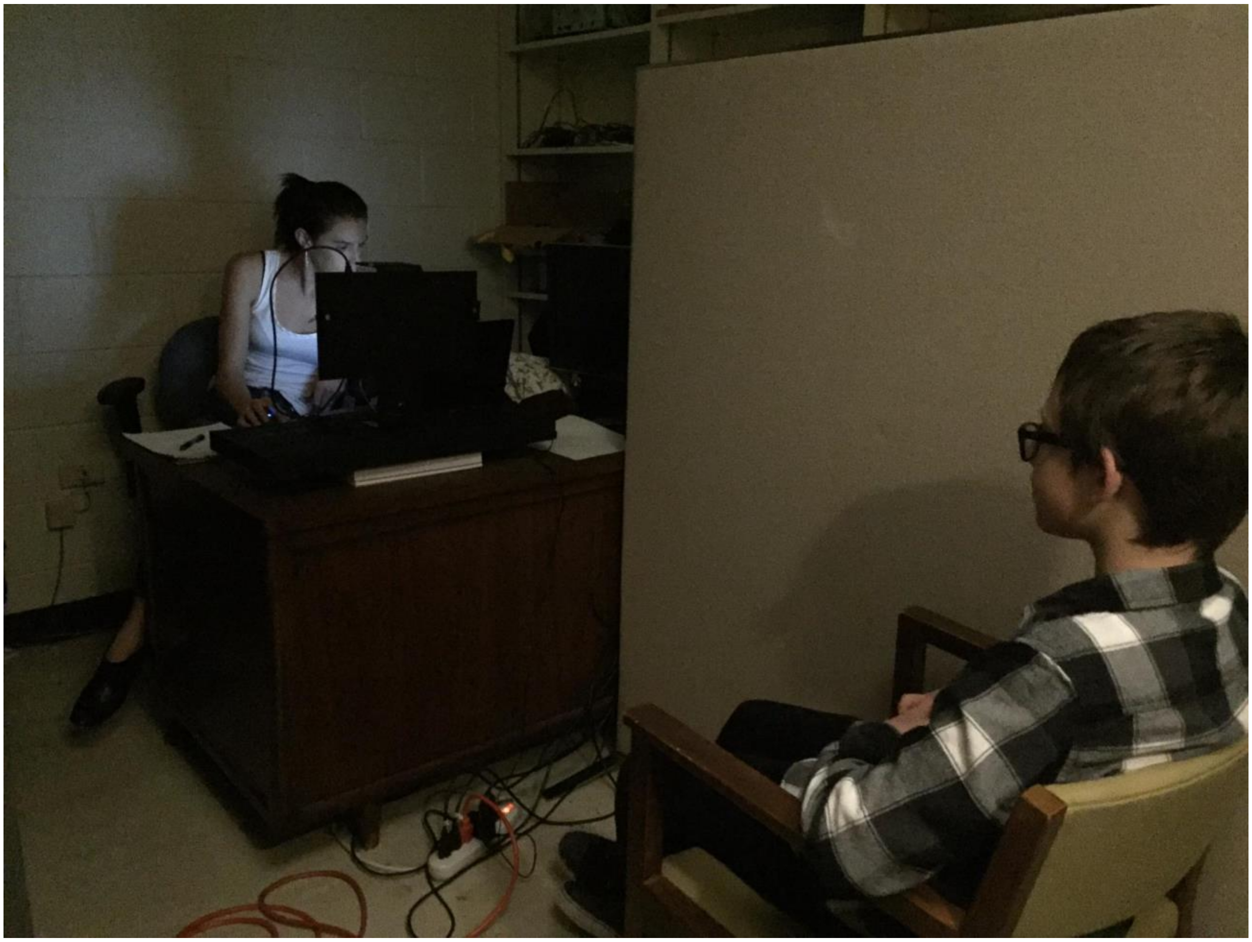

Figure 5. Photograph of a testing session.

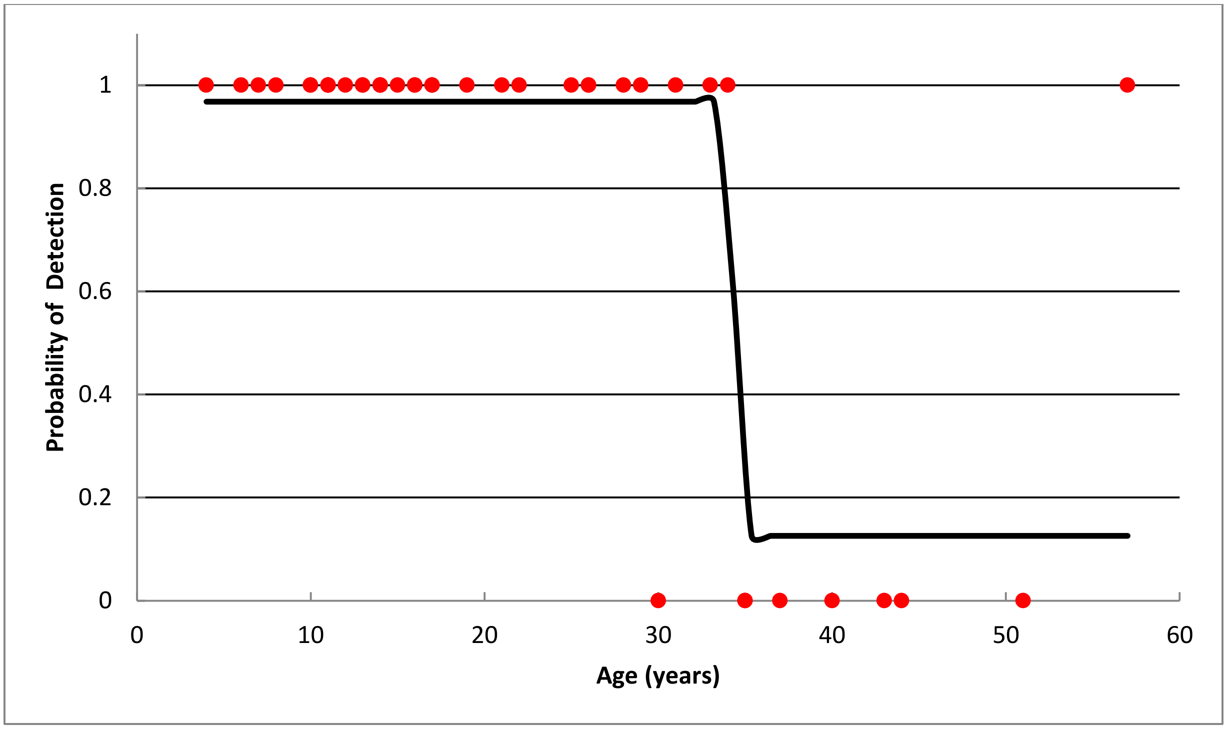

Figure 6. The relationship between UV detection and age.

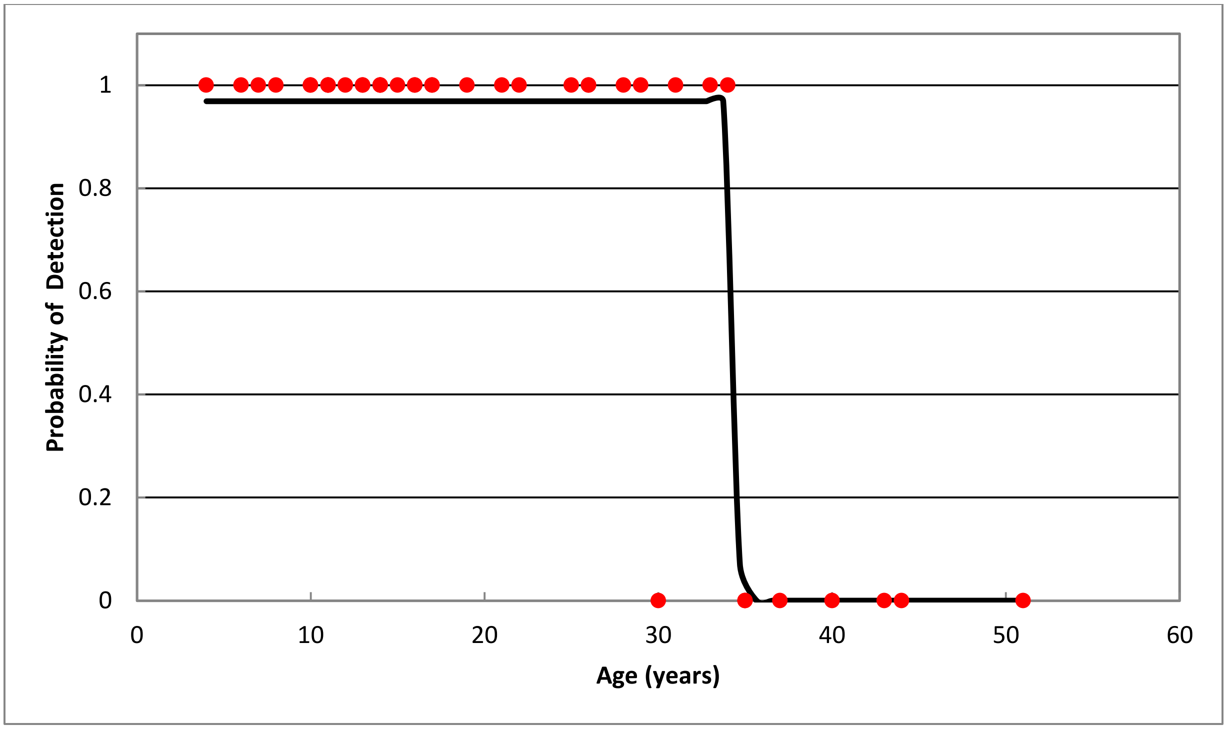

Figure 7. The relationship between UV detection and age (outlier removed).

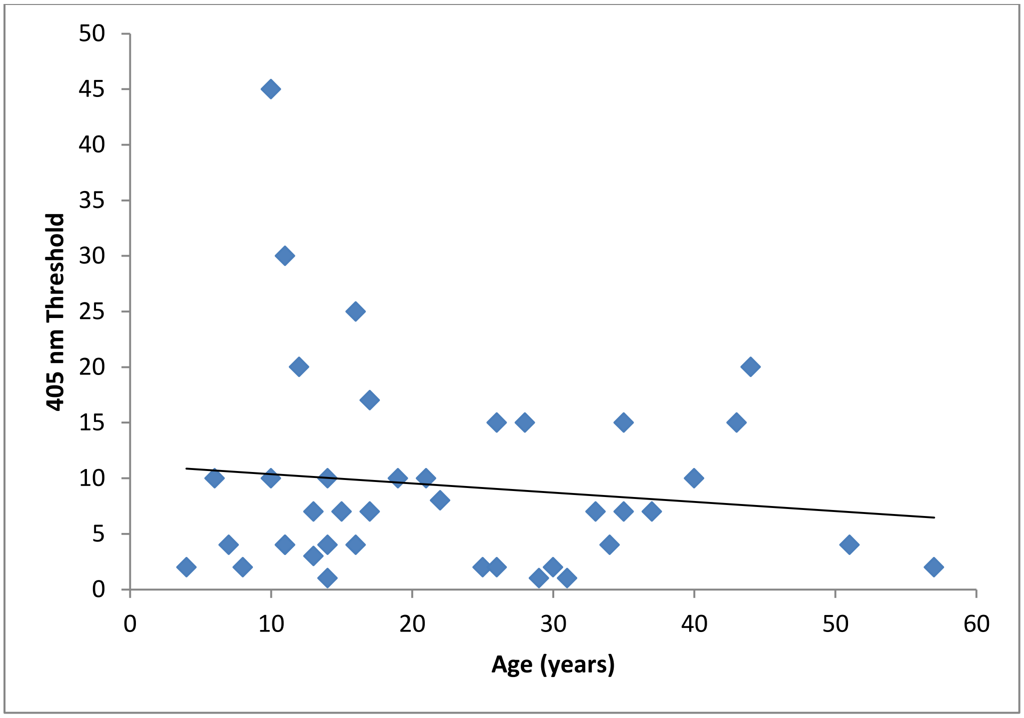

Figure 8. The relationship between age and threshold for the 405 nm stimulus.

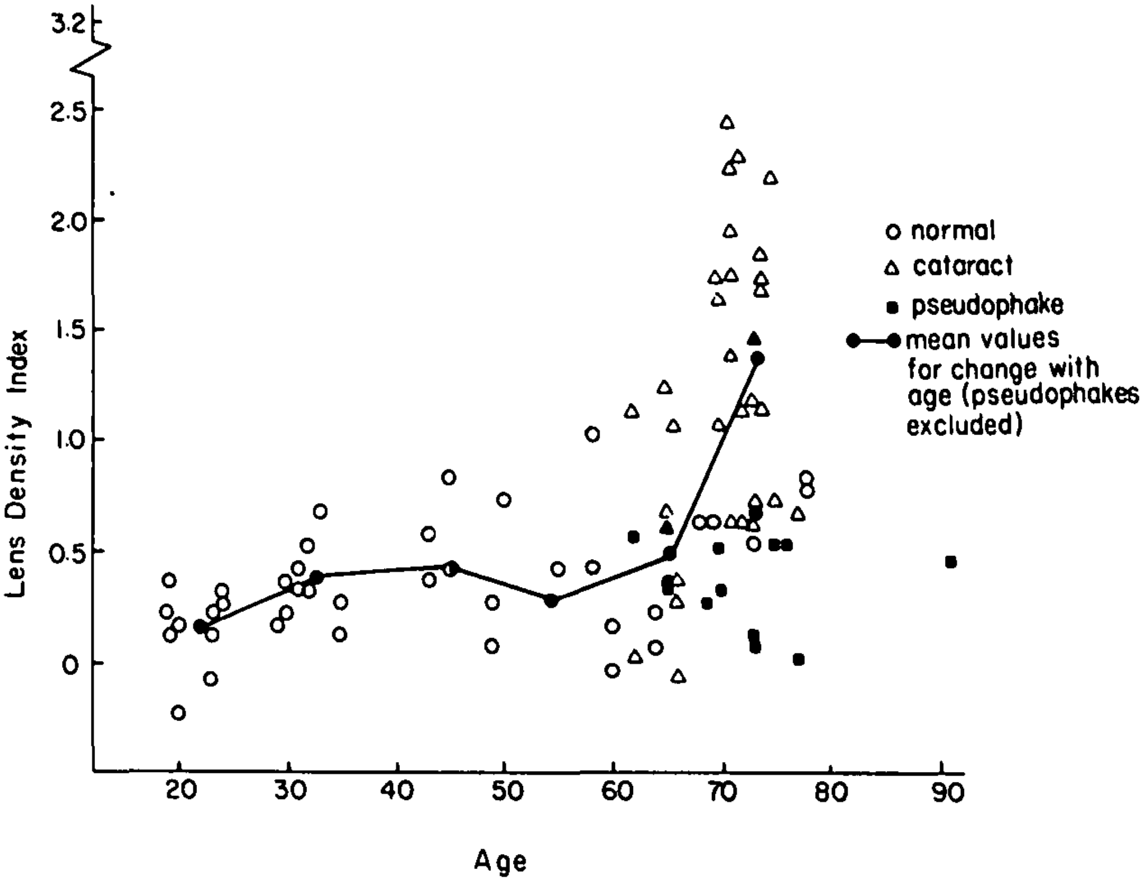

Figure 9. Lens density index as a function of age (reproduced from Sample, et al., 1988).

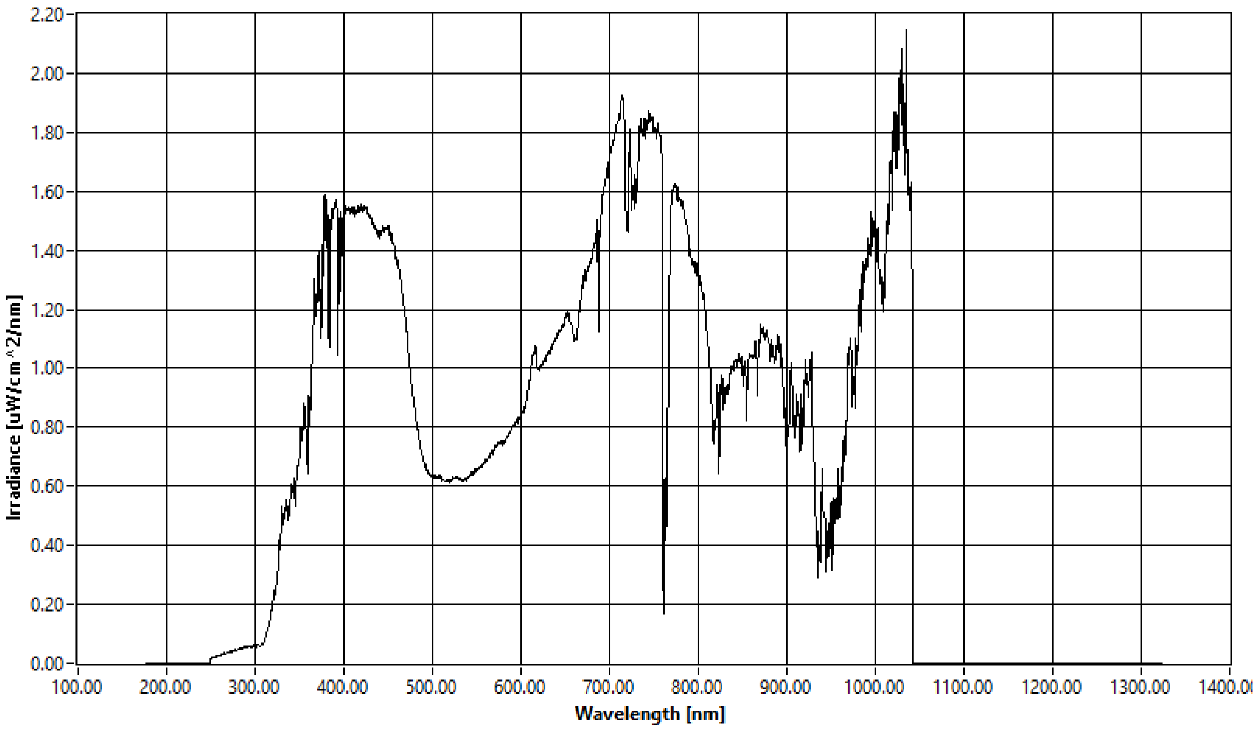

Figure 10. Spectral content of sunlight (4 p.m. on an overcast day in southern California through an open 30° NNE facing window).