THE EFFECT OF MACULAR PIGMENT OPTICAL DENSITY ON RESOLUTION ACUITY AND HYPERACUITY IN YOUNG SUBJECTS

by

MICHAEL P. ENGLES

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

ABSTRACT

Schültze (1866) proposed that macular pigment (MP) serves to improve acuity by reducing the deleterious effects of chromatic aberration. Although proposed well over a century ago, the hypothesis has never been tested. We chose to begin evaluating the Acuity Hypothesis by measuring MP levels and acuity and hyperacuity in the same observers. In the two experiments, the Acuity Hypothesis was not supported as tested by our stimulus configuration. Acuity could be related to MP density via a protective mechanism but older subjects showing loss would need to be tested to address this possibility. A novel finding, however, as shown by the difference in thresholds in the hyperacuity task, indicates that hyperacuity processing may be facilitated by chromatic content.

INDEX WORDS: macular pigment, resolution, hyperacuity, Acuity Hypothesis

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MICHAEL P. ENGLES

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MICHAEL P. ENGLES

Major Professor:	Billy R. Hammond Jr.
Committee:	James M. Brown Ronald A. Schuchard

Electronic Version Approved:

Maureen Grasso
Dean of the Graduate School
The University of Georgia
May 2005

DEDICATION

When dedicating a document, the writer will typically choose the person or persons closest and most influential in their lives. I wish to continue this age-old tradition by making mention of the two most important individuals in my life. It is impossible to imagine how I could have accomplished anything without them. They have supported me through those difficult days, and the long and laborious nights. They have provided me the strength and endurance to pursue excellence and great achievement. Mr. Coffee®, and Dr. Pepper®. Thanks guys.

Seriously though, I would like to dedicate this thesis to my parents who really have supported me my whole life, and to my brother, who always stood by me. Thank you for believing that I could achieve so much. Special thanks to my mother, who *perpetually* reminded me to do my homework, run those important errands, ask [someone] about the [something], eat, pay my bills, and most importantly to get out and to have some fun. Special thanks also to my father, who gave me critical advice and who helped me find the motivation within myself to achieve more.

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CHAPTER 1

INTRODUCTION

Overview

The macular pigment (MP) is a yellowish blue-absorbing chromophore within the retina composed of the carotenoids lutein (L) and zeaxanthin (Z) and can be found in some primates, including humans. Although L and Z exist in trace amounts throughout the entire eye, they are primarily concentrated in the central fovea anterior to the cones. Before reaching the receptors, light must pass through the MP. Consequently, it screens out a significant amount of short-wave (SW) energy. Variation in peak absorbance (460nm) among individuals can be quite large ranging from nearly 0.0 up to 1.5 log units.

Several important functions for MP have been proposed. For example, the Protection Hypothesis posits that MP serves to protect the retina. This can be accomplished by two independent and non-exclusive mechanisms. For example, MP passively absorbs actinic SW light prior to reaching the delicate cones, which are responsible for producing the highest visual acuity. Additionally, MP may protect the retinal tissues by actively quenching highly reactive free radicals and reactive oxygen species generated by metabolic activity. These reactive species damage retinal tissue and contribute heavily to the onset of degenerative diseases such as age-related macular degeneration, the most common form of blindness in the world. Another functional hypothesis, proposed nearly 140 years ago, the Acuity Hypothesis posits that MP may serve to improve acuity by absorbing poorly focused SW light that results from the eye's chromatic aberration.

Although feasible, this latter hypothesis has never been directly tested. This was the goal of the current study. To address this goal, MP was measured in a group of young healthy adults and the relation to acuity was evaluated. Two types of acuity were assessed: resolution acuity and positional hyperacuity. These measures of spatial vision were made under different spectral conditions: a "white" light condition which contained significant portions of SW-light and therefore would be expected to be influenced by the optical filtering of MP, and a "yellow" light condition which contained no SW-light and therefore is unaffected by MP absorbance.

Brief History

The first mentions of MP coincided with the discovery of the foveal pit made more than two hundred years ago by Soemmering (1795). This initial identification was later confirmed by Home (1798). At this time, the fovea was thought to be a lymphatic vessel and the pigment to be a post-mortem artifact. Whereas the function of the fovea quickly became clear, the ensuing debate as to whether the MP was a post-mortem artifact or a feature of the living retina persisted. In 1851, Herman von Helmholtz invented the ophthalmoscope, effectively allowing one to view and diagram the retina *in vivo* (Sherman, 1989). Despite this technological advancement, the debate intensified. As Nussbaum *et al* (1981) points out, this was most likely due to the diverse sources of illumination for various ophthalmoscopes in use at the time. Those who were using lamps that emitted SW light could more easily identify the existence of the pigment; whereas those who were using lamps producing mainly longer-wave light found it difficult, if not impossible to verify this feature. Consequently, this controversy continued until the mid 20th century when more advanced ophthalmoscopic techniques were developed and the appropriate lighting conditions could be generated to view the MP reliably.

In an early experiment, Schültze (1866) was the first to note the strong absorption of blue light by placing colored glass over extracted macular samples and viewing them through a microscope. These preliminary findings were later corroborated by Hering (1885), who although expanding on Schültze's analysis using a color matching technique, also noted a weak absorption of mid-wave, but not of long-wave light. Wald (1945) psychophysically measured foveal and peripheral spectral sensitivity functions in human subjects and was able to derive a rough spectral profile of the MP. These visual estimates demonstrated a peak absorbance between 430nm – 490nm, a modest absorption at 400nm, and a minimal absorption beyond 550nm (see Figures 1 & 2).

The Macular Pigment

Wald (1945) identified MP to be composed of a xanthophyllic carotenoid such as L, given that their spectral characteristics closely parallel. Bone *et al* (1985), using extracted retinas and a chemical identification technique known as high performance liquid chromatography (HPLC), identified the specific composition of MP to be that of the dietary derived carotenoids L and Z. These findings were then replicated by Handelmann *et al* (1988), thus firmly establishing the composition of MP to be of the two carotenoids L and Z.

Although carotenoids exist in all tissues of the eye (Bernstein *et al*, 2001), they are only optically dense in the macular region of the retina (Snodderly, 1995; Hammond *et al*, 1997a). Investigations regarding the spatial distribution of MP have revealed that it is most dense at its center and declines in concentration symmetrically and exponentially with eccentricity until reaching negligible quantities after 5° (Snodderly *et al*, 1984a,b; Hammond *et al*, 1997a,b). MP is located in the Henle layer between the receptor fiber layer and the inner plexiform layer

(Schültze, 1866; Snodderly *et al*, 1984a,b) and positioned centrally around the macular cup (for a complete review of the anatomy see Snodderly, 1995; see also Figures 1a & 1b).

As noted earlier, MP is a yellowish blue-absorbing spot centrally located over the fovea (thus the common clinical designation, macula lutea or "yellow spot"). Precise measurement of the spectral profile has shown MP to exhibit a peak absorbance in the blue-green region (460nm) flanked by a sharp decline from 490nm to 550nm in the longer wavelengths, and a modest decline from 440nm to the ultra-violet in the shorter wavelengths (Ruddock, 1963; Wyszecki & Stiles, 1982; Snodderly, 1984a,b; Pease *et al*, 1987) (see Figure 2). The density and spatial profile of MP can vary quite widely, in some individuals reaching a maximum of 1.5 log optical density (OD) units, analogous to 3% transmission of light measured at 460nm, to nearly 0.0 log OD units, analogous to 100% transmission (Hammond, 1997a).

CHAPTER 2

THE ACUITY HYPOTHESIS

The Acuity Hypothesis

Nearly 140 years ago in the preliminary investigations documented in his 1866 publication regarding the properties of MP, Max Schültze theorized that MP might serve to improve visual functioning in broadband illumination by filtering the poorly focused and easily scattered portion of the visible spectrum (as translated from German in Werner *et al*, 1987). Termed the Acuity Hypothesis (Hammond *et al*, 2001), it predicts that MP serves to improve visual function by reducing the adverse effects of chromatic aberration (CA). This is accomplished by removing the SW portion of the visible spectrum. This hypothesis is the oldest and most widely accepted proposed function for MP (Werner *et al*, 1987; Walls & Judd, 1933). Often it is stated in text-books as the only function for MP. For example, the following two quotes have been provided as representative statements:

> "Surrounding the fovea is a region of the retina referred to as the macula lutea. The macula lutea contains nonphotosensitive yellow pigment, located in the inner retina. This pigment absorbs blue light (maximal absorption is in the region of 460nm) and may aid vision by reducing light scatter or minimizing the effects of chromatic aberration."
>
> De Valois RL, De Valois KK (1988) Spatial Vision

> "There are no short-wavelength cones in the primate fovea, and a collection of yellow pigment in the front of the fovea, the macula lutea, filters out short wavelengths. This reduces the effects of chromatic aberration due to stronger refraction of short wavelengths than of long wavelengths."
>
> Special Topics in Vision

Additionally, even in texts that include other functions of MP, reference is still made to it as an optical filter which serves to reduce the deleterious effects of chromatic aberration:

> "The pigment is thought to fulfill three roles. As a carotenoid it may facilitate the transfer of oxygen in a retinal area not supplied with a rich retinal vasculature system. In view of its absorption spectrum, it has been seen as a useful filter serving to reduce the untoward effects of chromatic aberration in a retinal region that might be sensitive to them. And, thirdly, it may form a protection against potential retinal damage from short-wavelength radiations. Despite powerful advocacy, the experimental evidence for the last is open to argument."
>
> Weale RA (1992) The Senescence of Human Vision

Chromatic Aberration

The Acuity Hypothesis is based on a well-known property of the wave nature of light and of optical systems, called chromatic aberration (CA). First described by Sir Isaac Newton in 1672, the constituent wavelengths of an incident white source are not all refracted at the same angle. More specifically, blue light (SW) was identified to be more strongly refracted than red light (longer wavelengths) (see Figure 3).

Modern understanding of CA allows one to discriminate between two types based upon their effects on the retinal image (Thibos *et al*, 1990). The first type is known as longitudinal CA, or the chromatic difference of focus, which states that the focal length of a lens is proportional to the wavelength of the light propagated through it (Newton, 1672; Wald & Griffin, 1947; Bedford & Wyszecki, 1957; Reading & Weale, 1974; Wyszecki & Stiles, 1982; Thibos *et al*, 1990; Wooten & Hammond, 2002). Given the spectral content of daylight and the peak photopic sensitivity value, the eye is typically emmetropic for mid-wave (550 nm) light. Consequently it is ametropic for all other wavelengths, that is, myopic for SW light and hyperopic for long-wave light (Gilmartin & Hogan, 1985; Howarth & Bradely, 1986; Wyszecki

& Stiles, 1982). For example, for 460nm light (peak absorbance of MP), the magnitude of the chromatic difference of focus is approximately -1.2 diopters (Wyszecki & Stiles, 1982), placing the shorter wavelengths severely out of focus. The second type is known as lateral CA (Bennett & Rabbetts, 1984). There are two components to lateral CA, namely the chromatic differences of magnification and of position. Specifically this means the shorter the wavelength the larger the retinal image. Therefore, when one views a polychromatic source, color fringing occurs which, theoretically could reduce the contrast and visibility of a visual target.

By filtering out such light before it reaches the photoreceptors, MP could sharpen images and improve acuity (Reading & Weale, 1974). Due to the dense packing of the cones, the fovea is responsible for producing the highest visual acuity and is therefore the most vulnerable to optical aberrations. Interestingly, some studies have demonstrated wide inter-observer variability at the shorter wavelengths when measuring CA, especially at or near 460nm (Mordi & Adrian, 1985; Howarth *et al*, 1988). Reading & Weale (1974) calculated that the spectral characteristics of MP were optimal for reducing potential blurring of an image due to CA. To date, however, no one has measured individual MP levels to determine whether MP actually does serve this function.

Diffraction

In addition to CA, other optical phenomena exist that may also exert an effect on visual perception. For example, optical blur due to diffraction poses an additional theoretical limit to visual resolution. As with CA, diffraction is an inherent property of the wave nature of light (Allen, 1949). Because of diffraction, light brought to a sharp focus will be surrounded by a blurred edge. This phenomenon can be seen when viewing Airy's disc (Westheimer, 1964) (see Figures 4a and 4b). The diameter of this field is inversely proportional to the diameter of the aperture (Westheimer, 1964), and in certain circumstances, diffraction and CA in addition to other optical aberrations are claimed to compensate for one another. For example, McLellan *et al* (2002) demonstrated that when one accounts for the major optical phenomena (e.g. CA, spherical aberration, diffraction, & the Stiles-Crawford effect) they appear to 'correct' for one another. McLellan *et al* (2002) argued this result contradicts the Acuity Hypothesis since CA would be effectively cancelled by the other aberrations. McLellan *et al* (2002)'s conclusions, however, may have been influenced by limitations of their methods. For instance, only three subjects were used with fully dilated pupils (many aberrations would therefore arise from the edges of the lens that would not normally be present). Also spherical aberration from the cornea, which is typically negligible due to the small aperture size of the pupil, would have been successfully transmitted to the retina. Most pupils are not 6+ mm rather, they are commonly 3 – 4mm, and serve to reduce the amount of aberration transmitted to the retina by restricting light entry to a small area centered around the optical axis. Furthermore, the amount of dilating agent, namely 0.5% tropicamide, was not sufficient to prevent accommodation, thus it has been suggested that the modulation transfer function (MTF) may have been artificially improved (Davies & Morland, 2004). Lastly, MPOD was not directly measured, but was instead mathematically constructed based on average values and inferred point spread functions (PSF). This is not an accurate method of measuring MPOD since it can vary widely between observers and fails to account for the spatial distribution of the pigment density. Based on these limitations, the question of whether MP improves acuity by removing the effects of CA remains unresolved. In order to answer this 140 year old question, direct empirical study is needed.

CHAPTER 3

SPATIAL VISION

In order to evaluate MP's role in improving acuity, the question of how to measure acuity must be addressed. Measurement of static spatial vision can be accomplished via a variety of tasks: whether it is simply the confirmation of the existence of an object (minimum visible); the distinction between one versus two point sources (minimum resolvable); or the detection of the minimum offset of position (Wyszecki & Stiles, 1982). In this study, we chose to measure resolution acuity (RA) and positional hyperacuity (HA).

Resolution Acuity

RA, can be defined as the minimum perceivable angular distance subtended by the centers of two point sources to be reliably identified as two points as opposed to one (Helmholtz, 1867; Lord Rayleigh, 1879; Westheimer, 2001; 2003a; 2005). This threshold is known to be determined by at least two factors: (1) the packing density and ganglion convergence of the photoreceptors (Westheimer, 2001; 2003a), and (2) the optical quality of the image (e.g. the lack of anterior vasculature in the fovea might reduce intraocular scattering in that area). With regards to the latter, in order for two points to be resolved, the blurring of the two points (due largely to aberrations, diffraction, etc.) must not overlap to a point where the individual points cannot be discerned (Figure 5). With regards to the former, the lower threshold for RA is limited by the diameter of the cones. Robert Hooke, a scientist of the 17th century and contemporary to Sir Isaac Newton first identified and measured the lower limit of RA to be 1' of arc. Fincham's (1951) photomicrographic images of the retina determined the cone width to be 2.5 microns.

Assuming an eye of axial length of 17.5mm, this estimation is consistent with the current values of inter-cone spacing of approximately 30" (Marcos *et al*, 1996; Nestares *et al*, 2003). This is also the typical minimum visual angle for resolving two lines (Westheimer, 1981). Thus, in order for a pair of point sources to be reliably resolved, the angular distance subtended between the two peaks must exceed the diameter of the retinal cone elements.

SW light, with respect to the optics, appears to be the principal contributor to diminished image quality (see Figure 3). The level of defocus due to CA in addition to the typical diffraction pattern would additively combine and widen Airy's disc. According to the Acuity Hypothesis, MP would remove the SW portion, in effect sacrificing a small loss in illumination for a narrower diffraction pattern. As a result, contrast would be increased and thus so would RA. Additionally, while the retinal grain apparently represents a lower limit in resolution, sharpening the retinal image to more closely match the inter-cone spacing by narrowing the diffraction patterns might make resolution an easier task.

Ancillary Evidence

Although the Acuity Hypothesis has yet to be directly tested, there is indirect evidence that supports its feasibility. Males tend to have both a higher MPOD (Hammond *et al*, 1996; Hammond & Caruso-Avery, 2000) and better acuity on average (Brabyn & McGuiness, 1979). Serendipitously, yellow or amber filters, often with absorbance spectra similar to MP, have been recommended to improve rifle marksmanship for hunters (Provines *et al*, 1997), to reduce aberrations in telescopic equipment and improve resolution for Navy Opticalmen (Carson, 1997), and by physicians to patients (Zigman & Harris, 1990). Even Schültze (1866) was convinced that by placing a yellow filter in front of his eye he was able to improve his visual acuity. Of empirical value, many studies have experimentally examined the use of colored filters and their influence on visual capacity. Clark (1969; as cited in Wooten & Hammond, 2002) amassed and reviewed nearly 100 studies examining the use of colored filters. Clark (1969) ultimately concluded that there was no visual benefit from yellow filtered as opposed to spectrally flat lenses. As with the CA studies, MP was not a tested parameter in any of the color filter studies, nor were the spectral transmittance properties of the filters clearly defined. Furthermore, Wooten & Hammond (2002) emphasize that although Clark's (1969) survey appeared largely negative, there were a few studies that reported visual improvement. Additionally, even in the studies where results were negative, remarkable improvements were shown to occur in some observers. Critically, no studies attempted to match the spectral absorbance profile of MP. Thus, variability in results may have been due to accidentally approximating the absorbance of MP in some cases but not in others. This is consistent with recent data by Engles *et al* (2005a,b). Using tinted glasses closely matched to the combined spectral absorption profile of the human lens and MP (equivalent to 0.7 log relative MPOD units), improvement in visual acuity as measured by Landolt Cs (Engles *et al*, 2005a), and contrast sensitivity (Engles *et al*, 2005b) was observed. Wooten & Hammond (2002) have recently argued that other optical mechanisms quite different than CA could improve visual performance under the type of conditions where most yellow glasses show improvements (this was termed the Visibility Hypothesis of MP). The question of whether MP is related to CA therefore remains unclear.

Hyperacuity

Westheimer (1975) originally used the term 'hyperacuity' to describe extremely detailed visual discriminations. A number of various stimulus configurations can generate thresholds of the hyperacuity type (for review see Westheimer, 1977). One such type first described by Wülfing (1892), called vernier acuity, is essentially two vertically oriented and abutting lines. In this scenario, one line is adjusted horizontally such that an offset from perfect alignment is introduced and the threshold is determined as the minimum offset required to obtain a Just Noticeable Difference. Offsets as small as 2-4" of arc can be detected reliably (Westhiemer, 1977). This minimum is approximately one full order of magnitude smaller than the width of a cone photoreceptor (Anderson & Weymouth, 1923; Foley-Fisher, 1973; Westheimer, 1977; Geisler, 1984; Carney & Klein, 1997). Furthermore, if given the proper cues thresholds can be reduced to nearly 1" of arc (Klein & Levi, 1985). Additionally, this phenomenon is apparently very robust, as it is resistant to changes in spatial configuration (Westheimer, 1977; Geisler, 1984).

Unlike RA, retinal mosaic configuration (Anderson & Weymouth, 1923), eye movements (Keesey, 1960; Fender & Nye, 1962), and various degrees of optical blur (Williams *et al*, 1984) appear to play a relatively small role. Hyperacuity also appears to have a strong computational (e.g. neural processing) component. Even with minimal blur (Williams *et al*, 1984) or the absence of eye movements (Keesey, 1960) one is still able to compensate to some degree and provide hyperacuity thresholds. In summary, hyperacuity is not limited by the same factors as RA, or at least not to the same degree.

Since the Acuity Hypothesis is based on the idea that MP improves acuity by optical filtering, and since HA appears to be only minimally influenced by optical distortion, it is not clear whether MP would be expected to be related to HA. There is, however, some evidence that suggest that HA might also be influenced by the chromatic content of stimuli. For instance, in blue light testing conditions, HA thresholds have been shown to be poorer than when tested in white light or other chromatic backgrounds (Ferree & Rand, 1942; Baker, 1949; Foley-Fisher, 1968; as cited in Foley-Fisher, 1973; Rüttiger & Lee, 2000). At first glance, this would suggest that severe optical blur increases thresholds, but this would be in contradiction to studies showing that hyperacuity is strongly resistant to optical degradation (Stigmar, 1971; Westheimer, 1979; Williams *et al*, 1984), even when that degradation is due to cataract (Essock *et al*, 1984). Therefore, the degree to which MP would improve hyperacuity thresholds, or if it would elicit improvement at all, is unknown and speculation is difficult. Consequently, to determine MP's effect on hyperacuity thresholds, it was included as a parameter in this study.

CHAPTER 4

CURRENT PROJECT

The purpose of this project is as follows: (1) to empirically evaluate the Acuity Hypothesis originally proposed by Schültze (1866) as it applies to RA, and (2) to empirically evaluate whether the Acuity Hypothesis as proposed by Schültze (1866) can be extended to include the hyperacuities. In order to accomplish these goals, MPOD and RA and HA will be directly measured in a representative group of young participants. As predicted by the Acuity Hypothesis, it is anticipated that both RA and HA thresholds will be lower for those individuals with higher MPOD.

Methods

Apparatus for measuring resolution and hyperacuity:

The stimuli in both experiments (RA and HA) consisted of a pair of black vertically oriented lines superimposed on a diffusing plate and backlit by Light-Emitting Diodes (LEDs) to create one of two background lighting conditions, either an achromatic "white" (absorbed by MP; the stimulus was judged to be a perceptual white in a control experiment using five participants) or a chromatic "yellow" (not absorbed by MP). The "white" background (CIE coordinates x = .317, y = .324) was displayed at a luminance of 17.0cd/m^2. This was accomplished by combined illumination of the blue (peak λ = 460 nm) and yellow (peak λ = 570 nm) LEDs (see Figure 6). The "yellow" (CIE coordinates x = .460, y = .537) background was displayed at a luminance of 15.7cd/m^2 (using only the yellow LED). The vernier lines were 1' arc wide and 14’ arc long, when separated by a 1’ arc gap. See Figure 7 for a diagram of the stimulus configuration.

While making spatial judgments, participants sat 5.33m from the stimulus in a dark room behind a back-illuminated white screen ($11.7cd/m^2$ – illumination maintained by two 24in fluorescent bulbs). A hole was cut through the center to allow for viewing of the target (5.83° diameter). This ensured that observers maintained photopic sensitivity. The participant’s head was held steady by a chin and head rest assembly. All testing took place under monocular (right eye only, left eye patched) viewing conditions.

The square background subtended an angle of 30’ arc, and was viewed through a circular hole cut in the center of a baffle with a manually operated shutter. When closed (as it would be for configuration changes) the stimulus was completely obscured from the participant. During a configuration change participants fixated on a small cross located 12.85 deg below the target drawn on the white screen to help maintain photopic sensitivity. A verbal cue was provided to indicate that the change was complete and the baffle was open. Participants freely viewed the stimulus until a judgment was made and the baffle was closed again, whereby the participant recommenced fixation on the cross until the next verbal cue was given. A typical judgment was made in 1 – 3 sec. Judgments taking longer than 3 sec were discarded and that trial was re-presented later during testing. Testing extended over a 2-3hr period. This period was broken up into 20-30 minute testing blocks with short breaks that were used to avoid problems with adaptation and fatigue. During breaks the room lights were turned on and participants were allowed to move about freely until comfortable or otherwise sufficiently rested. After each break, the testing parameters were reset to their pre-break settings and measurement continued.

To prevent order effects, the "white" and "yellow" conditions were counter-balanced between participants.

Apparatus for measuring macular pigment:

MPOD was assessed in the right eye only by a Macular Metrics densitometer, which utilizes heterochromatic flicker photometry (Wooten *et al*, 1999). Participants were stabilized by resting their chin in a headrest assembly, adjusted such that they could clearly and easily view the test stimulus. The stimulus consisted of a circular test field comprised of two wavelengths, "blue" and "green" (peak $\lambda = 460$nm [max absorbance by MP]; peak $\lambda = 570$nm [no absorbance by MP] respectively), alternating in a square-wave fashion so as to create the perception of flicker. The task required the participant to fixate on a small dot at the center of the test field and to make an adjustment (an adjustment being a change in the relative radiance of the two LEDs) until the sensation of flicker ceased. Measurements were taken at the following eccentricities: 15' arc, 30' arc, 1° arc, 1.75° arc, and a 7° reference. MPOD was calculated by subtracting the log of the ratio "blue" to "green" radiance values of the peripheral test from those of the central test. See Figure 8 for a diagram of the stimulus configuration used to measure MPOD.

Although MPOD at 15' represents a measure that would logically demonstrate a correlation with acuity, as all spatial vision measurements were made well within 15' of the central fovea, MPOD at 30' was used because it typically represents a more stable measure of MPOD (Snodderly *et al*, 2004). To demonstrate that the two are yoked however, Pearson R correlations were conducted on MPOD 15' and MPOD 30' scores for both samples. For Experiment 1's sample, MPOD 30' was significantly correlated to MPOD 15' ($N = 20$, $y = 0.873x + 0.197$, $r = 0.802$, $p < 0.05$) (Figure 9). For Experiment 2's sample, MPOD 30' was significantly correlated to MPOD 15’ ($N = 21$, $y = 0.533x + 0.357$, $r = 0.618$, $p < 0.05$; see Figure 10).

Experiment 1: Resolution Acuity

Participants:

RA and MPOD measurements were obtained from 20 undergraduate students attending Introductory Psychology courses at the University of Georgia and were awarded course credit for their involvement. All participants were in good ocular health with no color deficits or past eye trauma (self report) and had Snellen acuity of at least 20/20 as measured by a wall chart (corrected if necessary either by prescription or by trial lens). All participants were treated ethically and briefed prior to and following experimentation in compliance with the Tenets of the Declaration of Helsinki.

Procedure:

To measure RA, thresholds were obtained by using the method of constant stimuli. Pseudo-random offsets were made by vertically displacing the bottom vernier line such that the gap subtended between the tips of the two bars was either increased or decreased. This could be accomplished in incremental steps as small as 1-5" arc, but was most commonly done in 10" arc increments. The minimum step size and range could be adjusted to accurately encompass each participant’s threshold. Changes to the standard method were based on the following criterion: if the typical step size (10" arc) did not generate enough data points to produce an accurate psychometric function, then the step size was halved and as many intermediate configurations as necessary were introduced without the participant’s awareness. Each configuration was presented at least 10 times. To be certain that the participants were responding appropriately, 20% of the presented configurations were catch trials. This was accomplished by presenting either a closed (no gap present) stimulus, or by creating an 'obvious' gap. Psychometric functions were generated using probit analysis (Finney, 1971), and thresholds were defined as 50% correctly identified (Figure 11).

Experiment 2: Hyperacuity

Participants:

HA and MPOD measurements were obtained from 21 undergraduate students attending Introductory Psychology courses at the University of Georgia and were awarded course credit for their involvement. All participants were in good ocular health with no color deficits or past eye trauma (self report) and had a Snellen acuity of at least 20/20 (corrected if necessary either by prescription or by trial lens) as measured by a wall chart. Participants were treated ethically and briefed prior to and following experimentation in compliance with the Tenets of the Declaration of Helsinki.

Procedure:

HA was assessed using a two alternative forced-choice paradigm. Participants were asked to judge whether the bottom line appeared laterally displaced to the left or to the right relative to the top line (see Figure 7). This was done in 2" arc increments to a max offset of 20" arc, plus one centrally aligned configuration. The lines were always separated by a vertical distance of 1' arc during testing. Ten presentations were made for each configuration (total average number of presentations were 215). Offsets made to the left were computationally considered as negative in terms of distance. Thresholds were determined as the average of the 25% and 75% correct points, thus allowing the 50% correct point to act as a measure of response bias (see Figure 11). It is well known that perceptual learning is a factor in hyperacuity tasks, thus, feedback was not given during experimentation as this is known to influence the observer's responses (McKee & Westheimer, 1978; Shiu & Pashler, 1992; Fahle & Edelman, 1993; Fahle *et al*, 1995; Herzog & Fahle, 1997; Folta, 2003).

Results

Experiment 1: Macular Pigment and Resolution Acuity

MPOD for the entire sample ranged from 0.14 to 1.00 at 30' (mean = 0.45 ±.22). RA thresholds also varied widely across participants for both conditions (W: range = 14.8" – 73.10"; mean = 37.03" ±13.85; Y: range = 16.30" – 66.80"; mean = 35.03" ±12.52). These statistics are shown in Table 1.

To determine the reliability of the RA measurements, Pearson R correlations were conducted on "white" and "yellow" resolution thresholds. The resolution thresholds as measured for the two conditions were significantly correlated to one another (N = 20, y = .867x + 6.528, r = 0.77, p = 0.000) suggesting that the measures were reliable and that learning (e.g. improvement between sessions) was not a factor (Figure 12). In fact, despite the large differences in the spectral content of the "white" and "yellow" RA tasks, no significant difference was observed between the two testing conditions ((19) t = 0.890, p = 0.508) (Figure 13).

As a means of controlling for individual differences in RA, we subtracted the RA values obtained in the "white" light condition (filtered by MP) from the RA values obtained in the "yellow" light condition (not filtered by MP). This procedure should isolate the component of RA most influenced by MP (this derived measure we termed the magnitude of difference in resolution [MDR]). As shown in Figure 14, no relation between MPOD 30' and MDR was observed (N = 20, y = 9.843x – 2.638, r = 0.23, p = 0.320).

Experiment 2: Macular Pigment and Hyperacuity

As with Experiment 1, a wide range of MPOD was found for the sample of 21 participants (range = 0.07 – 0.79 at 30'; mean = 0.43 ±.2). HA thresholds were also found to vary widely between participants in both chromatic conditions (W: range = 1.25" – 12.40"; mean = 6.28" ±0.63; Y: range = 1.00" – 13.02"; mean = 4.80" ±0.66) (for a summary see Table 2).

To determine HA measurement reliability, Pearson R correlations were conducted on "white" and "yellow" thresholds. The HA thresholds for the two conditions were significantly correlated to one another (N = 21, y = 0.747x + 2.691, r = 0.78, p = 0.000) suggesting that the measures were taken reliably and that learning (e.g. improved thresholds between sessions) was not a factor (Figure 15). A t-test revealed however, that the "yellow" HA values were significantly higher than the "white" HA values (t = 3.430, p = 0.023) (Figure 16). This effect was independent of MP.

As a means of controlling for individual differences in HA, we subtracted the HA values obtained in the "white" light condition (filtered by MP) from the HA values obtained in the "yellow" light condition (not filtered by MP). This procedure should isolate the component of HA most influenced by MP (this derived measure we termed the magnitude of difference in hyperacuity [MDH]).

To test the Acuity Hypothesis a Pearson R correlation was conducted for MPOD 30' and MDH. As shown in Figure 17, however no relation between MPOD 30' and MDH was observed (N = 21, y = 1.956x + .627, r = 0.19, p = 0.399).

CHAPTER 5

DISCUSSION

The Acuity Hypothesis: Resolution Acuity

As demonstrated by the results, MPOD did not appear to influence RA thresholds. It should be noted, however, that this result is very specific to the stimulus conditions used in our experiment. This result cannot be generalized, for instance, to other stimulus conditions (e.g. filtering may be more important in low luminance conditions). The stimulus configuration used in this study is not equivalent to measuring RA using two point sources of illumination, rather it is equivalent to two dark points against an illuminated surface. As discussed by Westheimer (2001) in the case of two point sources of illumination, blur would cause the two points to subjectively 'widen' or blur together. In this situation, resolution is dependent on one's ability to discriminate intensity, that is, the peak-to-trough ratio of the two blur patches must equal one's intensity difference discrimination threshold. The current study's contrast polarity was reversed (dark bars on a bright background) and therefore is more taxing to the visual system in terms of RA. With increased optical blur, two dark points against an illuminated background would be more difficult to detect and to resolve. This is because a given observer's intensity difference discrimination threshold is a constant ratio, and therefore the two points must be moved further apart in order for the illuminated area between them to appear just noticeably dimmer than the more brightly illuminated background (Figure 18). In short, it is easier to detect a very small amount of illumination while in a dark room, than it is to detect a slightly darker patch when in a fully illuminated room.

In terms of the current stimulus configuration, the pins would be subjectively made ‘thinner’ and ‘pushed apart’ by optical blur. Consequently, even in the presence of MP, optical blur from other wavelengths not absorbed by MP will still subjectively push the bar tips apart, reducing RA. Therefore, while the Acuity Hypothesis was not supported using our stimulus conditions, MP could still improve acuity for reversed contrast tests, essentially illuminated bars against a dark background.

Additionally, as Wooten and Hammond (2002) point out, a modern view of spatial acuity holds that RA using high contrast targets (e.g. Snellen test letters or Landolt C’s), merely represents but a single point in the broader contrast sensitivity function (CSF). Higher spatial frequencies are more vulnerable to optical degradation due to blur because contrast would suffer; whereas mid- or lower-spatial frequencies might prove to be more resistant. Consistent with this view, Thibos (1989) originally calculated that MP would be most likely to improve the high-frequency portion of the CSF. Thus, future studies should be directed toward evaluating the Acuity Hypothesis as it applies to the entire gamut of the CSF.

The Acuity Hypothesis: Hyperacuity

As with RA, the results show that no relation exists between MPOD and HA (again based on the stimulus conditions). Thus it would appear that the Acuity Hypothesis cannot be extended to include at least this type of HA. This may be due largely to the neural computations involved when one is making HA judgments. For example, HA may be determined by pooling of information across the retinal elements as suggested by Westheimer and McKee (1976). Recall that even when severe optical degradation is introduced to the target, HA thresholds can still be maintained with only a small loss (Westheimer, 1981; Essock *et al*, 1984; Williams *et al*, 1984; Enoch, 1998). This means that HA is not dependent on high spatial frequencies for accuracy, provided that a ‘center of gravity’ is visible in the stimulus (Williams *et al*, 1984). Thus, it would appear that despite the defocus caused by the presence of SW light, MP’s role is minimal, even if it successfully removed a considerable amount of blur.

Compared with past studies, the stimulus configuration used for this study is fundamentally different, in that the contrast polarity was opposite and chromaticity was carefully controlled. Therefore, one might argue that MP’s role in this HA configuration was negligible because, as with the RA stimulus configuration, a dark bar on a bright background blurs toward the center, so as to make the bars subjectively ‘thinner.’ In this situation, MP’s role would not influence HA thresholds, however, MP could re-tune the light distribution of the stimulus so as to render a more accurate profile of the bars.

Interestingly, HA thresholds taken on the “yellow” background were significantly better than those on the “white” background. This difference cannot be explained due to the small differences in target luminance (approx. 1cd/m^2 difference). For Example, studies have shown that HA is relatively independent of moderate changes in target luminance (Bedell, 1987; Waugh & Levi, 1993). Since MP was unrelated to this difference, the improvement in acuity for the “yellow” condition seems to be linked to the chromatic content of the stimulus. This interpretation implies that chromatic channels may process spatial stimuli differently than achromatic channels. The Y-B channel has been shown to demonstrate lower spatial resolution (Rüttiger & Lee, 2000). This idea could be tested by also determining HA in a blue light condition. Since HA does involve neural computation (Snyder, 1982), the idea that chromatic content could facilitate such computation is feasible.

Summary and Future Directions

While the Acuity Hypothesis was not supported by these data, influences of MP on other forms of acuity are possible. Nonetheless, these data do suggest that for moderate luminance (e.g. daylight conditions), and easily viewed stimuli (e.g. mid-spatial frequencies at high contrast), the effects of MP on improving acuity by filtering blur due to SW light is minimal. This finding is consistent with data showing that filters used to correct for chromatic aberration (e.g. Powell achromatizing lens) do not show dramatic improvements in acuity (Bradley *et al*, 1989). This may be due to the fact that SW blur is a constant feature of our environment. Based purely on the optics of the eye, most objects viewed in bright white sunlight should be surrounded by a bluish fringe (even if MP removed this aberration it would be seen by those individuals with relatively low MP and lenticular density). The fact that most individuals do not have such experiences suggests that the visual system may dynamically correct for this constant feature of our visual environment. In addition to neural adaptation, several other factors may limit the role of SW light in spatial vision. The lens strongly absorbs SW light and the human spectral sensitivity function is minimally sensitive to SW and LW light (the areas most prone to aberration). SW cones are relatively sparse compared to mid- and long-wave cones (Curcio *et al*, 1990) and probably do not contribute much to spatial tasks (De Valois *et al*, 1982). Such a contribution of factors may make additional subtraction of sunlight by MP superfluous or even deleterious in low-light conditions.

In summary, while the Acuity Hypothesis was not supported using these test parameters, testing should be expanded to include different types of visual stimuli, such as illuminated points or bars against a dark background. In addition to modified stimuli, testing should be expanded to include the entire CSF, as one might expect an attenuation of high spatial frequencies due to blur and perhaps a loss of the very low spatial frequencies. Additionally, while not a goal of this study, testing of the hyperacuities in chromatic vs. achromatic conditions has demonstrated a novel finding. Namely that, hyperacuity appears to be less sensitive for achromatic conditions than for chromatic conditions. This may be beneficial to understanding the underlying mechanisms responsible for the processing of relative position.

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TABLES

Table 1: Presents the number of participants and descriptive statistics for Experiment 1.

Variable			N	Range		Mean	Std. Dev.	SEM
				Min	Max			
MPOD 30’	Male		10	.29	1.00	.51	.25	.08
	Female		10	0.14	0.74	.41	.18	.06
	Total		20	0.14	1.00	0.45	0.22	0.05
Acuity (arc-sec)	“white”	Male	10	14.8	73.10	41.30	16.67	5.27
		Female	10	19.9	57.2	32.99	10.46	3.31
		Total	20	14.80	73.10	37.03	13.85	3.02
	“yellow”	Male	10	17.9	66.8	37.42	15.00	4.74
		Female	10	16.3	50.8	33.17	9.78	3.09
		Total	20	16.30	66.80	35.30	12.52	2.80
MDR		Male	10	-11.6	28.60	3.88	11.29	3.57
		Female	10	-16.4	6.40	-0.18	6.77	2.14
		Total	20	-16.40	28.60	1.85	9.30	2.07

Table 2: Presents the number of participants and descriptive statistics for Experiment 2.

Variable		N	Range		Mean	Std. Dev.	SEM
			Min	Max			
MPOD 30’		21	0.07	0.79	0.43	0.20	0.04
Hyper-acuity (arc-sec)	“white”	21	1.25	12.40	6.28	2.90	0.63
	“yellow”	21	1.00	13.02	4.80	3.04	0.66
MDH		21	-1.40	6.75	1.48	1.97	0.43

FIGURES

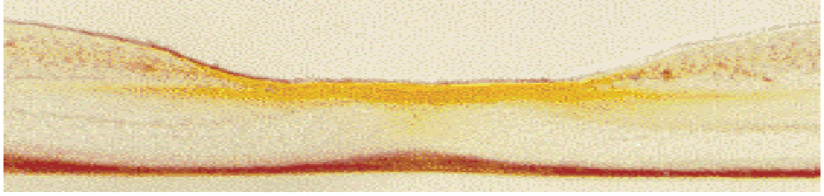

Figure 1a: Macular Pigment photomicrograph taken in yellow light.

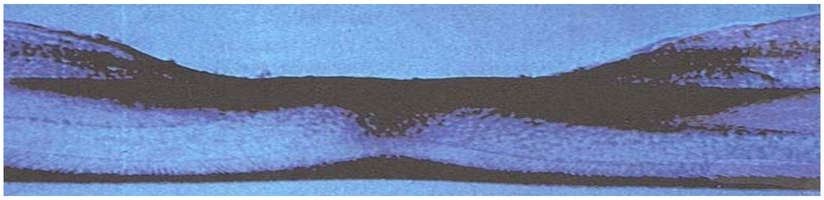

Figure 1b: Macular Pigment photomicrograph taken in blue light. Images obtained from D. Max Snodderly from retinal preparations published in Snodderly *et al* (1984).

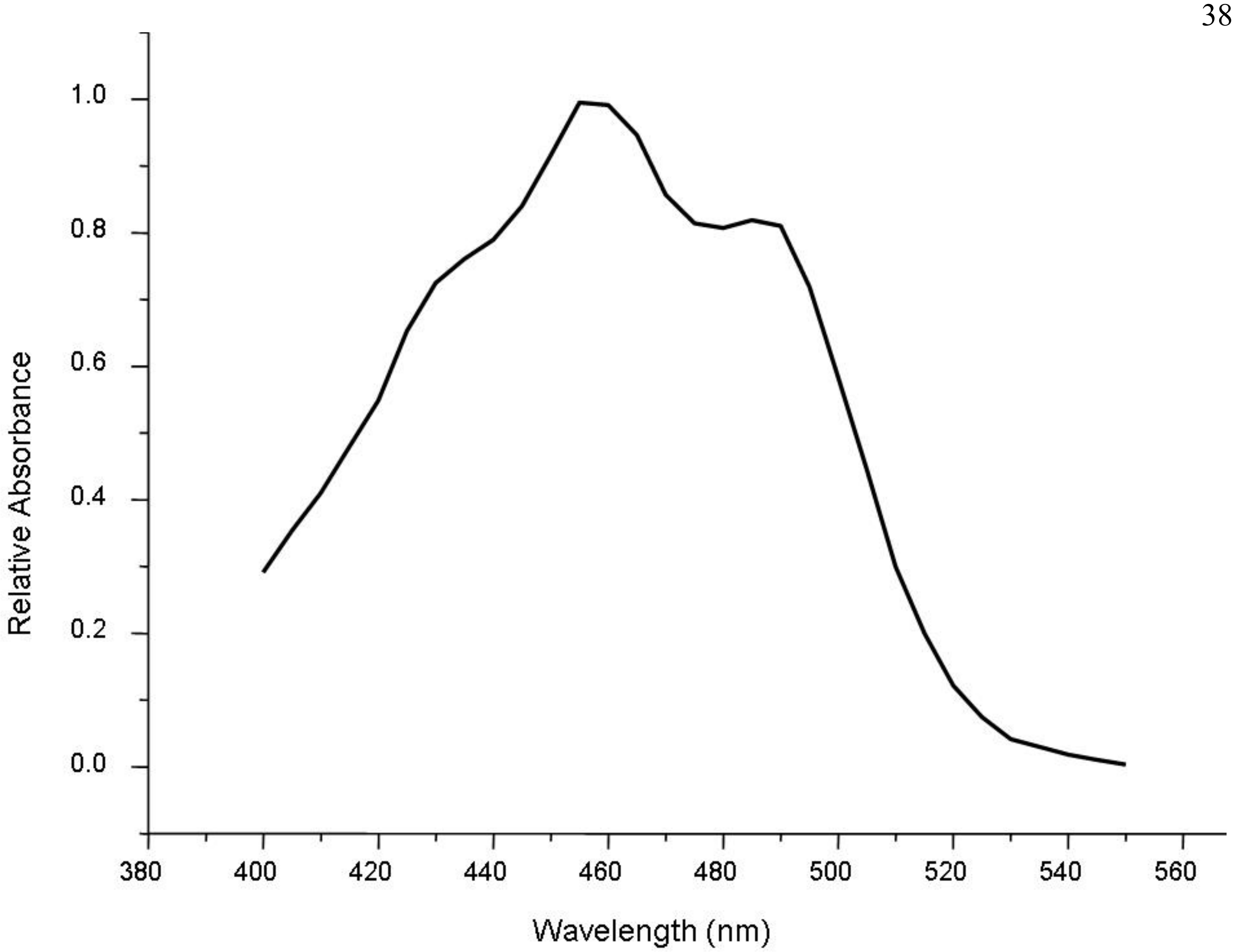

Figure 2: MP's relative absorbance by wavelength. Data derived from Wyszecki & Stiles (1982).

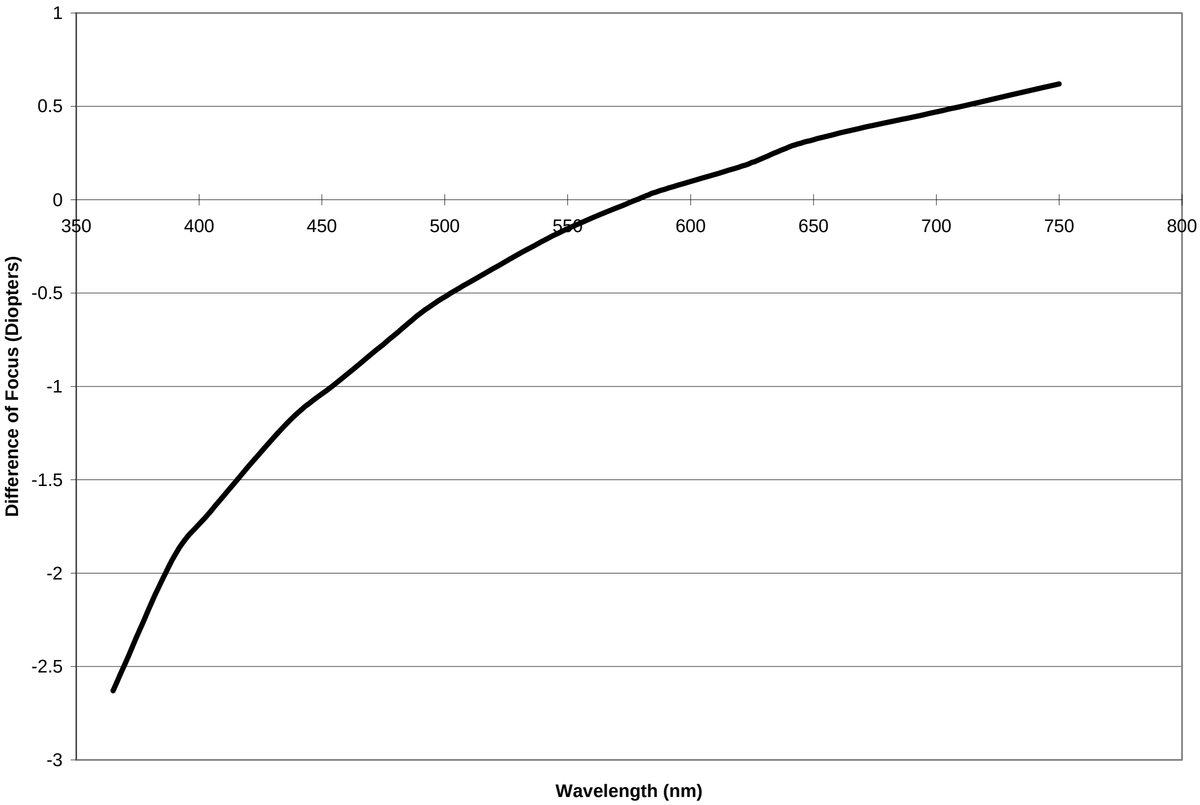

Figure 3: Longitudinal chromatic aberration as a function of wavelength. Data derived from Wyszecki & Stiles (1982).

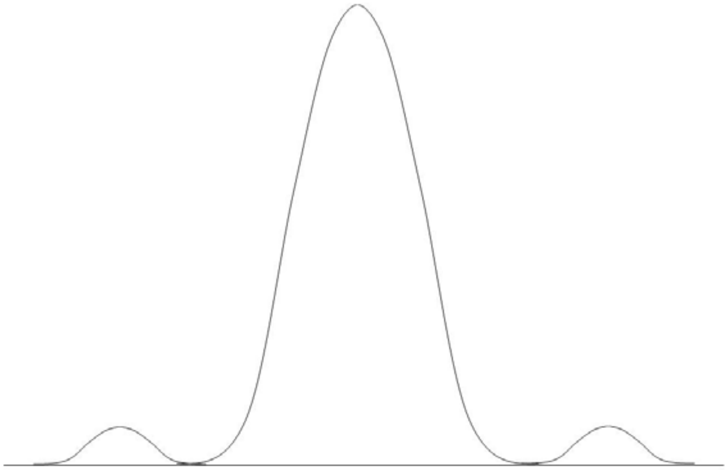

Figure 4a: The typical shape of the diffraction pattern plotted by retinal light distribution.

Figure 4b: Shape of Airy's disc as formed by the retinal light distribution due to diffraction.

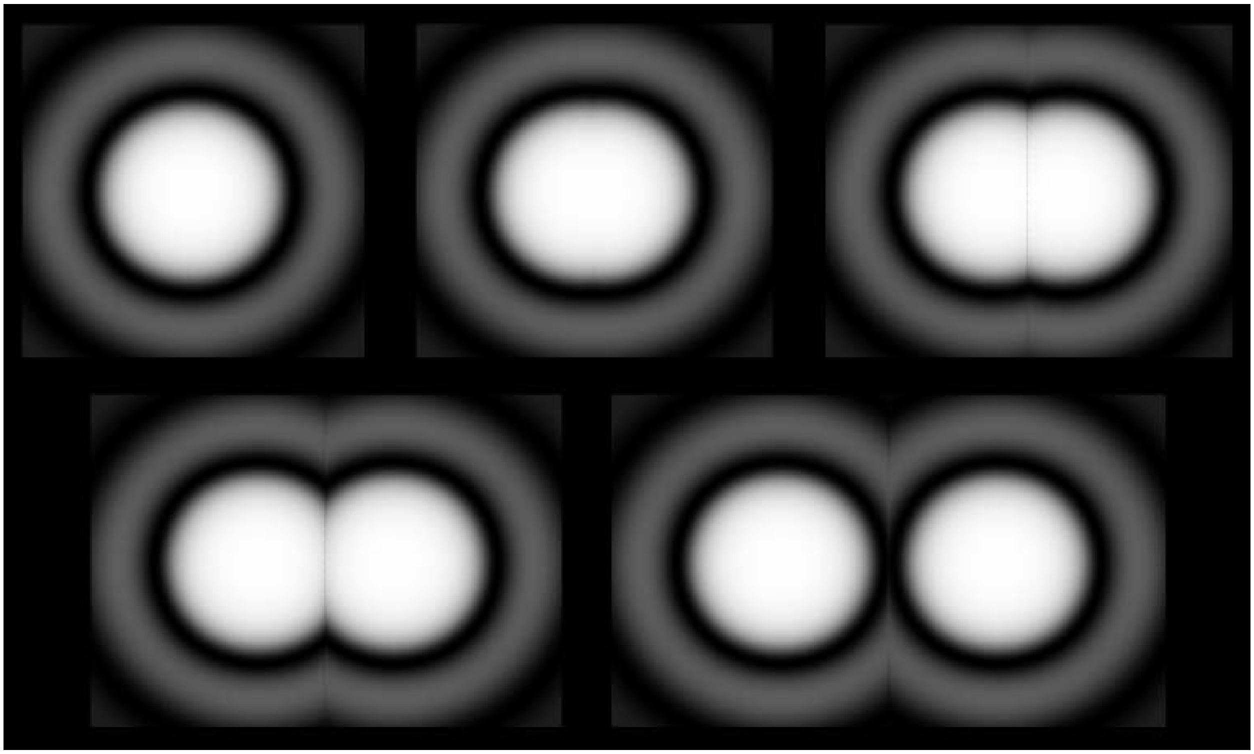

Figure 5: In order for two point sources to be resolved, the low point between two luminance distributions must be of sufficient depth such that the difference in illumination from peak to trough is detectable to the underlying cones.

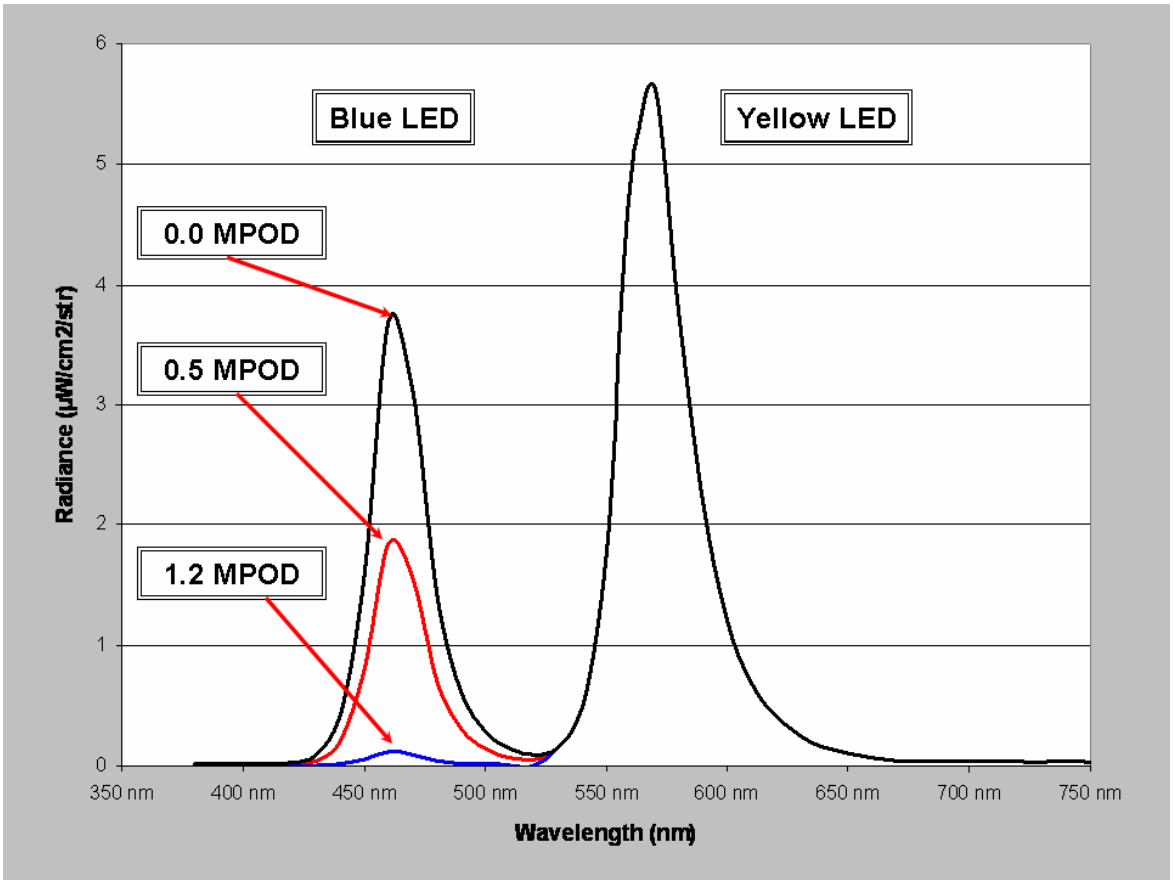

Figure 6: The radiant output of the blue (peak output = 460nm; max absorbance by MP) and yellow (peak output = 570nm; no absorbance by MP) LEDs combined (as shown here) to create the "white" light condition. The blue LED was turned off to create the "yellow" light condition. Notice that as MPOD absorbance increases, the relative luminance of the blue LED diminishes and more closely matches the "yellow" condition.

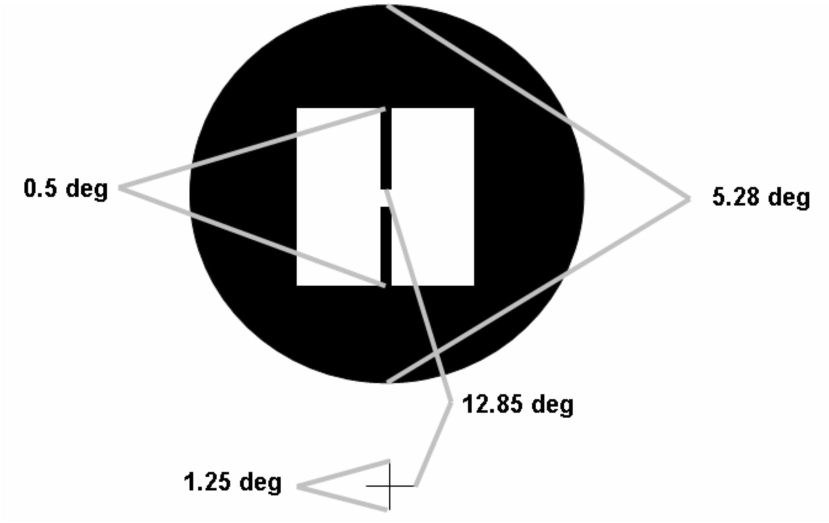

Figure 7: Diagram of the apparatus used to measure both types of spatial vision. The bars in the center could be adjusted in either of two directions, vertically, so as to be moved apart, or horizontally, so as to introduce misalignment.

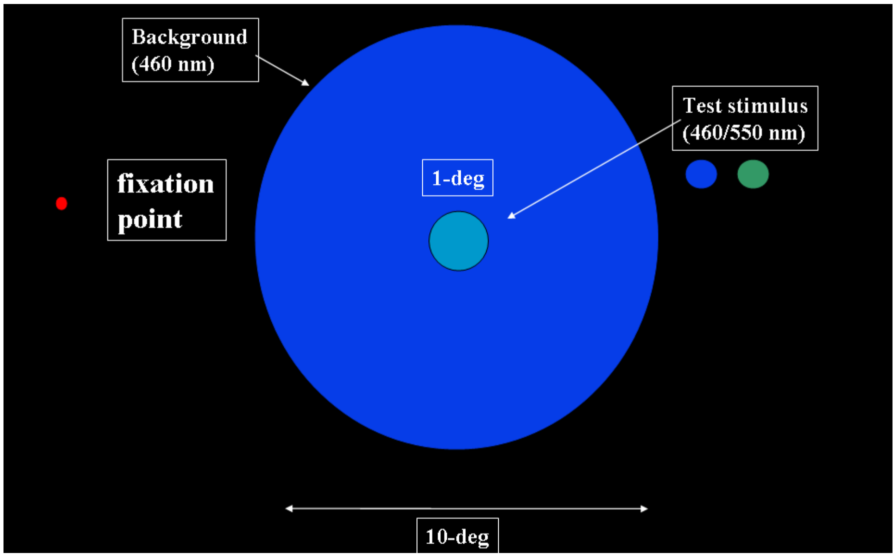

Figure 8: Stimulus configuration used to measure MPOD as seen by participants.

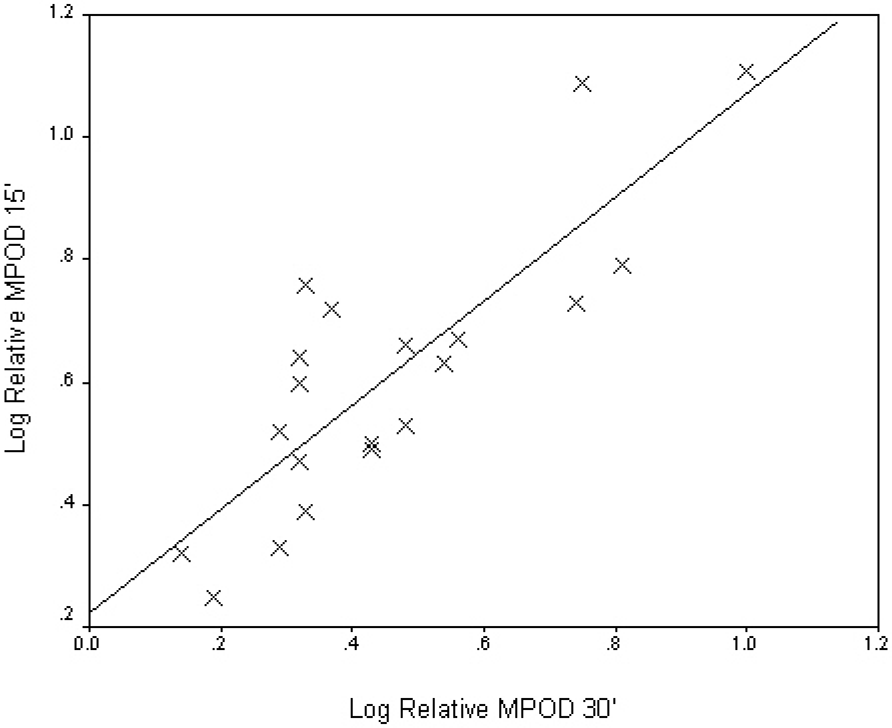

Figure 9: Correlation between MPOD 30’ and MPOD 15’ for Experiment 1 (r = 0.802).

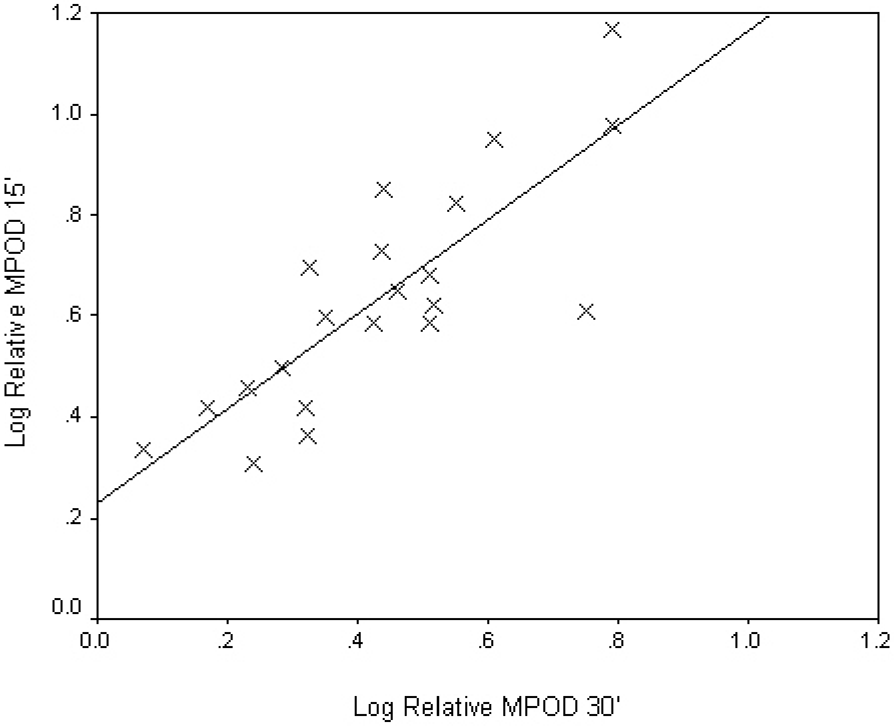

Figure 10: Correlation between MPOD 30’ and MPOD 15’ for Experiment 2 (r = 0.815).

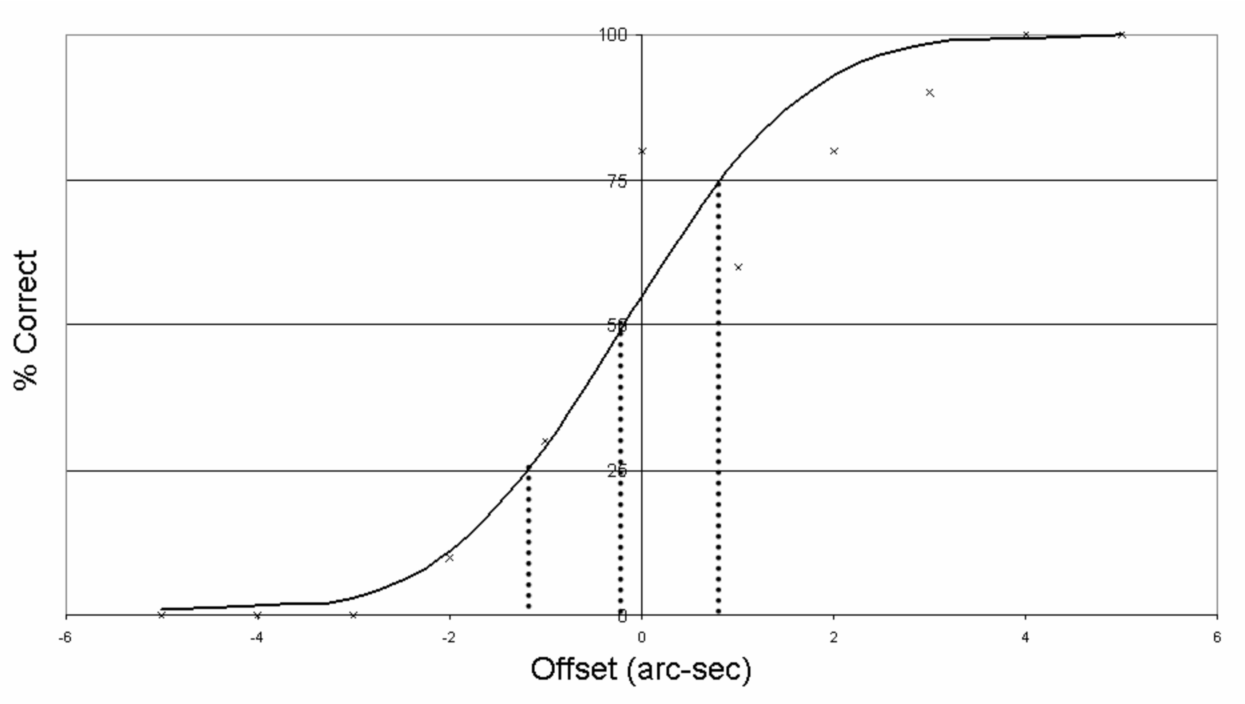

Figure 11: Standard psychometric function generated by Probit analysis. Threshold was calculated by averaging the 25% and 75% correct responses; 50% correct response was used as a measure of bias.

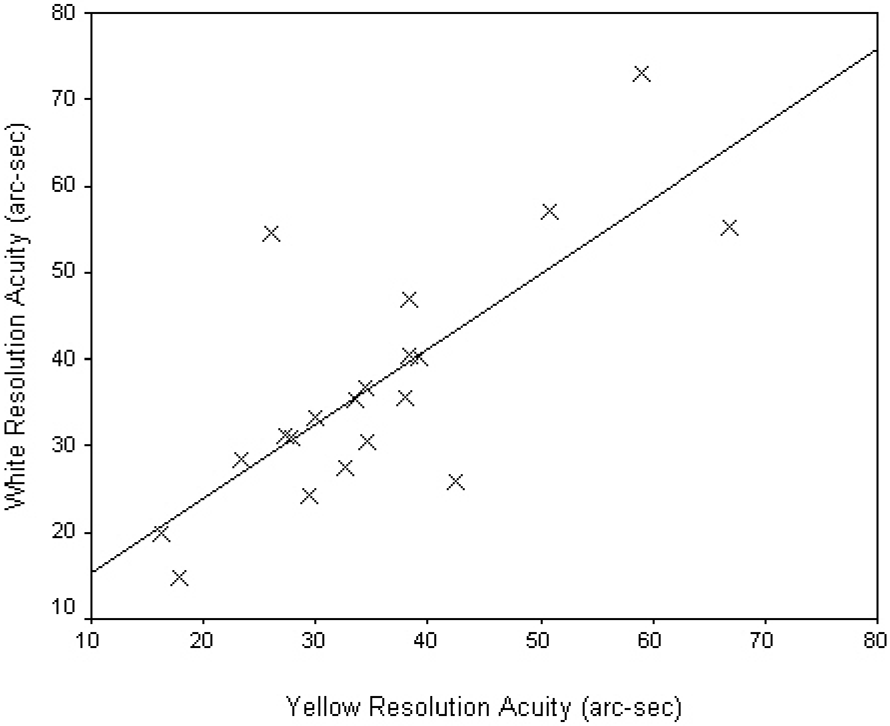

Figure 12: Correlation between “yellow” thresholds and “white” thresholds for RA.

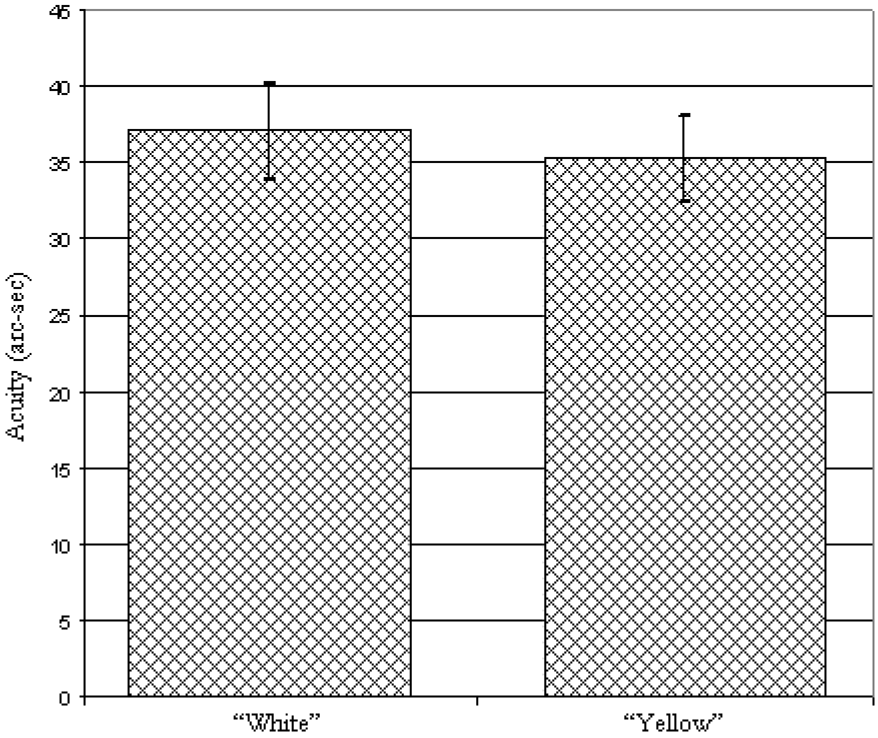

Figure 13: Average "white" and "yellow" thresholds for RA. Error bars represent the standard error of the mean.

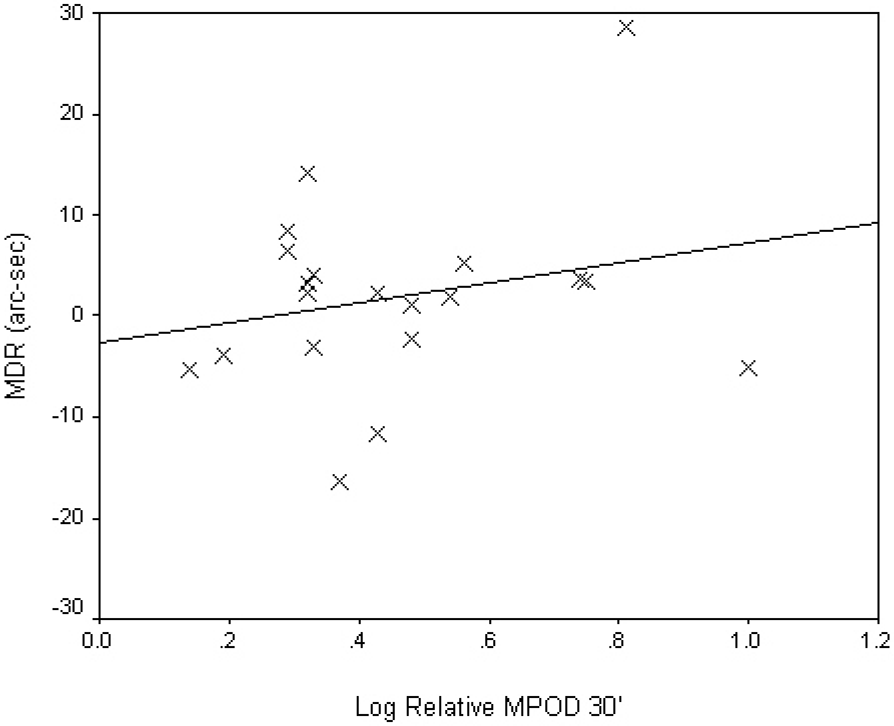

Figure 14: Correlation between log relative MPOD 30’ and MDR.

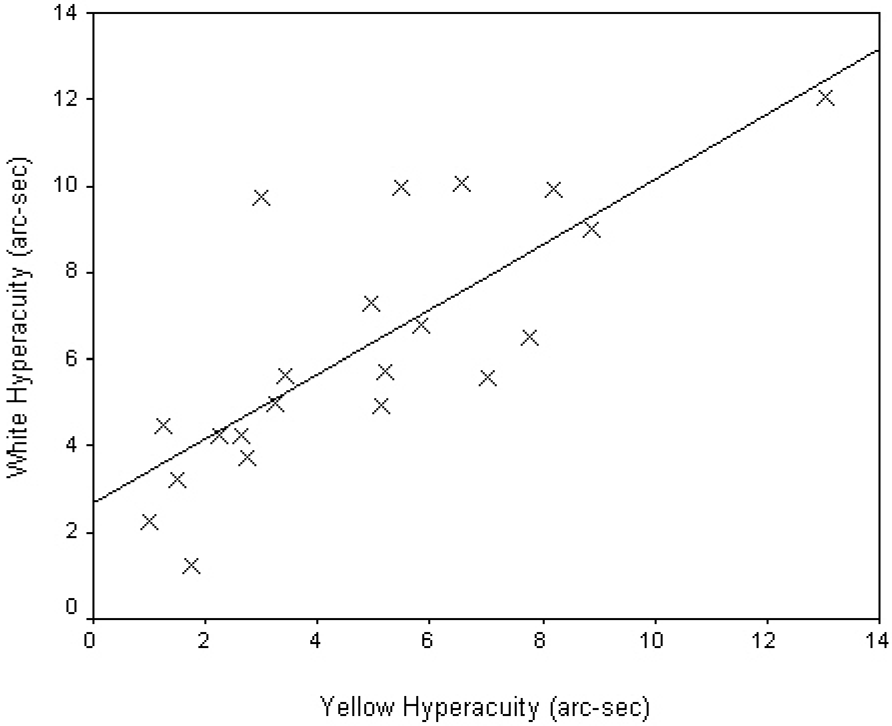

Figure 15: Correlation between “yellow” thresholds and “white” thresholds for HA.

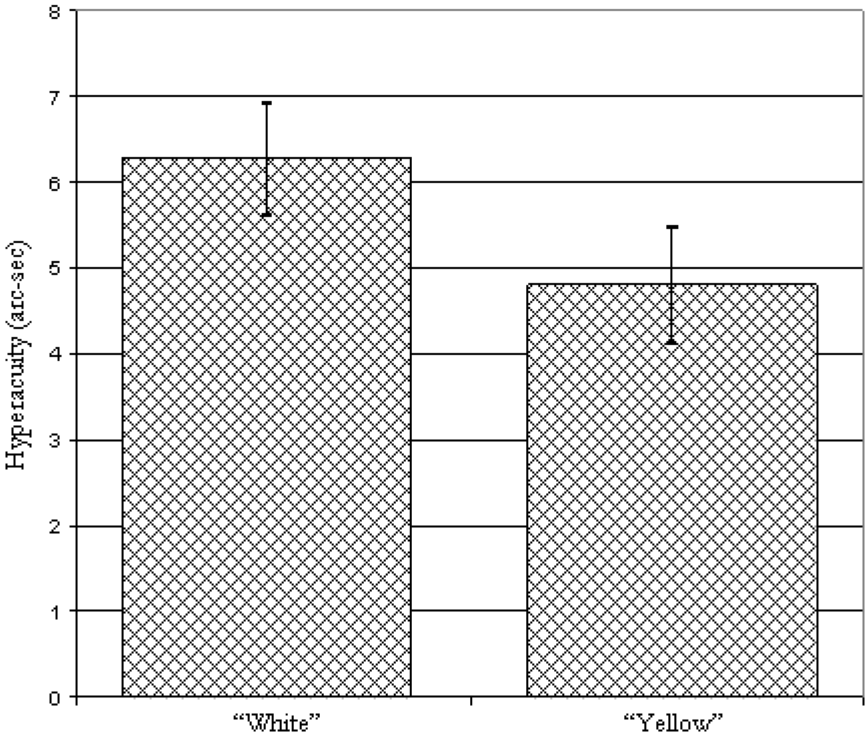

Figure 16: Average "white" and "yellow" thresholds for HA. Error bars represent the standard error of the mean.

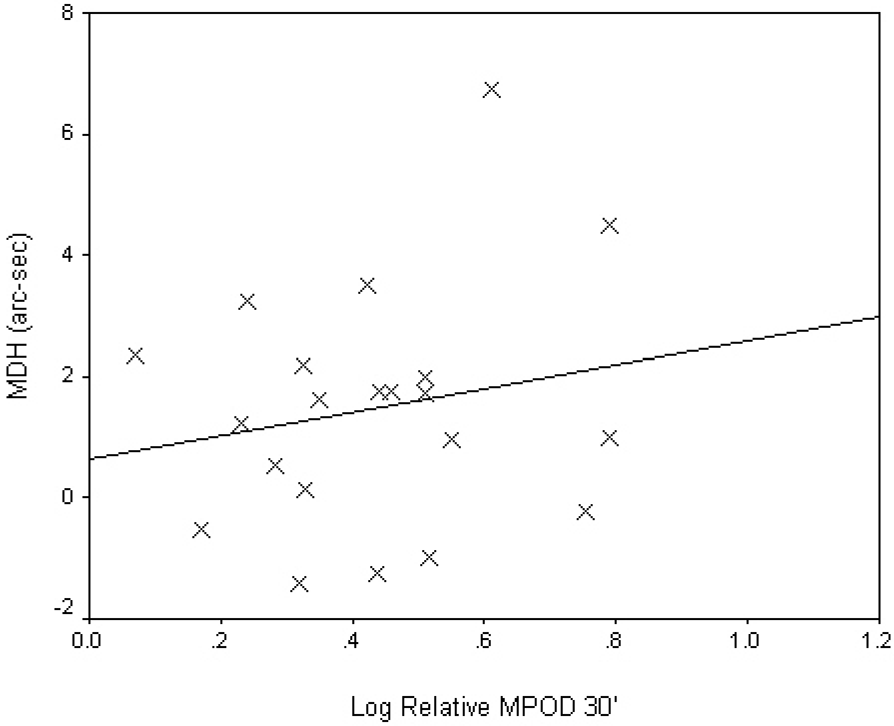

Figure 17: Correlation between MPOD 30’ and MDH.

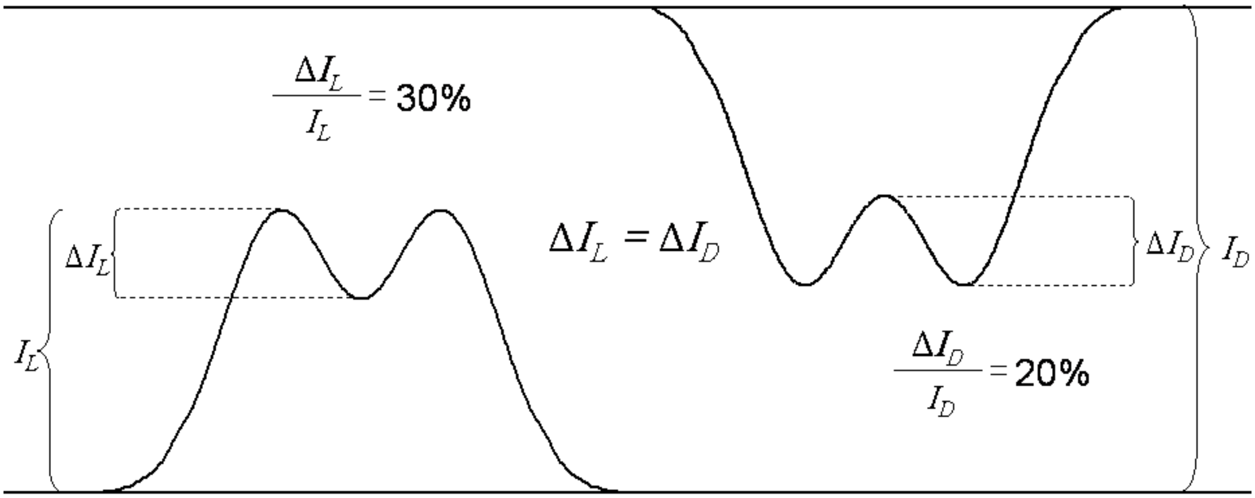

Figure 18: On the left is a diffraction pattern representing a pair of bright points against a dark backgound; on the right is a diffraction pattern representing a pair of dark points against a bright background. Notice that although the difference in illumination from peak to trough in both patterns are equal, resolution is easier when using a bright source against a dark background.