COLOR, TILT, AND THE HERMANN GRID ILLUSION

A thesis presented to the graduate faculty of The New England College of Optometry in partial fulfillment of the requirements for the degree of Master of Science

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Abstract

The Hermann grid illusion has long be attributed to the effects of concentric lateral inhibition and receptive field organization. However, experiments using two variations of the grid do not support this explanation. The first is that the illusion diminishes when the grid is tilted. The second is that chromatic assimilation occurs for colored grids instead of the expected chromatic contrast. The present work quantified these two effects in order to examine their roles in producing the illusion. It was confirmed that luminance contrast is the most important factor for producing a strong illusion, even for chromatic grids. The experiments also showed that the effects of tilt and color on the illusion were independent of one another. The effect of tilt was attributed to orientation specific S1 cells in the striate cortex. There are a greater number of these lightness/darkness processing cells oriented in horizontal and vertical directions than in oblique directions. Therefore, obliquely presented grids are processed differently than vertical/horizontal grids. This is the same explanation used to describe the oblique effect. However, this is not an example of the oblique effect; rather, it is a version of it. The role of color was determined to be very minor in inducing the Hermann grid illusion and even shows a mild diminishing effect for grids with higher luminance contrast. However, chromatic Herman grids produce illusions that demonstrate chromatic assimilation even though they are predicted to illicit chromatic contrast. It is postulated that this assimilation occurs because of color coding that occurs after the luminance processing that is the basis of the illusion.

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Introduction

The Hermann Grid

The Hermann grid illusion was first described by L. Hermann in 1870. Its classic form consists of intersecting horizontal and vertical white bars placed on a black background, yielding illusory grey smudges at the intersections of the white bars. See Figure 1. Several attempts have been made to explain the processes behind this illusion. Baumgartner (1960) proposed that the illusion was due to lateral inhibition circuitry within the retina. He argued that the dark smudges were the result of increased lateral inhibition of on-center receptive fields. When an intersection coincides with an on-center receptive field, there will be more inhibition from the surround than when the same field coincides with a bar alone. The result is an apparent decrease in brightness observed at the intersections compared to the bars. The same holds true for black bars on a white background, except instead of on-center cells, off-center cells are displaying the lateral inhibition. This explanation has been used and developed further to account for their variations on the grid (Spillman and Levine, 1971; Berbaum and Chung, 1981; Oehler and Spillman, 1981; Wolfe, 1984; Spillman, 1994). In support of this theory, neurophysiologists have demonstrated center/surround antagonism in retinal ganglion cells (Kuffler, 1953; Werblin and Dowling 1969). The fact that one does not typically observe the illusion in the center of gaze does not contradict this explanation. In the fovea, there is a dense packing of cone photoreceptors. The ganglion cells responding to these photoreceptors then have correspondingly small receptive fields. There would be several receptive fields completely within the intersection of the grid as well as in the bar regions adjacent to the intersection. Therefore, the receptive fields exhibit the same

stimulation in the bars as in the intersection leading to no apparent darkening/lightening of the intersection.

A problem with Baumgartner's theory was shown by Spillmann in 1971. He demonstrated that if the grid was rotated by 45º the illusion was greatly diminished. See Figure 2. If the retinal lateral inhibition theory was correct, one would expect the illusion to remain constant at all degrees of rotation. More recent work has shown, quantitatively, that the illusion diminishes the further it is rotated from the horizontal/vertical position to a minimum at 45º (de Lafuente and Ruiz, 2004; Ash, Comerford, and Thorn, 2003). These works suggest that there needs to be a cortical mechanism to account for the perceived illusion. One possibility is the oblique effect (Appelle, 1972). The oblique effect causes an increase in the threshold of certain visual perception tasks, such as acuity and contrast detection, when targets are presented obliquely (Campbell, Kulikowski, and Levinson, 1966). Subjects demonstrate lower thresholds with these tasks when the targets are aligned vertically or horizontally, indicating that orientation selective cells may play a role in the illusion. Orientation selective neurons are first seen in the visual pathway in the striate cortex in the form of simple and complex cells (Hubel and Wiesel, 1962; 1968).

The next problem with the lateral inhibition model came from experiments using colored versions of the grid as opposed to the standard achromatic form (McCarter, 1979; Levine, Spillmann, and Wolf, 1980). The results of these experiments showed that the illusion was still observed when using chromatic stimuli. However, the illusory spots appeared to be of similar color to the background presented. See Figure 3. This finding contradicted the predictions of Baumgartner's (1960) center-surround receptive field

hypothesis, and McCarter (1979) proposed that the illusory spots were due to double-opponent cells. A double-opponent cell, for example, is a cell with a receptive field consisting of an on-red/off-green center with an off-red/on-green surround. In this case, if the receptive field was at the intersection of green bars on a red background, the red would have stronger excitation (due to less off-red stimulation) and the green would have less inhibitory effect (due to more on-green stimulation) than the same receptive field located on a bar alone. These double opponent cells have not been found in the primate retina (Daw, 1972), although they have been found in the visual cortex (Livingstone and Hubel, 1984). However, these cells exhibit very little orientation selectivity and have circular symmetric receptive fields (Conway, 2001).

Oehler and Spillmann (1981) proposed that the illusion was mediated by R and G cones only. Their experiments used colors that coincided with different tritanopic confusion lines on the CIE diagram. These colors can only be distinguished by differences in excitation of the B cones. The colors that belonged to the same confusion line were easily interchanged with little effect on the strength of the perceived illusion. It was concluded that the B cones had very little effect on the intensity of the illusion. They showed that for a strong illusion to occur, the tritanopic purity difference between the underlying stripe and the background had to be greater than the tritanopic purity difference between the overlying stripe and the background.

The most recent attempt at explaining the Hermann grid illusion came from Schiller and Carvey (2005). They provided various other examples in which the retinal ganglion cell theory proposed by Baumgartner could not fully explain their observations. They

manipulated the grid in various ways that did not alter the center/surround activation of the retinal ganglion cells and showed a reduction of the illusion. Furthermore, they showed that by adding more intersecting bars (diagonally through the intersections) the illusion did not gain in magnitude even though the center/surround antagonism was increased. All of these changes were not shown experimentally, but were presented in the paper as demonstrations for the reader.

Schiller and Carvey's (2005) theory involves the S1 type simple cells in the visual cortex. These S1 cells consist of one subfield that is either excited by the ON retinal ganglion cell system (the ON system is excitatory for light increment (Kuffler, 1953)) or the OFF system (excitatory for light decrement). Thus, ON S1 cells are excited by light edges that correspond to their receptive fields and conversely, OFF S1 cells are excited by dark edges (Schiller, 1976). These S1 type simple cells also demonstrate orientation selectivity with elongated receptive fields, of varying lengths, along their axis of orientation. When one of these elongated receptive fields corresponds to an intersection of the same orientation, there is no continuous edge, thus producing a relative decreased response compared to similar oriented cells that fall completely on a single bar. This decreased response is interpreted as a darker (or lighter with dark bars) area, hence the illusion of smudges at the intersections. In addition, Schiller and Carvey assume that some of these S1 type cells are also color selective. They make this assumption based on the fact that some cells in area V1 receive selective input from the midget retinal ganglion cells (Schiller and Logothetis, 1990) and that the koniocellular system (some blue/yellow mediation) terminates in V1 (Chatterjee and Callaway, 2003). Therefore, they propose that the illusory effects seen in the Hermann

grid, both achromatic and chromatic, are the product of the co-activation of color selective S1 cells, ON selective S1 cells, and OFF selective S1 cells.

Figure 1 – The Hermann Grid

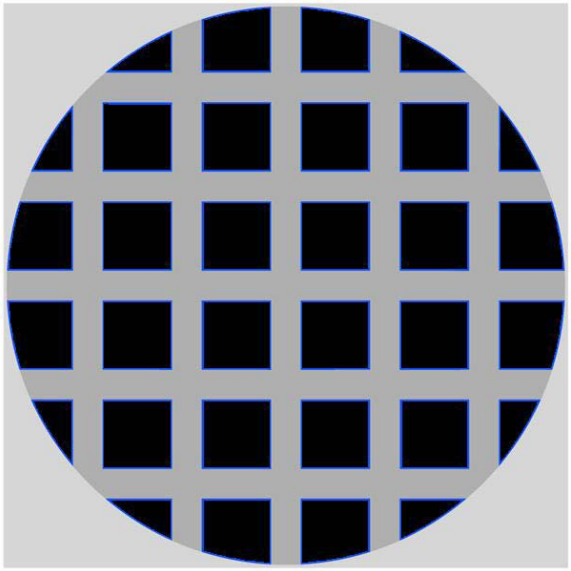


Figure 2 – The Hermann Grid Rotated 45°

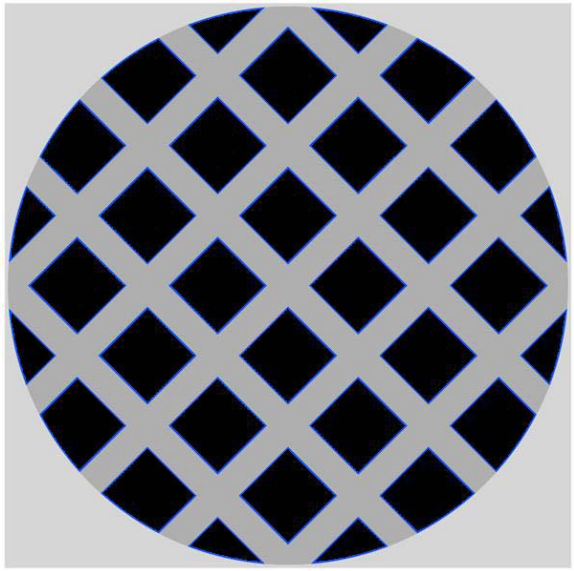
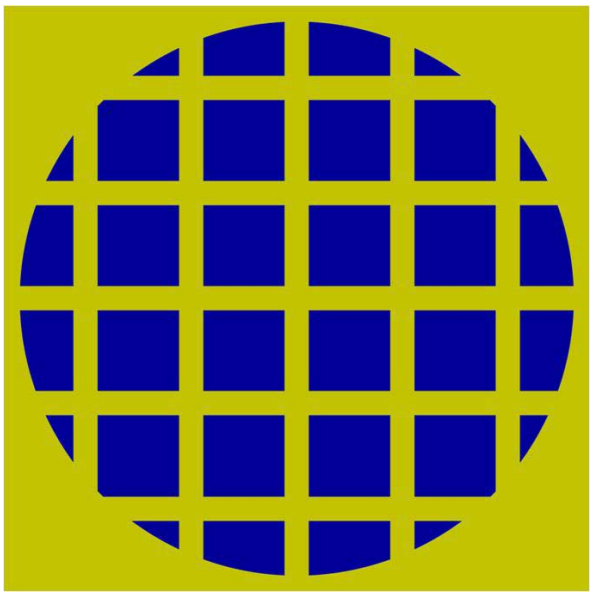


Figure 3 – Chromatic Hermann Grid



Orientation

It is widely accepted that orientation plays a large role in visual perception. Appelle (1972) coined the term "oblique effect" to describe the phenomenon where humans perform better on visual tasks involving stimuli oriented vertically or horizontally. This has been demonstrated in many experiments involving spatial acuity thresholds (Berkley, Kitterle, and Watkins, 1975), contrast sensitivity (Campbell and Kulikowski, 1966), orientation discrimination (Bouma and Andriessen, 1968), vernier acuity (Saarinen and Levi 1995), motion discrimination (Ball and Sekuler 1980), and reaction time (Attneave and Olson 1967).

Early studies believed these anisotropies were the result of physical properties of the visual system and attributed the oblique effect to astigmatism, spherical aberrations (Leibowitz, 1953), diffraction (Weymouth, 1959), density of photopreceptors (Shlaer, 1937; Hartridge, 1947), and microsaccadic eye movements (Brown, 1949). However, experimental data has since revealed there to be no significant contribution from these physical factors (Higgins and Stultz, 1950; Nachmias, 1960). In fact, the effect has clearly been shown to have a neural basis (Campbell and Kulikowski, 1966; Maffei and Campbell, 1970; Li, Peterson, and Freeman, 2003).

The recent work of Li et al (2003) has given much more insight into the oblique effect. They found more horizontally biased cells in the primary visual cortex (of cats) than both vertically and obliquely biased cells. These horizontally biased cells also have a more narrowly tuned response compared to their counterparts. This finding agrees with several psychophysical studies for orientation discrimination (Mustillo, Francis, Oross, Fox, and Orban, 1988), orientation detection (Heeley and Buchanan-Smith, 1990), spatial resolution

(Coletta, Segu, and Tiana, 1993), and contrast sensitivity (Mitchell, Freeman, and Westheimer, 1967). Li et al (2003) also conclude there to be a slight vertical preference over oblique stimuli due only to the greater number of cells tuned to vertical orientation. The tuning widths of these two cell types were not found to be significantly different. They were also able to provide evidence that contradicted Vidyasagar and Urbas' (1982) proposed linear feed-forward theory. That theory suggested that slight orientation biases found in the lateral geniculate nucleus (LGN) (experiment done with cats) could, via linear feed-forward connections, play a significant role in orientation selectivity in the primary visual cortex. Li et al (2003) demonstrated a non-linear intracortical mechanism to be responsible for orientation preferences in the primary visual cortex. Another conclusion from Li et al (2003) was that meridional anisotropies are only found in V1 simple cells, not complex cells. This contradicts the classic model of simple cells feeding into complex cells with both showing orientation selectivity (Hubel and Wiesel, 1962 and 1968). This finding implies that not all simple cells connect directly with complex cells and therefore, possibly link straight into visual processing areas responsible for our perception of the environment. The last finding from their work reveals that these simple cells that demonstrate orientation selectivity are only those that prefer relatively high spatial frequencies. This is consistent with the findings of Berkley et al (1975) that show there to be no oblique effect present for grating stimuli with spatial frequencies ≤ 8 cycles per degree.

This last finding implies we should not experience an oblique effect with our Hermann grids because they are comprised of approximate square wave patterns with half cycle spatial frequencies calculated to be < 8 cycles per degree. These half cycle spatial

frequencies were calculated using the width of the bars in the grid pattern as a half cycle of the highest spatial frequency observed. This does not factor in higher order harmonics that would also be present, albeit at a much lower amplitude. Also, the oblique effect is a threshold phenomenon, further discounting its role in the perception of the Hermann grid illusion which is presented at suprathreshold levels.

Chromatic Induction

One visual process that might help explain the Hermann grid illusion is chromatic induction. Chromatic induction refers to the perceived color change of a stimulus induced by a nearby chromatic stimulus in the same field of view (Wyszecki, 1986). There are two types of classic chromatic induction – chromatic contrast and chromatic assimilation. Chromatic contrast refers to an induced color change that is the opposite or complementary to the inducing stimulus. For example, a white test field would appear green when viewed with a red inducing field. Chromatic assimilation occurs when the induced color change is similar to the inducing stimulus. For example, a white test field would appear red when viewed with a red inducing field.

Several studies have shown that the most important factor for determining the type of induction is the geometry of the stimulus display (Helson and Joy, 1962; Helson, 1963; Fach and Sharpe, 1986; Smith, Jin, and Pokorny, 2001). These studies show that color contrast tends to occur for simple displays whereas assimilation occurs with more complex displays. Indeed, assimilation is more common in our daily visual scenes than contrast (De Valois and De Valois, 1988). One key factor is in the spatial frequency of the display. A simple square

wave pattern can show both contrast and assimilation depending on its spatial frequency. Fach and Sharpe (1986) showed that with a square wave pattern, the change from chromatic contrast to chromatic assimilation occurs at 4-6.7 cpd. Based on these findings, we would expect to see chromatic contrast when viewing chromatic Hermann grids. Our grids are very simple displays with approximate square wave gratings with spatial frequency < 4cpd. However, the illusory spots perceived with our grids demonstrate what appears to be chromatic assimilation at first inspection.

Chromatic contrast has long been explained by the two-process theory of chromatic adaptation (Jameson and Hurvich, 1972; Shevell, 1978: from Shevell, 2003). This model says that the appearance of the test field is affected by the inducing field in two ways. First, the inducing field determines the gain of the receptor signals that encode the inducer. This is similar to the von Kries Coefficient Law (Von Kries, 1905 as cited in Shevell, 2003). The von Kries Coefficient Law says that chromatic adaptation sets the amplitude of the response associated with each type of color receptor. It assumes that the relative sensitivity to different wavelengths for each type of receptor is unaltered. Second, it causes an additive shift to chromatic opponent neural systems. These opponent systems, red/green, blue/yellow, and white/black, receive a weighted combination of the signals from the three color receptor types. Therefore, a chromatic surround alters the receptoral gain which then induces an additive gain away from the appearance of the surround. For example, a red surround would cause an adaptation that lowers the response to red by the cones; this causes a shift towards green at the opponent neural system.

The process behind chromatic assimilation was first thought to be the result of optical aberration and light scatter in the eye. Later studies proposed a possible neural mechanism to explain assimilation (Hurvich and Jameson, 1974; Sugita, 1995). Hurvich and Jameson proposed a post-receptoral model that employed parallel processing using multiple size receptive fields. With a grating pattern, neurons with large receptive fields would encompass many bars and respond as if the light was mixed. Neurons with small receptive fields would respond to a single bar. This results in both a blending of light (assimilation) and a preservation of spatial pattern. Indeed, it has been shown that color selective cells have larger receptive fields and respond to lower spatial frequencies (De Valois and De Valois, 1993). A more recent study has once again shown that optical aberrations play a role in chromatic assimilation in a grating pattern (Smith et al, 2001). The purpose was to use a line spread function to calculate the amount of light scatter in their stimuli. The theoretical calculations of Smith et al (2001) agreed with the data they obtained from observers in the experiment. They observed a change to chromatic assimilation above 4 cpd, which is the same point at which their line spread calculations predicted that spread light was negligible. However, as shown by de Weert and van Kruysbergen (1997), optical aberrations and light scatter cannot fully explain the chromatic assimilation observed in more complex stimuli.

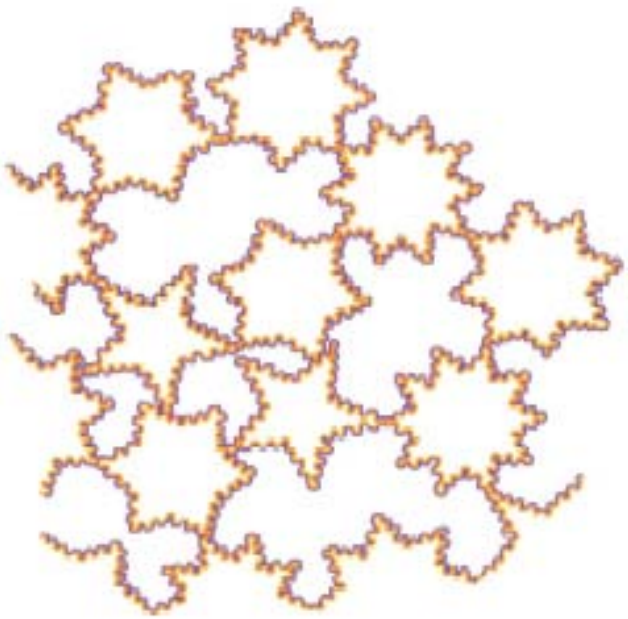
These studies all demonstrated short-range color assimilation. The Watercolor Effect is an example of long-range color assimilation. The Watercolor Effect, first described by Pinna (1987), is observed when a test field assumes the color attribute of the contour that surrounds the field. See Figure 4. The perceived color remains uniform across the entire field and continues to be present up to about 45º of visual angle (Pinna, Brelstaff, and

Spillmann, 2001). The effect is strongest for a thin (6 arcmin) light contour surrounded by a thin dark contour. It is dependent on luminance contrast of the two contours and becomes very weak at isoluminance (Pinna, 2005; Devinck, Delahunt, Hardy, Spillmann, and Werner, 2005). Chromatic aberrations play a role in the effect, but only at higher spatial frequencies with small areas of induction (Devinck, Delahunt, Hardy, Spillmann, and Werner, 2006). It is proposed that the effect is the result of a neural two stream parallel system as predicted by the FACADE model (Pinna and Grossberg, 2005). These two processes, boundary grouping and surface filling in, are carried out by a boundary contour system (BCS) and a feature contour system (FCS) (Grossberg and Mingolla, 1985a; 1985b). In the BCS, edge contrast determines boundary strength and nearby boundaries compete with each other through inhibition. A high contrast boundary will actually inhibit a nearby boundary of lesser contrast. The FCS involves the filling-in processes of color and brightness. When a boundary is weakened by a competing boundary, it allows for the outflow of color and brightness information into the adjacent area. This spreading therefore would not occur at the stronger boundary. This explanation also holds for another color assimilation effect - neon color spreading (Pinna and Grossberg, 2005).

The Hermann grid has a low spatial frequency (< 4 cpd) and is a very simple visual target. Based on these two facts, we would expect to observe basic chromatic contrast with the chromatic grids. However, what is perceived appears to be chromatic assimilation. We know that simple chromatic assimilation does not occur based on previous studies using square wave gratings (Fach and Sharpe, 1986; Smith et al, 2001). Those studies

demonstrated the shift from chromatic contrast to chromatic assimilation occurs between 4 and 6.7 cpd.

Figure 4 – Example of the Watercolor Effect



©Pinna et al, 2001

Purpose

The purpose of this project was to test three hypotheses regarding the effect of color and orientation on the perception of the Hermann Grid Illusion. The first experiment tests the hypothesis that luminance differences alone do not mediate the illusion. The second experiment tests the idea that chromatic grids will behave similarly to achromatic grids when

viewed at different angles of tilt. The third experiment sought to isolate the chromatic portion of the tilted grids in order to study the effect of color alone on the illusion.

Experiments

Subjects

All subjects tested were subject to the same criteria. They had to be correctable to 20/20 acuity with their habitual correction. They could not have any color vision defects or ocular pathologies. Color vision was assessed using the Farnsworth D-15 test and subjects were questioned about their eye history. They were required to have had a complete eye exam within the previous 6 months. All but one subject was enrolled in the Doctor of Optometry degree program at the New England College of Optometry, therefore participating in several eye examinations per year as test subjects for their classmates during clinical lab sessions. The non degree candidate was personally assessed by Dr. Bodkin prior to participating in the study. They were asked to read and sign an informed consent form prior to testing and were compensated for their time. All experiments were conducted in accordance with the guidelines provided by the Declaration of Helsinki and were approved by the Internal Review Board of the New England College of Optometry.

Experiment 1

Purpose

The purpose of this experiment was to study the effect of luminance contrast on the chromatic Hermann grid illusion.

Methods

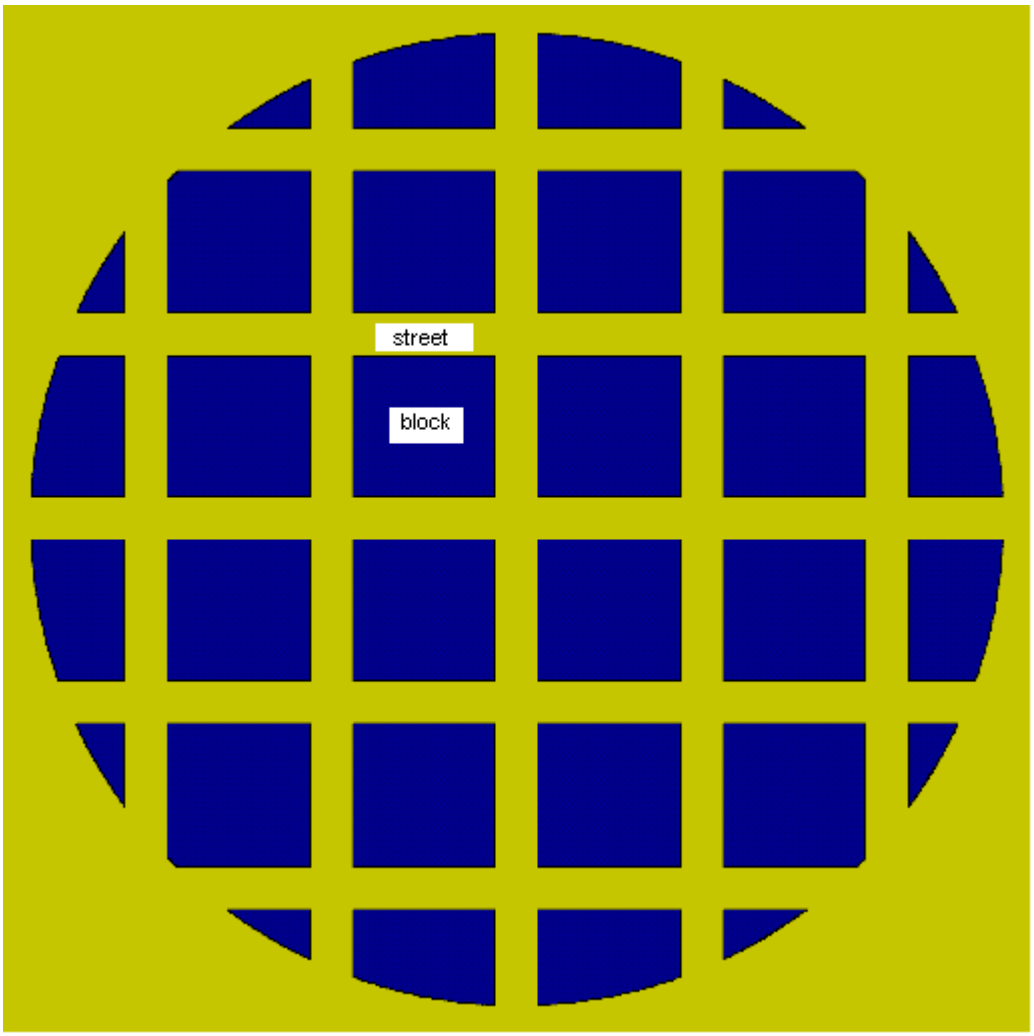
A circular Hermann Grid composed of 5 vertical and 5 horizontal bars (See Figure 5) was presented to subjects on an Image Systems 17 inch computer screen. The grids were created and presented using Macromedia Director 6.0 on a Macintosh 9.0 operating system. The circle was 17 centimeters in diameter, each line was 0.75 centimeters in width and they were separated by 2.5 centimeters. The test distance was 3 meters. Viewing the grids from this distance produces an angular subtense of 0.143° for the lines. This results in a highest half cycle spatial frequency of 3.49 cycles per degree. Half cycle spatial frequency was defined by using the width of the bars in the stimuli as representing a half cycle. The spatial frequency determined does not account for lower amplitude harmonics that would be present. Seven sets of grids were shown to 7 subjects. The stimuli were defined by grey bars seen against a black background, grey against red, grey against green, grey against blue, green against red, red against green, and yellow against blue. Each set was presented with 18 different contrast levels defining the bars. The order of the presentation of the stimuli was randomized within a given set. Two randomly picked stimuli were tested a second time to check for variability. These were tested after all 18 grids in each set had been presented. If a subject varied by more than 1 unit of estimation for either repeated stimulus, the data were discarded. The subjects were asked to use a rating scale of 1-5 to rate the magnitude of the illusion – 1 being unseen and 5 being the strongest illusion. The 5 rating was based on a set grey on black grid (98% contrast) presented to each subject before the test was administered. The subjects were encouraged to use any real number to describe the illusion. They were

allowed to use numbers greater than 5 if they felt it necessary. The subjects were also asked to name the color of the hue of the illusion for each grid.

Luminance values of the grids were measured using a PhotoResearch Spectra® Pritchard® photometer. All readings were taken under the same testing conditions used in the experiment. Three readings were taken for 5 different areas on the lines (variable) for each grid and averaged. One reading was taken at 4 different locations of the background (constant) color for each grid and averaged. The difference in luminance was then calculated for each grid. The isoluminant point was defined by the point tested with the difference in luminance value closest to 0. One limitation with the Macromedia Director software and designing the grids is that one cannot always create the exact luminance values desired. It was a challenge to get exactly zero luminance difference between the colors used for the grids. Many different combinations were tested for making each color. Then a red/green and blue/yellow were chosen that resulted in the least difference with the most leeway to change the luminance in either direction. Therefore, an isoluminant point had to be defined. Magnitude estimation data obtained were averaged and plotted against contrast. Percent contrast was calculated using the Michaelson ratio:

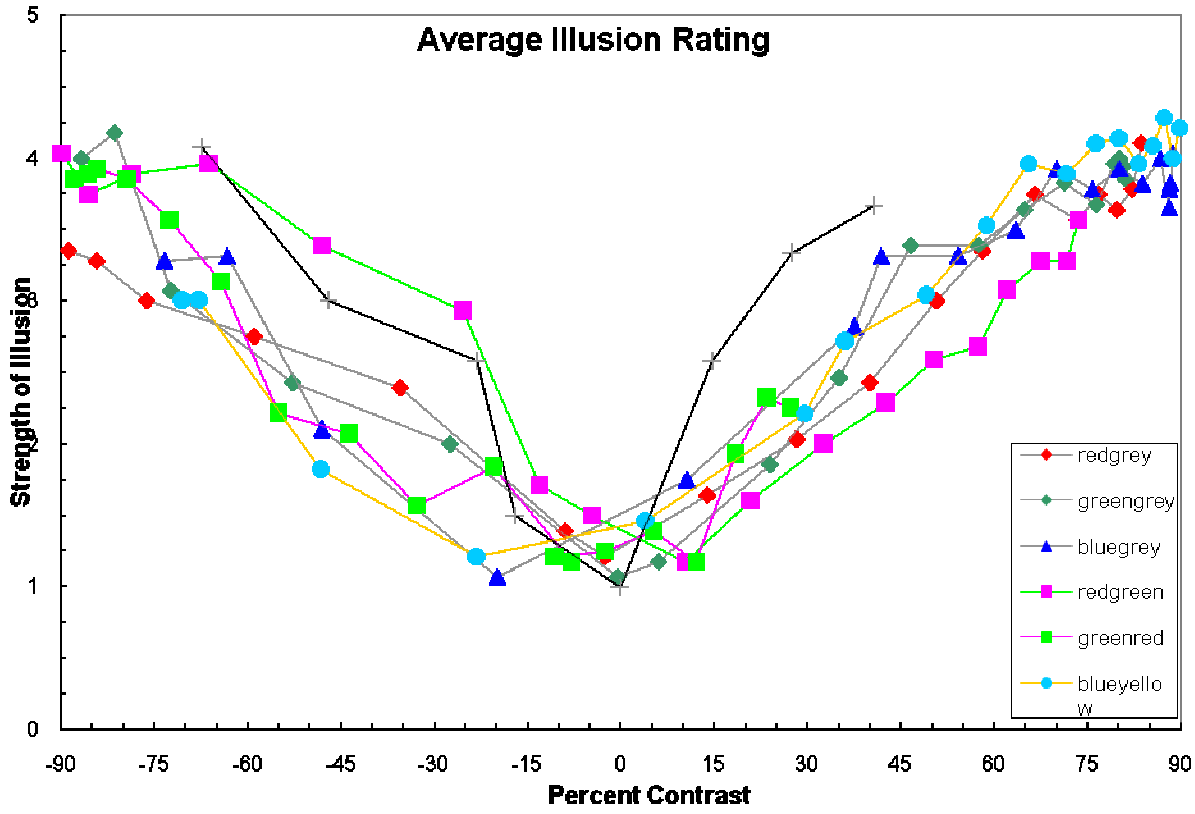
$$\% \text{ contrast} = (\text{Luminance}_{bar} - \text{Luminance}_{block})/(\text{Luminance}_{bar} + \text{Luminance}_{block}) \times 100$$

Figure 5 – Example of Grid Used in Experiment 1



Results

Graph 1 – Average Illusion Rating, Experiment 1



All subjects perceived the Chromatic Hermann Grid Illusion. For all conditions tested, the lowest average rating occurred at or near the defined isoluminant point and the highest average rating coincided with maximum or near maximum contrast. See Table 1. For the grids comprised of grey bars, subjects rarely perceived an illusion at the defined isoluminant point. In contrast, for the grids containing chromatic bars, a slight majority perceived a weak illusion at the isoluminant point. See Table 2. For grids incorporating an achromatic stripe, the subjects reported that the illusion appeared to be either similar to the color of the blocks or grey. The green stripes on the red blocks resulted in 5 subjects

reporting a reddish hue, 1 and orange hue, and 1 a greenish hue. For the red on green condition, 5 reported seeing a greenish hue, 1 a grey, and 1 a reddish hue (this subject also reported the greenish illusion for the green on red grids). Interestingly, for the yellow on blue grids, 5 observers reported a green illusion while only 2 reported a blue one. All grid combinations showed a decrease in the magnitude of the illusion as they approached isoluminance. See Graph 1.

Table 1 – Lowest and Highest Average Illusion Rating, Experiment 1

Condition Tested	Lowest Avg Rating (% Contrast Tested)	Highest Avg Rating (% Contrast Tested)
grey on grey	1.00 (**0%**)	4.11 (**67%**)
grey on red	1.21 (**2%**)	4.11 (**84%**)
grey on green	1.07 (**0.5%**)	4.18 (81%)
grey on blue	1.07 (**10%**)	4.04 (**89%**)
green on red	1.18 (10%)	4.04 (**90%**)
red on green	1.18 (8%)	3.92 (84%)
yellow on blue	1.21 (23%)	4.28 (87%)

Bold: lowest/highest contrast tested

Table 2 – Subjects Reporting No Illusion at Isoluminant Point

Condition Tested	% reporting no illusion at isoluminant point (n=7)
grey on grey	100
grey on red	71
grey on green	86
grey on blue	86
green on red	43
red on green	43
yellow on blue	43

Discussion

It is evident that luminance contrast plays a large role in the perception of the chromatic Hermann grid illusion. The magnitude of the illusion diminishes as the contrast between the bars and blocks decreases reaching a minimum at or near isoluminance. This agrees with the findings of Spillmann and Levine (1971) and Oehler and Spillmann (1981). It is interesting to note that all but one of the chromatic grids showed a lower magnitude of illusion for higher contrasts when compared to the achromatic grid. This suggests that there is a mild diminishing effect to the illusion attributable to color.

One interesting point from Table 1 is that the three all chromatic conditions tested showed their lowest average rating at contrast levels above the lowest one displayed. This could mean that at isoluminance, chromatic differences may play a role in determining the strength of the illusion.

The next step in attempting to understand the Hermann grid illusion is to study the effect of tilting the grid. Obliquely presented achromatic grids result in a decrease in the perceived magnitude of the illusion. The next experiment will compare any differences the effect of orientation has on the illusion between the achromatic and chromatic versions. It is expected that the chromatic illusion will diminish with increasing tilt away from the cardinal directions. Also, based on the previous results, we expect that the magnitude of the chromatic illusion will be slightly less than that of an achromatic version.

Experiment 2

Purpose

The purpose of this experiment was to study the effect of tilt on the chromatic Hermann grid illusion.

Methods

The test stimulus was a circular Hermann Grid with a diameter of 12.5 centimeters. The grid consisted of 5 lines intersecting orthogonally with 5 other lines. These lines have a width of 0.65 centimeters and are separated by 1.55 centimeters. The stimulus was presented to the subject in a dimly lit room at a distance of 1 meter. At this test distance, the lines correspond to a 0.372° angular subtense. This resulted in a highest half cycle spatial frequency of 1.34 cycles per degree. This Hermann Grid, consisting of 21 intersections and a 50% contrast level (contrast was determined using the same technique as in Experiment 1), was presented to subjects on an Apple Studio Display 17 inch computer monitor. Three sets of 10 grids were shown to 16 subjects. The 3 sets were defined by grey grids on a grey background, grey on blue, and grey on red. Each set was presented at 0°, ±5°, ±10°, ±15°, ±30°, and 45° of rotation. The subjects viewed the grids through their habitual refractive prescription. They were asked to use a magnitude estimation technique, based on a 98% contrast standard grid, to rate the illusion seen. The rating scale was from 1-5, where 1 designated no illusion and 5 being the strength of the illusion for the standard grid. Subjects were encouraged to use any real number on the scale and were allowed to use numbers greater than 5 if they deemed it necessary.

To control for the oblique effect, 2 additional achromatic sets were tested. These 2 sets consisted of 11 different contrast levels (5 positive, 5 negative, and isoluminant). They were presented at 0° and 45°. Since the oblique effect is a threshold phenomenon, the purpose of these two control sets was determine if there was a change in the threshold at which the grid, not the illusion, could be detected based on its orientation. In this control test, the subjects reported whether or not they were able to observe a grid (not the illusion) at each contrast level.

The experiment was run on each subject at 2 separate times, a minimum of 20 minutes between runs, and grids were presented in a random order within each set. The grids were created and presented using Macromedia Director 6.0 software on a Macintosh 9.0 operating system.

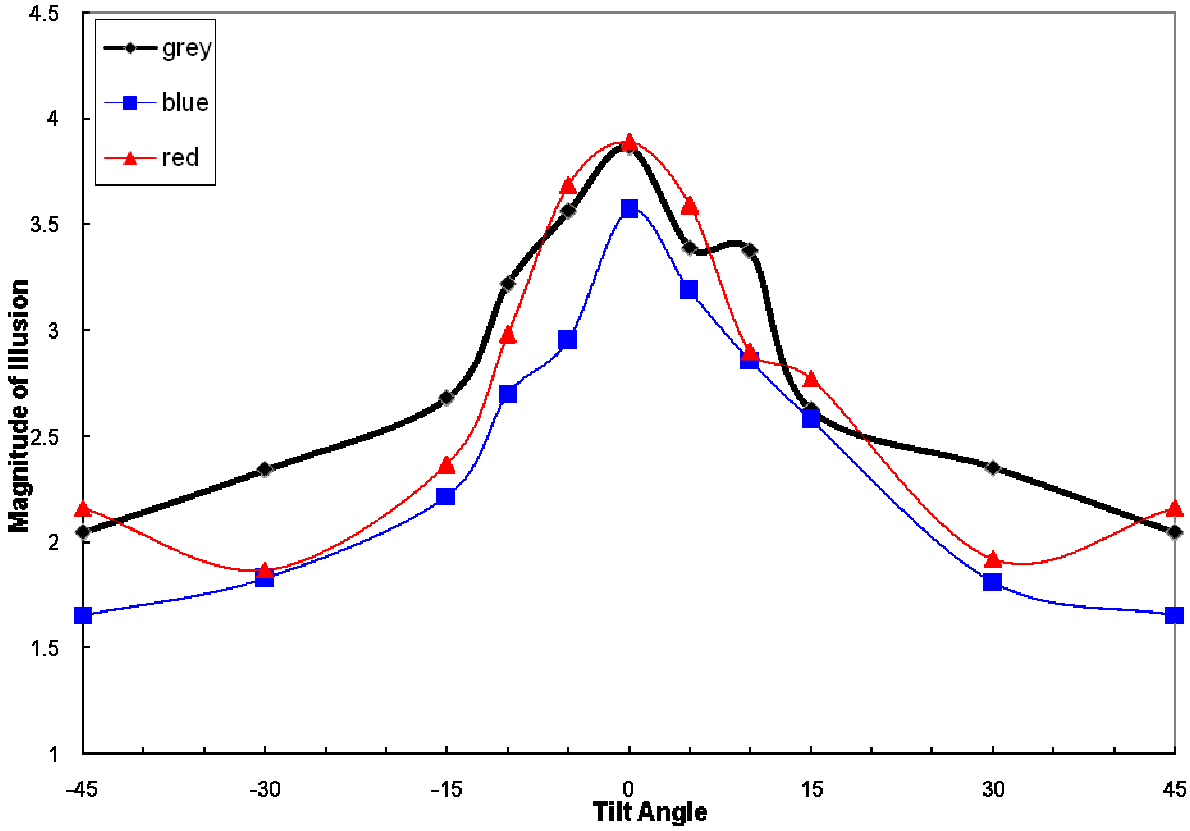
According the Oehler and Spillmann (1981), tritanopic purities of the grid elements play an important role in determining the strength of the illusion. Therefore, tritanopic purities (p_t) were calculated for the chromatic grids using a modified version of the tritanopic purity equation developed by Valberg and Tansley (1977) (Oehler and Spillmann, 1981). The equation is as follows:

$$p_t = 0.77\ X - 0.49Y - 0.28\ Z$$

where X, Y, and Z denote tristimulus values. Our values were obtained using The Digital Color Meter software. The Digital Color Meter is proprietary software for the Macintosh operating system that displays approximate chromatic information about the point on the diplay where the cursor is set.

Results

Graph 2 – Average Illusion Rating, Experiment 2



In the first part of the experiment (control), contrast thresholds for detecting the grid, 2 subjects (13%) demonstrated a higher contrast threshold for the oblique grid, 1 subject (6%) had a lower threshold, and 13 (81%) displayed no difference in their contrast thresholds for the 2 orientations of the grid. Tilt had no significant effect on contrast threshold for the Hermann Grid.

For the second part of the experiment, magnitude estimations for the illusion, all 16 subjects reported perceiving the illusion. There were 3 data sets produced – grey on grey, grey on blue, and grey on red. For all three conditions, most of the subjects perceived the

strongest illusion for grids presented with ≤5° of tilt. The weakest illusion was observed a majority of the time for grids with 45° ± 15° of rotation. See Table 3. The magnitude of the illusion diminished with tilt angle in all three sets tested. The average diminishing of the illusion at 45° of tilt was 69.4%. See Table 4, See Graph 2

An ANOVA was performed on the data set. A linear regression for magnitude versus tilt was found for all 3 groups of stimuli. The regression slopes for all 3 groups were essentially equal - 0.040, 0.042, 0.045 (grey, blue, red). All 3 groups also showed significance – $p < 0.0001$, $p < 0.0001$, $p = 0.0013$. All 3 groups also had very high correlations – $R = 0.933$, $R = 0.937$, $R = 0.864$. Between groups, the only significant finding was the difference in magnitude of the illusion between the grey grids and the blue grids ($p = 0.0032$). The blue grids versus the red grids showed a borderline significance ($p = 0.0512$) and the grey grids versus the red grids showed no significance ($p = 0.4663$).

Tritanopic purity differences were as follows – difference between the grey lines and blue background was 6.808 and the difference between the grey lines and red background was 6.792. The purity differences between the underlying stripe/background and overlying stripe/background were 0 since both stripes were the same.

Table 3 – Orientation of Strongest and Weakest Illusion Perceived

Condition tested	Strongest illusion perceived at ≤ 5° of tilt (n=16)	Weakest illusion perceived at 45° ± 15° of tilt (n=16)
Grey on grey	81%	88%
Grey on blue	88%	81%
Grey on red	100%	75%

Table 4 – Lowest and Highest Average Rating, Experiment 2

Condition Tested	Lowest Avg Rating (Tilt)	Highest Avg Rating (Tilt)
Grey on grey	2.04 (45°)	3.86 (0°)
Grey on blue	1.65 (45°)	3.57 (0°)
Grey on red	1.87 (30°)	3.89 (0°)

Discussion

As expected, tilting of the chromatic Hermann grid resulted in a decrease in the perceived strength of the illusion. One might assume that this is caused by an oblique effect. That is unlikely for two reasons. First, the oblique effect was measured during the experiment and was shown to have no impact on the grids tested. Second, the oblique effect only occurs for stimuli with spatial frequencies ≥ 8 cycles per degree. Therefore, there is some other factor that causes this decline in magnitude for obliquely presented grids.

The next experiment will look at the interaction between color and tilt in the Hermann grid illusion. According to the results of Conway (2001), chromatic processing in the visual cortex shows very little, if any, orientation selectivity. Therefore, it is expected that these two factors will act independently of one another.

Experiment 3

Purpose

The purpose of this experiment was to isolate the effects of color and tilt, so that we can observe the possible interactions between the two effects.

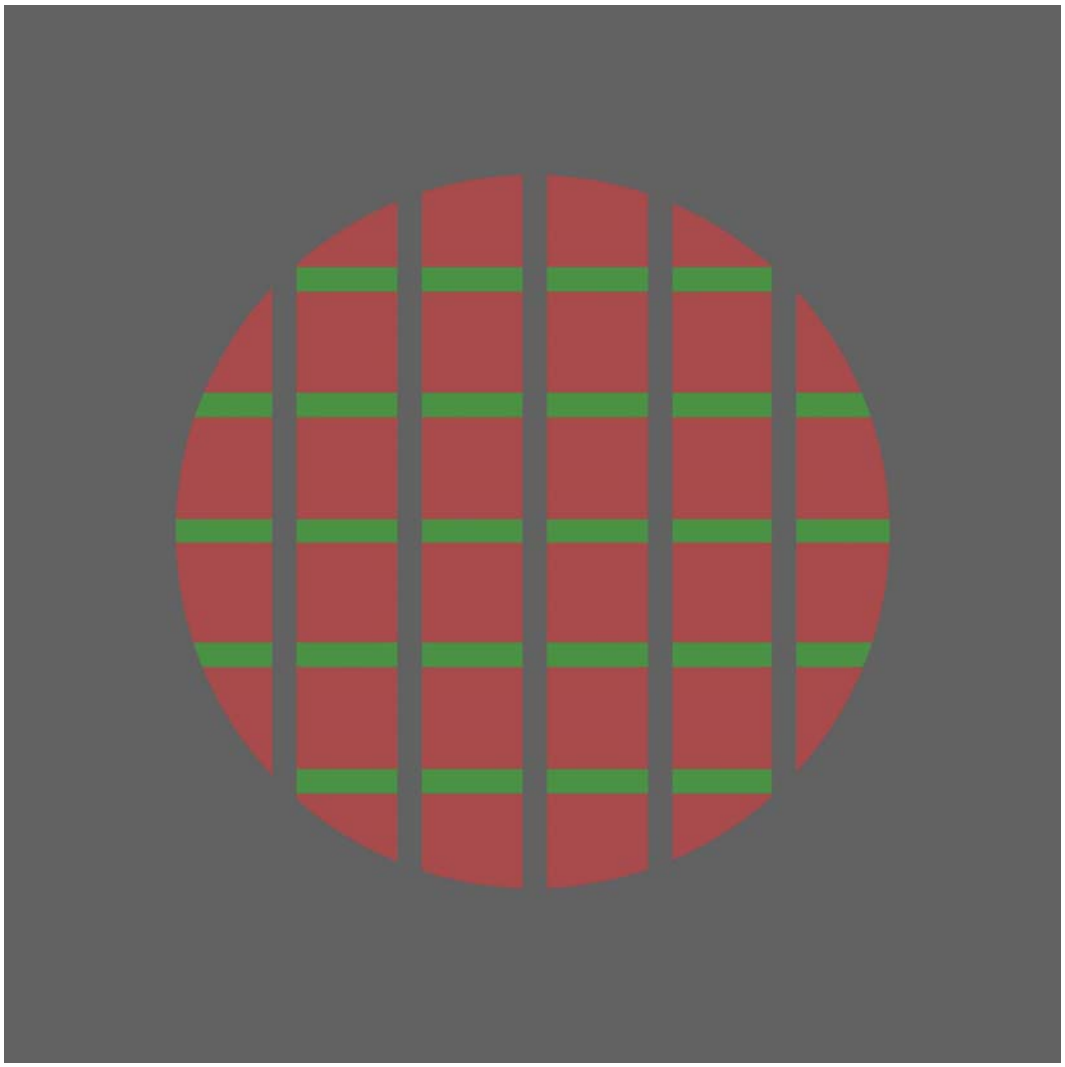
Methods

The test stimulus was a circular Hermann grid with a diameter of 8.7 centimeters. There were 5 stripes of 0.45 centimeter width orthogonal to 5 other stripes of 0.45 centimeter width. The stripes were separated by 1.1 centimeters. The stimulus was viewed at a distance of 1 meter. Therefore, the stripes subtend a 0.258° angle at this viewing distance. This results in a highest half cycle spatial frequency of 1.94 cycles per degree. The stimuli were presented on a 17 inch Apple Studio Display using Microsoft PowerPoint on a Macintosh OS 10. The stimuli were changed from experiments 1 and 2 to have an underlying stripe and an overlying stripe. See Figure 6. The grids were changed based on the work of Spillmann and Levine (1971), Levine et al (1980), and Oehler and Spillmann (1981). Their work used an underlying stripe (intersected) and an overlying stripe (intersecting). They demonstrated that this design allows for a stronger perceived illusion. This was achieved when the overlying stripe and the background were similar in contrast or color group and the underlying stripe was at maximum contrast difference or different color group than the overlying stripe. This difference in color group was the basis for the tritanopic purity difference theory from Oehler and Spillmann (1981). There were 4 groups of stimuli. One group had green blocks, red underlying stripes, and grey overlying stripes; one had red blocks, green underlying stripes, and grey overlying stripes; one had blue blocks, yellow underlying stripes, and grey overlying bars; and one had yellow blocks, blue underlying stripes and grey overlying stripes. Within each color group, there were 7 different orientations of the grid. The underlying (colored) stripes were set at 0°, 15°, 30°, 45°, 60°, 75°, and 90°. All color grids had a 50% contrast (contrast determined using same method as in Experiment 1).

Additionally, there were 2 standard grids with grey boxes with grey stripes. One grid had 98% contrast and the other had 5% contrast. There were 3 different slide shows composed with all grids arranged in a random order. Each show started with a comparison slide that showed both the high contrast and the low contrast grey grids. This served as a basis for estimating the magnitude of all future grids. The high contrast grid was assigned a magnitude of 5 and the low contrast grid was assigned a magnitude of 0. The subjects were instructed to use any real number to estimate the magnitude of the illusion seen in the test grids based on this standard criterion. This included allowing the subjects to use numbers greater than 5. The comparison slide was shown after every 5 test grids to remind the subjects of the basis for their estimations. After each grid, a blank slide was presented to control for afterimages. Subjects were asked to tell if they saw a strong, weak, or no afterimage while looking at the blank slide. Once the subject claimed the afterimage was no longer visible, they were allowed to continue to the next slide. Each subject was tested on 2 of the 3 shows with a minimum of 5 minutes between each run.

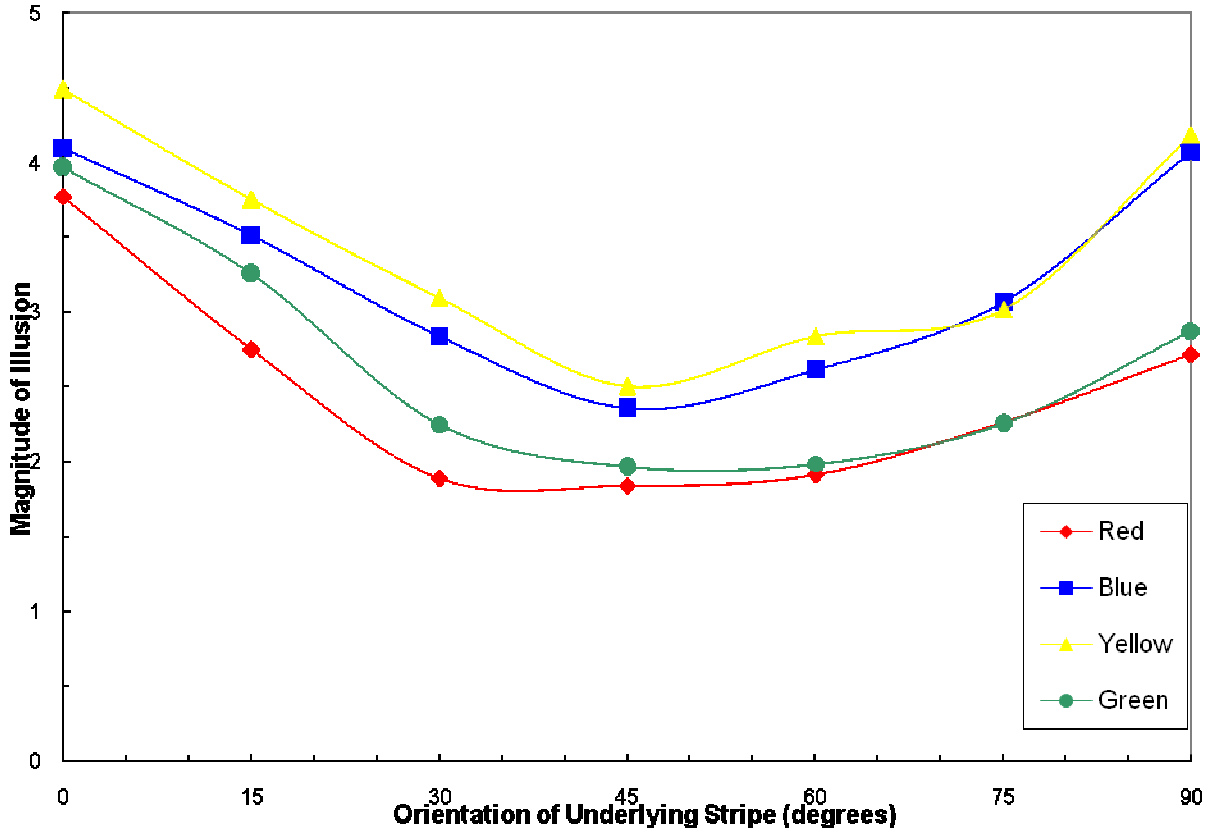
Again, tritanopic purities were calculated using the same method as in Experiment 2.

Figure 6 – Example of Grid Used in Experiment 3



Results

Graph 3 – Average Illusion Rating, Experiment 3



All 14 subjects perceived the illusion. For the blue background grids, 12/14 (86%) subjects perceived the strongest illusion at 0° or 90° orientations for the underlying (colored) stripe. Ten subjects (71%) observed the weakest illusion at 30°, 45°, or 60°. For the yellow grids, the strongest illusion was seen at 0°or 90° for 13 subjects (93%), while the weakest was perceived at 30°, 45°, or 60° for 13 subjects (93%). For the green background, 13 (93%) subjects reported the strongest illusion at 0° or 90° and 12 (86%) reported the weakest illusion at 30°, 45°, or 60°. For the red grids, 14 (100%) subjects perceived the strongest

illusion at 0° or 90° while 11 (79%) observed the weakest illusion at 30°, 45°, or 90°. The average diminishing of the illusion at 45° of tilt was 47.1%. See Table 5, See Graph 3

The ANOVA for the overall tilt effect was highly significant ($P < 0.000001$). In fact, using a Fisher's protected least significance difference test (PLSD), the data showed a significant illusion strength difference between most tilt conditions. See Appendix 1. The strength of the illusion also differed between colors. Fisher's PLSD tests show that the blue and yellow conditions do not differ from each other and the green and red conditions do not differ as well. It shows the strength of the illusion is significantly greater for the blue and yellow conditions than for the green and red conditions. See Appendix 2. The significance of the color x tilt interaction was equivocal ($P = 0.067$). There was no significant interaction effect for the blue and yellow conditions ($P = 0.92$), nor between the red and green backgrounds ($P = 0.32$). The blue and yellow grids have symmetry in the strength of the illusion at 0° and 90°, whereas the red and green grids show significantly stronger illusions for the 0° than the 90° orientation. This shows a possible color x tilt interaction that was not seen with the ANOVA analysis.

Tritanopic purity differences were higher for the blue/yellow conditions than for the red and green conditions. See Table 6

Two sets of trials were run for each subject. There was no significant difference between trials one and two, nor did any of the trials' interactions with stimulus conditions approach significance.

Table 5 – Lowest and Highest Average Illusion Rating, Experiment 3

Condition Tested	Lowest Avg Rating (Tilt)	Highest Avg Rating (Tilt)
blue background	2.36 (45°)	4.10 (0°)
yellow background	2.50 (45°)	4.49 (0°)
green background	1.96 (45°)	3.96 (0°)
red background	1.84 (45°)	3.77 (0°)

Table 6 – Tritanopic Purity Differences

block/US/OS	p(t) difference
red/green/grey	0.43134
blue/yellow/grey	1.38901
yellow/blue/grey	1.38628
green/red/grey	0.49896

US: underlying stripe, OS: overlying stripe

Discussion

The results show that there is no interaction between color and orientation in the perception of the Hermann grid illusion. Color processing and orientation processing are acting independently in the production of the illusory spots. Therefore, we can think of each process separately and try to look at how they are combined to give the final resulting illusion.

One interesting result in experiment 3 – the lowest average rating, occurring at the highest degree of tilt, was higher than that found for experiment 2. Both experiments showed an average lowest rating near 2, however, the scales were different. In experiment 2, the lowest possible rating was a 1. That was changed to a 0 for experiment 3. It was expected that the lowest average rating should have been between 1 and 1.5 for this data set. A

possible explanation is the difference in stimuli. The grids now contain an underlying stripe of color and an achromatic overlying stripe. This results in tritanopic purity differences between the background/underlying stripe and the background/overlying stripe that are not present in experiment 2 (overlying and underlying stripe are the same). According to Oehler and Spillmann (1981), this is the cause for a stronger illusion. Comparing the maximums in experiment 3 to experiment 2, there is also a slightly stronger illusion seen in experiment 3 even though the upper limit of the estimation scale was not changed. This further supports Oehler and Spillmann's idea of tritanopic purity difference as the driving force behind the strength of the illusion.

The data from experiments 2 and 3 agree well with previously published studies of the effect of tilt on the Hermann grid illusion. Oehler and Spillmann (1981) reported a 40% reduction in response frequencies with 45° of rotation (using grids with underlying and overlying stripes). This is similar to the findings in experiment 3 which showed a reduction of 47.1%. More recently, de Lafuente and Ruiz (2004) showed approximately a 2/3 reduction in the magnitude of the illusion with the grid rotated 45°. Experiment 2 resulted in a 69.4% reduction.

General Discussion

Luminance Contrast

Luminance contrast is the driving force behind the Hermann grid illusion. The illusion diminishes quickly as the contrast decreases. In fact, the illusory effect is minimal, if present at all, at isoluminance, even for chromatic grids. This agrees with the findings of

Spillmann and Levine (1971) and Oehler and Spillmann (1981). Oehler and Spillmann also showed that the illusion did not increase in strength if the overall brightness of the grid increased, as long as the contrast remained at isoluminance. It is easy to comprehend why luminance plays such a vital role in the production of the illusion; after all, the illusion is a perceived change in luminance at the intersections. There must be a change produced within the ON and OFF systems that results in this apparent change.

Orientation

Orientation of the Hermann grid also plays an important role in generating the illusion. The illusion shows a systematic decline in magnitude the further the grid is rotated from the standard vertical/horizontal positioning and is minimal for obliquely presented grids. At first glance, this appears to be a phenomenon associated with the oblique effect. However, the oblique effect was measured in experiment 2, shown not to exist, and therefore could not have any effect on the outcome. The grids used in the experiments were presented well above the threshold criterion. The threshold for observing the grid pattern was not altered by orienting the grid at 45º. Also, the oblique effect has been shown to be absent for stimuli with spatial frequencies ≤ 8 cycles per degree (Berkley et al, 1975), which is in the range of all of our stimuli. The highest half cycle spatial frequency tested was 3.49 cycles per degree. There would be higher harmonic frequencies present for our stimuli. These higher spatial frequencies have very low amplitudes and therefore were not considered to have a significant effect on the perception of the illusion.

So, what is causing this perceived diminishing of the illusion in obliquely presented grids? There must be orientation biased cells responsible for some aspect of the illusion. The first place orientation selective neurons are seen in the visual pathway is in the striate cortex, specifically area V1, in the form of simple cells (Hubel and Wiesel, 1962; 1968). There are several classes of simple cells that receive input into one or more subfields. These subfields are either part of the ON retinal ganglion system or the OFF system, where the ON system conveys lightness and the OFF system conveys darkness. According to Schiller (2005), the simple cells with only one subfield (S1), either ON or OFF, would be well suited for contributing to the perception of lightness and darkness. These simple cells also show a high degree of orientation selectivity that is very narrowly tuned, especially for horizontally biased cells (Li et al, 2003). Li et al (2003) also showed there to be more horizontally biased cells than vertically biased cells which were more numerous than obliquely biased cells. The receptive fields for these simple cells are elongated about the axis of their orientation.

As described by Schiller (2005) these S1 cells may mediate the perception of the illusion. When a particular ON cell's receptive field is aligned with one of the edges of the lines that create the grid, it has a constant activation that is equal to that of an OFF cell of similar orientation bias. When these same cells coincide with an intersection, they no longer correspond to a continuous edge. This causes them to have a decreased response in comparison to the aforementioned cells. This renders a perceived darkening of the area, hence the smudges are seen. The rest of the areas of the grid are processed by non-orientation specific cells that process lightness and darkness.

If now we consider the disproportionate numbers of simple cells tuned to each orientation, we can easily see why tilting the grid has such an effect. In the standard horizontal/vertical presentation, there are a lot of horizontally biased cells coinciding with the horizontal lines of the grid and to a lesser extent, many vertically tuned cells coinciding with the vertical lines. Therefore, there is an ample amount of orientation specific cells contributing to the perception of lightness and darkness to go along with the normal non-oriented contribution. This leads to a strong illusion as long as the difference between lightness and darkness is substantial. On the other hand, there are fewer obliquely tuned simple cells in V1. When viewing an obliquely presented grid, there is much less input coming from these orientation specific cells compared to the standard presentation. Thus, the non-oriented system overpowers the meager contributions from this system and a much weaker illusion is perceived.

This same reasoning is used to describe the oblique effect. There are more horizontally and vertically biased cells in the primary visual cortex which lead to visual anisotropies. However, what we are observing is not considered the classic oblique effect due to the low spatial frequencies used in the experiments. In fact, Berkley et al (1975) showed there to be no oblique effect present for grating stimuli with spatial frequencies ≤ 8 cycles per degree.

Color

Color appears to play a minor role in inducing the Hermann grid illusion. While color contrast alone may illicit a very weak, if any, illusion for an isoluminant grid, the

overall role of the color system appears to be a mild diminishing effect. Both color sets tested – red/green and blue/yellow – showed a slight decrease in the magnitude of the illusion compared to achromatic versions of the grid. However, this was only shown to be statistically significant for the blue/grey condition in experiment 2. Furthermore, in experiment 3, the red/green grids produced a significantly weaker illusion than their blue/yellow counterparts. This can be the result of different response rates of the L and M cones. Oehler and Spillmann (1981) proposed that the chromatic Hermann grid illusion is mediated by the L and M cones, with little or no contribution from the S cones. Their theory involves the difference in tritanopic purity for elements in the grid as the primary factor behind the strength of the chromatic illusion. In particular, the tritanopic purity difference between the background and the underlying stripe must be greater than the difference between the overlying stripe and the background. In experiment 2, grey lines were used on blue and red backgrounds. In those grids, the blue and red grids had identical tritanopic purity differences. However, the blue grids showed a marginally significant ($p = 0.0512$) weaker illusion than the red grids tested. This does not necessarily contradict Oehler and Spillmann's theory. In these grids, the difference in tritanopic purities of the underlying stripe and background versus the overlying stripe and background is zero since the overlying stripe and underlying stripe were identical. In experiment 3, the blue and yellow grids showed a larger tritanopic purity difference compared to the red and green grids tested. As expected, the blue and yellow presentations had a significantly higher estimated strength of illusion compared to the red and green grids, agreeing with the theory proposed by Oehler and Spillmann.

The more interesting aspect of color processing in the Hermann grid illusion is the type of induction perceived – assimilation. That is, the hue of the illusory spots appears to be similar to that of the background color. According to Fach and Sharpe (1986), chromatic induction changes from chromatic contrast to assimilation between 4 and 6.7 cpd for simple square wave patterns. The Hermann grids tested in all 3 experiments had a highest spatial frequency of 3.49 cpd. The fact that assimilation occurs is contradictory to all previous studies on color induction. One possible explanation for this phenomenon is a double opponent cell theory (McCarter, 1979). That theory suggests there are double opponent chromatic cells which account for the apparent assimilation. However, this theory cannot account for the perceived weakening of the illusion as the orientation of the grid is rotated. Indeed, Conway (2001) showed that chromatic visual processing by these double-opponent cells in the visual cortex has little, if any orientation selectivity. It is possible that the chromatic induction occurs after the processing of the luminance for the grid pattern. This is discussed further in the next section.

Luminance x Color

There appears to be no interaction between color and orientation in the perception of the Hermann grid illusion; that is, color and orientation act independently. From these experiments, it is impossible to determine if the color of the smudges is produced before or after the production of the illusion by the simple cells. It is possible that the S1 cells receive color coded input prior to producing the illusion. Evidence has shown that color-selective midget cells and koniocellular neurons make connections within area V1 (Chatterjee and

Callaway, 2003; Doi, Inui, Lee, Wachtler, and Sejnowski, 2003). Conversely, it can be postulated that these connections are not made with the S1 selective cells in V1, but possibly other cells within the area. Color-opponent cells are found in every layer of V1, but they are most prevalent in layers 3 and 4. This suggests that a majority of the color processing in V1 is handled here. The pure chromatic cells in layer 3 have little to no pattern information and the bulk of neurons in layer 4 have poorly defined orientation selectivity, if any at all. This gives support to the finding that color and orientation appear to act independently in the perception of the Hermann grid illusion.

I believe it is more feasible to think that the color coding of the illusion occurs after the luminance processing that is the basis of the illusion. After the luminance contrast of the grid has been defined, the S1 cells send forward the signal that the intersections are different than the bars. At this point, the color system finishes the processing. The color system must be able to consistently represent the colors involved from the very beginning of the visual process. The color specific cells have large amorphic receptive fields. The location of colors relative to boundaries requires input from the luminance and spatial systems to assign these colors to objects within the scene. I hypothesize that after the color system receives this achromatic input, it fills in the chromaticity accordingly. For example, consider a blue grid with yellow bars. The chromatic processing has already defined there to be 2 colors in the presentation – blue and yellow. After it receives the luminance input, it now assigns the colors accordingly based on coinciding points. So, for a receptive field completely within a blue block which has a certain luminance value, it assigns the color blue. Likewise, for a receptive field within the yellow bar, which has a different luminance value, it now assigns

the color yellow. Finally, at the intersections, it is receiving luminance input that has been shifted from the value it knows for yellow towards that which it knows for blue. Therefore, it assigns the color of mostly blue with very little yellow (the color originally attributed to that area). Hence, we observe a bluish hue to the illusory smudges.

One possible fault with this hypothesis is the fact that a very weak illusion is perceived in isoluminant chromatic grids. One explanation for this is that the luminance inputs into V1 may have some influence from L and M cones, via the lateral geniculate nucleus (LGN), in determining luminance contrast. On average, cortical line detectors have a spectral sensitivity very similar to the photopic spectral sensitivity function. However, individual neurons may vary widely. There are random connections to these S1 cells from the L and M cones. Therefore, it is possible to get an S1 neuron with a majority of its connections from one cone type. This leads to different spectral sensitivities among individual cells. This can result in a minimal perception of contrast based on chromaticity alone which could very well be enough to produce a very negligible illusion. Another explanation for this could be observer bias. In my experiments, there were some subjects who were very tentative to say they did not perceive an illusion. This could be due to the subjects' awareness that they were to estimate a magnitude of illusion and thus felt there should always be some illusion present (even though they were instructed before testing that all estimations were feasible, including an estimation of no illusion seen).

Further work is needed to narrow down the exact mechanisms involved for the perception of the illusion. Showing that chromatic processing of the illusion occurs after the luminance processing could be a very daunting task, but one that would yield much insight

into visual processing. Once the entire process is understood, the next logical step would be to apply that knowledge clinically. From other work in this lab, the most apparent application would be as a possible screening/progression tool for Parkinsonism and Diabetes Mellitus. Patients with either disease show a pronounced deficit in the ability to perceive the Hermann grid illusion (Comerford, Pruszenski, Thorn, and Perryman, 1997). It is conceivable to think that one day eye care professionals would be able to administer a simple screening test involving a Hermann grid to aid in early detection of either disease.

Appendix 1

Fisher's PLSD for HG color tilt
Effect:tilt meridians
Significance Level: 5 %

	Mean Diff.	Crit. Diff	P-Value	
m0, m15	.811	.269	<.0001	S
m0, m30	1.598	.269	<.0001	S
m0, m45	1.946	.269	<.0001	S
m0, m60	1.784	.269	<.0001	S
m0, m75	1.401	.269	<.0001	S
m0, m90	.616	.269	<.0001	S
m15, m30	.787	.269	<.0001	S
m15, m45	1.136	.269	<.0001	S
m15, m60	.973	.269	<.0001	S
m15, m75	.590	.269	<.0001	S
m15, m90	-.195	.269	.1551	
m30, m45	.348	.269	.0115	S
m30, m60	.186	.269	.1748	
m30, m75	-.197	.269	.1495	
m30, m90	-.982	.269	<.0001	S
m45, m60	-.162	.269	.2348	
m45, m75	-.546	.269	<.0001	S
m45, m90	-1.330	.269	<.0001	S
m60, m75	-.383	.269	.0056	S
m60, m90	-1.168	.269	<.0001	S
m75, m90	-.785	.269	<.0001	S

Appendix 2

Fisher's PLSD for HG color tilt
Effect: Color
Significance Level: 5 %

	Mean Diff.	Crit. Diff	P-Value	
blue, yellow	-.176	.294	.2367	
blue, green	.495	.294	.0012	S
blue, red	.717	.294	<.0001	S
yellow, green	.671	.294	<.0001	S
yellow, red	.893	.294	<.0001	S
green, red	.221	.294	.1376	

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