Outer Plexiform Layer Receptive Fields As Underlying Factors Of The Hermann Grid Illusion

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Abstract—**The Hermann grid was first described and discussed by the physiologist Ludimar Hermann in 1870. It is composed of white horizontal and vertical bars on a black background [1]. Subjects perceive black or gray smudges at the intersections of white bars when looking at the grid. This effect was discussed by Baumgartner who proposed a theory related to ganglion cell receptive fields to explain the appearance of the smudges [2]. Since then, various versions of the Hermann grid have been experimented on which demonstrate that the theory breaks down due to inconstant effects [3]. However, Baumgartner's original arguments do not involve outer-plexiform layer (OPL) receptive fields and how they affect the receptive fields at the ganglion cell layer. Hence, this paper will present a verification of the Hermann grid effect by using a model of the retina that includes both outer and inner plexiform layers and will address the question of the role of the OPL in generating the Hermann grid illusion. The paper also discusses how these findings may have a direct impact on the design of retinal prostheses.**

Keywords: Hermann grid illusion, retina, receptive field.

I. INTRODUCTION

When people look at an image where the physical measurements of the image contradict what is perceived, people will experience a perceptual illusion. The illusion in this case is an optical illusion and different people usually experience it in a similar manner. There are many categories of optical illusions, e.g.: motion illusions, luminance and contrast illusions, color illusions and geometric and angle illusions [4]. Among the optical illusions, the luminance and contrast illusions described via the Hermann grid have received significant interest from psychologists as well as physiologists. A Hermann grid consists of horizontal and vertical white bars on a black background (or vice-versa) and hence forms an array of black squares as can be seen in Fig. 1. When looking at this grid, one can see the appearance of black or gray dots at the intersection of bars. One curious aspect is that this illusion does not happen at the center of view or at the point the eyes are looking at. This illusion also happens when the grid is displayed in inverted color whereby people will perceive white dots at the intersection instead, as can be seen in Fig. 1.

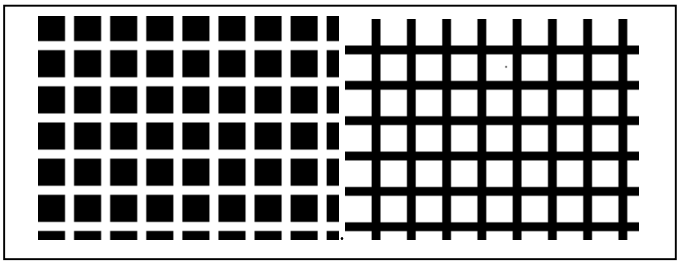

Figure 1: The original Hermann grid (left) and its inverted color version (right).

Although many theories attempting to explain the Hermann grid illusion have been proposed, the question with regards to the underlying neural and computational causes of the illusion is still not completely answered. In this paper we present several experiments on the Hermann grid using a simulation model of the retina and propose an explanation of the illusion wherein the outer-plexiform layer (OPL) plays a fundamental role.

II. WHAT DO WE KNOW SO FAR ABOUT THE HERMANN GRID ILLUSION?

In 1960 Baumgartner proposed a theory to explain this illusion based on lateral inhibition in the retina and argued that center-surround antagonism plays a major role in creating the illusion [5]. According to this argument, On-center ganglion cells when placed over the intersection get more inhibition

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than when placed over the bar portion of the grid (i.e. away from the intersection). This is because the total (inhibitory) surround area of the receptive field is larger than the total (excitatory) center area, so the total inhibition will be larger than the total excitation. A similar argument is applicable to the Off-center ganglion cell in the inverted grid (i.e. black bars on a white background) resulting in brighter smudges at the intersections. This argument also explains why people don't perceive the illusion in the center of gaze due to the small receptive fields of the fovea. If receptive fields are small enough, this leads to a balance between inhibition and excitation and the abolition of the illusion [3]. This explanation can be seen in Fig. 2.

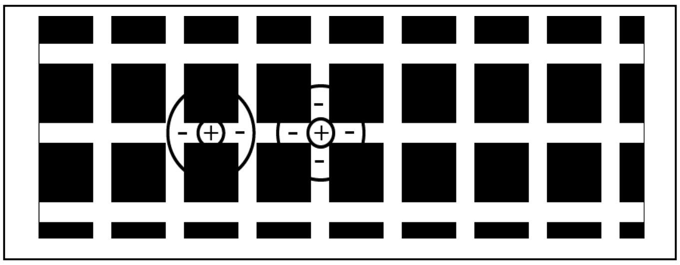

Figure 2: The explanation of Hermann grid illusion.

Although Baumgartner's theory has considerable explanatory power, it breaks down in the face of more recent experiments involving variations of the Herman grid. These variations belong to three main categories, i.e.: orientation, luminance and distortion.

In the first category, Spillmann in 1971 rotated the Hermann grid by 45° and observed that the illusion is reduced as a consequence of this rotation [5]. This is detrimental to Baumgartner's theory because according to the latter, rotating the grid by 45° should not affect the inhibition/excitation imbalance which produces the smudge effect. Recent research shows that the illusion is at its weakest when the grid is rotated by 45° [7][8]. Hubel and Wiesel suggested that the "orientation modulation" of the illusion might be explained by orientation selective neurons in the cortex [9]. The "orientation modulation" of the illusion can be easily verified in Fig. 3.

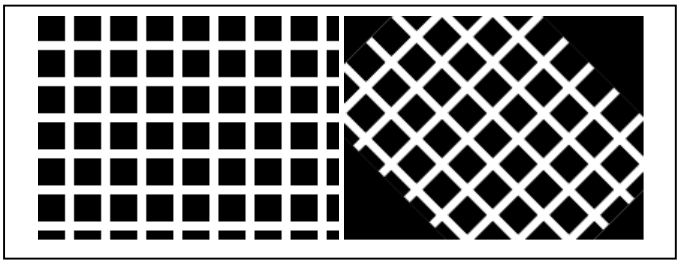

Figure 3: The original Hermann grid (left) and rotated by 45° grid (right).

In the second category, the grid is designed with different colors [10][11]. As a result, the illusion still occurs but the spot color is not black or white but the color of the square. McCarter proposed that the illusion is produced by the double-opponent cell, where the distribution of receptive fields consists of red-on/green-off center and red-off/green-on surround ganglion cells [10]. According to this argument, if the receptive field is placed at the intersection of green bars on a red background, excitation would be stronger due to more red-on stimulation and vice-versa for the green background. Also on this issue, Oehler and Spillmann also predicted that, in terms of photoreceptors, the illusion is based on red and green cones only. Their experiment showed that the intensity of the illusion does not depend much on blue cones [12]. Figure 4 illustrates how the illusion varies with bar color.

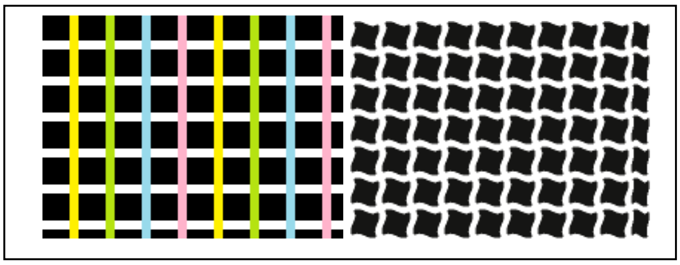

Figure 4: Color variant and distorted version of the Hermann grid.

In the last category, the Hermann grid pattern is geometrically distorted in different ways. In one specific distortion, bars are curved resulting in a sinusoid grid as seen in Fig. 4 (right-hand side). With this experiment, Janos Geier et al. concluded that the Hermann grid illusion also depends on straightness because as one can easily verify, the illusion disappears in the sinusoid grid. The authors concluded that the role of On and Off ganglion cells with regards to the illusion is not important and proposed a new theory to explain the Hermann grid illusion, a theory that could account for the elimination of the effect in the distorted case. At the core of this theory lies the "radiating edge hypothesis" which states that a segment of a white-black edge will radiate darkness and lightness on its dark and light side, respectively, whereby the magnitude of the radiation is directly proportional to the straightness of the edge and the direction of the radiation is perpendicular to the orientation of the edge [13].

In this paper, we propose another theory to explain the Hermann grid illusion, where the OPL plays a fundamental role and which accounts for the effect in the classical grid and its modern variations. This theory shows that the classical receptive field explanation of Baumgartner is still useful, after taking into consideration the OPL and a more detailed model of retinal processing.

III. Our Theory

Retinal bipolar cells are known for transferring data from photoreceptors to ganglion cells via chemical and electrical synapses. In the OPL of many retinae we find complex circuitry involving photoreceptors, horizontal cells and bipolar cells, exhibiting feedforward, lateral and feedback computations, mediated via chemical and electrical connections, and implementing diverse computational functions such as contrast enhancement, center-surround antagonism, color correction and so on [16][17][18][19]. In this paper, we concentrate on the center-surround antagonism exhibited especially by bipolar cells. This retinal function was first discovered by Kuffler in ganglion cells and was later claimed to exist in bipolar cells as well [20][21][22]. We believe that the limited number of connections between photoreceptors and bipolar cells and the resulting geometric heterogeneity of receptive field shapes might account for some of the modern variations of the effect apart from being capable of explaining the classical effect.

Normally small diffuse bipolar cell collect information from 5-7 cones for the center and 12-14 cones for the surround to form a center-surround receptive field [23]. A question here is how do the connectivity properties of bipolar cells with respect to photoreceptors affect their receptive field properties? And how do bipolar cell receptive fields explain the Hermann grid effect? By using our retinal model to simulate how the Hermann grid is processed by the retina, tentative answers for these questions and suggestions for future investigations can be obtained.

IV. METHOD

We use a model of the retina encompassing both the OPL and the inner plexiform layer (IPL) to experiment on the Hermann grid to see whether the outputs from ganglion cells are consistent or not with the Hermann grid illusion. We test the model on the original version of the Hermann grid and several variants pertaining to orientation, color and geometrical distortion. In the model all cell layers of the retina involving photoreceptors, bipolar, horizontal, amacrine and ganglion cells are represented and connected as can be seen in simplified form in Fig. 5. Here only major layers involving photoreceptors, bipolar cells and ganglion cells are illustrated. From top to bottom, the first layer is the photoreceptor layer, which receives the stimulus image and transfers information to horizontal cells (not shown here) and bipolar cells. Horizontal cells feedback to photoreceptors while bipolar cells, which are in the second layer receive information from both photoreceptors and horizontal cells, pass the results of their own computations to ganglion cells in third layer. The ganglion cell layer also receives information from amacrine cells (not shown in this figure), which in turn process information originating from bipolar cells. Notice that the highlighted circles in each layer are the cells covered in 1 receptive field. The Hermann grid images at each layer represent example outputs for each layer. There are two outputs for each one of the bipolar and ganglion cell layers which correspond to On and Off cells.

The connectivity between bipolar cells and photoreceptors is determined by a probability matrix. Each value in the matrix determines the probability of a connection at the corresponding coordinate. In this paper we use a 10x10 matrix where the probability of a connection is 10% for each coordinate, which maintains the number of input connections at each bipolar cell at 10 on average.

The model is implemented in C/C++ using the CUDA platform to speed up processing time. The GPU used in this model is NVidia Tesla C1060.

The input to the model consists of the original Hermann grid stimulus and its variants. The Hermann grid was generated using Adobe Illustrator. The bar width consists of 6 pixels and the square is 3 times larger than the bar as suggested by Schiller and Carve [2]. In order to make the output images clearer and easy to observe, the contrast of output images is enhanced using histogram normalization and equalization.

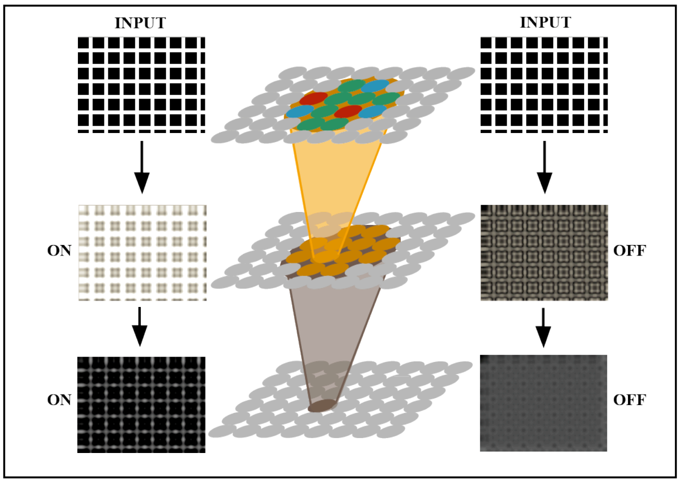

Figure 5: The retina model and its connectivity.

V. EXPERIMENTS

A. Line Width Ratio

The first experiment was conducted on the line width ratio property of the Hermann grid. In this experiment, the white bar width was changed while keeping the receptive field unchanged and vice-versa. The test cases are listed in Table 1.

TABLE I. RATIO TEST CASES

Receptive field size		**Ratio**			
		1:1		**1:3**	
		Hermann grid size		**Hermann grid size**	
Center	***Surround***	***Line***	***Square***	***Line***	***Square***
1-5	2-10	2	2	2	6
1-5	2-10	4	4	4	12
1-5	2-10	6	6	6	18
1-5	2-10	8	8	8	24
1-5	2-10	10	10	10	30

As can be seen in the table above, the ratio is changed from 1:1 to 1:3 for the width of the white bars and the black squares, respectively. According to Schiller and Carvey, the effect is reduced for the 1:1 case compared to the standard 1:3 ratio of the Hermann grid [2]. The receptive field center radius was also changed from 1 to 5 and the surround radius from 2 to 10, respectively. These parameters were chosen based on the experiment from Dacey et al. in which the surround of diffuse ganglion cell is said to be 2 to 5 times larger than the center [15]. Hence we set the ratio of receptive field surround/center to 2 and tested on Hermann grid stimuli with 1:1 and 1:3 ratios.

The results from our model can be seen in Fig. 6 and Fig. 7. The Hermann grid illusion is only visible (as a darkening smudge at the intersection of bars) in the bottom left image. It can be seen easily that the smudges appear when the grid is set to 1:3 ratio and the receptive field size matches the white bar width. The effect is strongest when the width of the bar of the grid equals the center receptive field diameter. In the case that the receptive field size is suitable but the ratio of the bar and the square is not 1:3, the effect is not shown as can be seen at the 1:1 ratio output in Fig. 6.

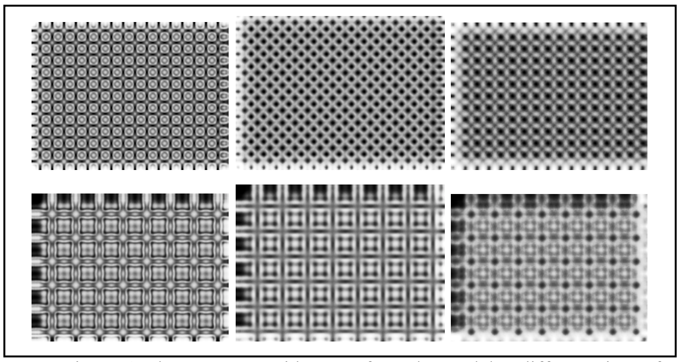

Figure 6: The Hermann grid output from the model at different sizes of receptive field at ratio 1:1 (three images on top) and ratio 1:3 (three images at bottom) with bipolar cells connected. The receptive field size is changed in range from 1:2 to 2:4 and 3:6 corresponding to three columns of images from left to right.

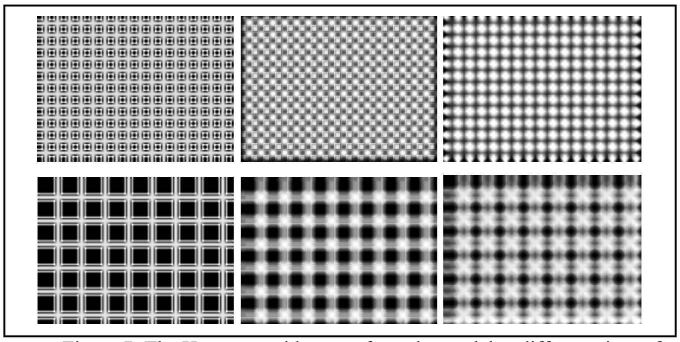

Figure 7: The Hermann grid output from the model at different sizes of receptive field at ratio 1:1 (three images on top) and ratio 1:3 (three images at bottom) with no bipolar cells connected. The receptive field size is changed in range from 1:2 to 2:4 and 3:6 corresponding to three columns of images from left to right.

B. Orientation

In this test case, the Herman grid was rotated at different angles, namely 15°, 30°, 45°, and 60°. In this case we used a fixed receptive field with a center diameter of 6 pixels and a surround of 18 pixels. Besides this, for the bar and square, widths of 6 and 18 pixels were used, respectively. These values were chosen because in the first test we can see that the effect is strongest when the grid had a 1:3 ratio and because larger widths allow the effect to be easily recognized by naked eye.

From the outputs in Fig. 8 and Fig. 9, one can see that the intensity of the output of Off-ganglion cells in rotated grids decreases (albeit subtly) as the angle of rotation increases up to 45°. So, as predicted from experiments on human subjects, the intensity of the smudges is weakest at 45°.

C. Distortion

The last experiment was constructed by distorting the grid geometrically. Figure 10 presents the Hermann grid after geometric distortion and the output from the model. The input and the configuration for the model is the same as the orientation test to maintain the observation of the effect when seen by human subjects. The distortion is set to the same parameter as in Janos Geier and his colleague's paper [13].

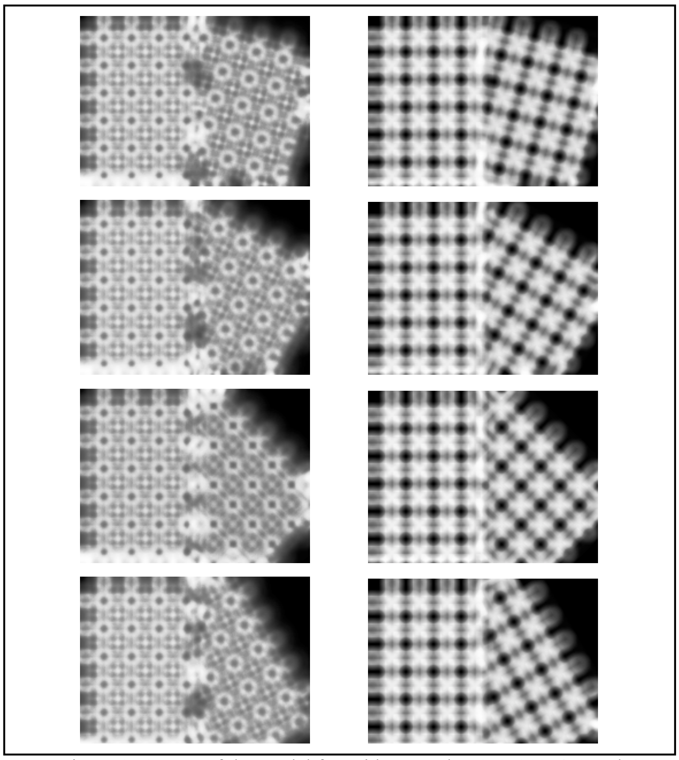

Figure 8: Output of the model for grids rotated at 15°, 30°, 45° and 60° with connectivity calculated using probability matrix. The output for each angle corresponds to each row in the figure. The left column contains images output from model with bipolar cells involved while on the right column the bipolar cells are not involved. When the bipolar cells are not involved (images in right column), the outputs from the model are the same for the original and rotated grids. The receptive field of the bipolar cells in this case is non-circular.

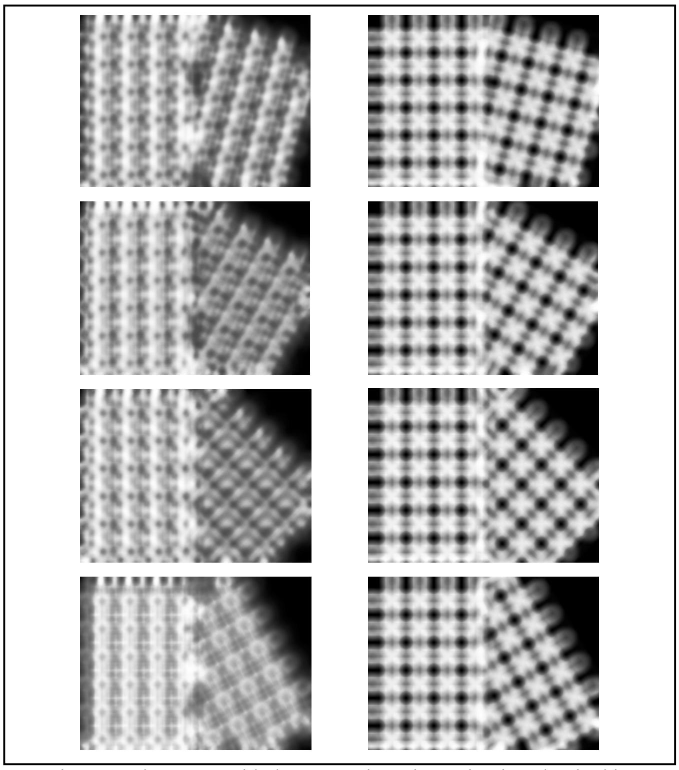

Figure 9: The output with the same orientation as in Fig. 8 but in this case the receptive field of the bipolar cells in this case is circular.

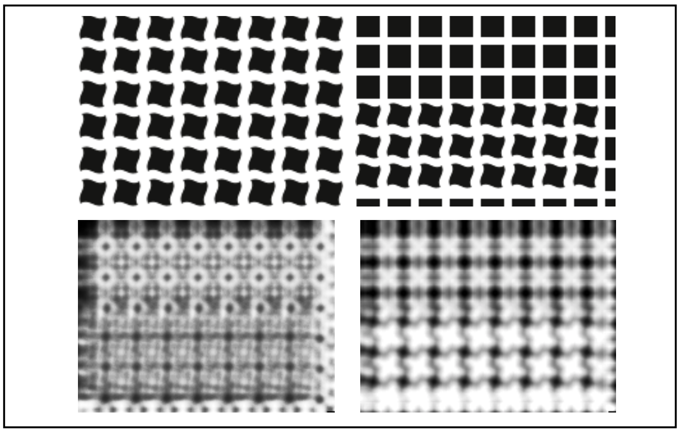

Figure 10: Distorted Hermann grid as input to and output from the model. Two images on top are input and bottom images at bottom are corresponding output from the model.

VI. DISCUSSIONS

From the outputs of the model in the bar/square ratio experiment, we can confirm that that ratio of the squares and the bars in the Hermann grid is an important factor in generating the smudge effect. In addition, this also shows the role of the bipolar cell receptive field in forming the effect at ganglion cell layer. When the bipolar cells are disconnected from the model, the smudges are no longer present at the output of the ganglion cell layer. When the bipolar cells are disconnected this means that the output from photoreceptors and horizontal cells are fed directly to ganglion cells as can be seen in Fig. 7. Even with the same setting as in Fig. 6 the results show that no smudge appears when bipolar cells are disconnected. This is positive evidence of the critical role bipolar cells play in producing the Hermann grid response at seen at the ganglion cell layer.

In the next experiment of orientation, one can see that our model can explain the "orientation modulation" effect of the rotated Hermann grid and therefore provides evidence of the critical role the OPL plays in the illusion and in the formation of the receptive field properties of ganglion cells. When there is no bipolar cell involvement, the output of the model at the ganglion cell layer, shows no trace of the "orientation modulation" effect as discussed by Sciller and Carvey as well as Janos Geie's paper [2][13]. When bipolar cells are involved, the "orientation modulation" effect is clearly visible. To make this experiment clearer, we used the Mean Square Error (MSE) to measure the difference between the output of the rotated grid and the rotated output of the original grid. The MSE can be seen in Table 2.

TABLE II. MSE BETWEEN THE OUTPUT OF ROTATED HERMANN GRID AND THE ROTATED OUTPUT OF THE ORIGINAL GRID

Orientation	Mean Square Error
15°	2.1840
30°	16.9023
45°	27.8667
60°	15.12146

We believe this orientation modulation effect can be explained by the sparse connectivity between photoreceptors and bipolar cells which in turn leads to heterogeneously and asymmetrically shaped receptive fields. The current paper at the very least provides strong evidence in favor of the previously unrecognized critical role of bipolar cells and hypothesizes that the effect is due to the heterogeneous shape of bipolar cell receptive fields. However, the precise relationship between the geometrical properties of bipolar cell receptive fields and the orientation modulation effect still remains to be investigated. An example bipolar receptive field from the model can be seen in Fig. 11 where white pixels represent the presence of a connection between a photoreceptor and bipolar cell.

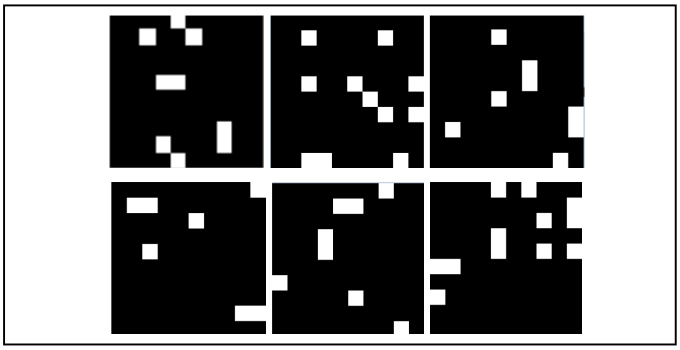

Figure 11: Binary maps of connectivity in bipolar receptive field.

One can easily see that the shape of the receptive field is not circular so when the grid is rotated by 45°, the output from this receptive field is not the same as in the circular receptive field. In the case where receptive fields are perfectly circular the orientation modulation effect is completely obliterated. In a parallel set of experiments we compared circular vs. non-circular ganglion cell receptive fields. For the circular case, the orientation modulation effect is absent whereas for the non-circular case, the effect is significant, as in our present experiments with bipolar cell receptive fields. This circular vs. non-circular explanation seems to support that the reason bipolar cells contributed towards the orientation modulation effect has to do with the non-circularity of their receptive fields. The precise geometrical relationships, as already mentioned, require further investigation, especially when we consider the overall effect of multiple receptive fields with different shapes.

Apart from the orientation modulation effect, in the 45° rotation case, one can easily perceive a "smudge diagonal". Janos Geier discussed this effect in his paper of factors behind the Hermann grid illusion. It turns out that 5%-10% of viewers can see these "diagonal smudges" in the original position but most subjects see them only in the 45° rotation case [13]. This fact is also consistent with the result from our model where one can see the "diagonal smudge" at 45° rotation. We propose that heterogeneously shaped receptive fields can also explain this effect. When receptive fields exhibit more circular properties this effect does not occur (Fig. 9). Combining this result and the MSE result above, this model shows that the rotation based Hermann grid effects can be explained by Baumgartner theory if we include the involvement of bipolar cells.

As can be seen in the model output in the last experiment, the effect disappears at the intersections and this result is matched when observing the distorted grid using human eyes.

The output again emphasizes the role of bipolar cell receptive fields in the retinal processing pathway. Without the bipolar cell receptive field, the output shows the same smudges at the intersection in both the original and distorted grids. In this case, the smudge intensity is larger than in the original case because the area in the intersection is larger. This explains why we see a brighter spot at the intersection in the distorted version when bipolar cells are disabled (right bottom image in Fig. 10). In the opposite case the smudges are present more strongly at the intersections of the original grid. In the distorted case "bar smudges" are also apparent, which is consistent with direct observation of the stimulus.

One weakness of the model pertains to shading variations of the Herman grid. When the background of the bar is shaded to grey and the intersection is still white, the model output is not consistent with what human eyes see. This failure needs more research in the future and may be addressed by adding further details and realism to the retinal model.

The above findings have at least one important medical implication in the form of new designs for retinal prostheses [24]. Researchers are increasingly giving importance to the question of what constitutes the right type of image processing that needs to be applied to raw video data before it is passed on to an array of electrodes. One way of putting it is that we need to "speak the language of the retina" before we can feed it with sensible information. One of the simplest forms of image processing is arguably center/surround saliency information, which is usually assumed to be conveyed via circular and symmetric receptive fields (or filters). This study alerts us to the possible need to consider heterogeneous and asymmetrical receptive fields. The closer we can replicate or emulate the types of signals cells expect, the easier it will be for the recipient brains to interpret the information carried by those signals.

VII. Conclusions

In this paper we present experiments on the Hermann grid in terms of bar width ratio, orientation and distortion to see the effect of bipolar receptive fields on the output of ganglion cells. When bipolar cell receptive fields are not involved, the outputs of the model ganglion cells are consistent with what has been discussed by former researchers and therefore exhibit several subtle innacuracies. When bipolar cells are added to the model, the outputs of ganglion cells are highly consistent with what human eyes perceive when looking at the Hermann grid. Although the model is far from matching the richness of the real retina and more test cases are needed, these experiments show that Baumgartner's explanation of the Hermann grid illusion when considered in conjunction with a more detailed model of the retina (e.g. OPL and IPL mechanisms), deserves further investigation in the near future.

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