
The Hermann grid illusion revisited

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Abstract. The Hermann grid illusion consists of smudges perceived at the intersections of a white grid presented on a black background. In 1960 the effect was first explained by a theory advanced by Baumgartner suggesting the illusory effect is due to differences in the discharge characteristics of retinal ganglion cells when their receptive fields fall along the intersections versus when they fall along non-intersecting regions of the grid. Since then, others have claimed that this theory might not be adequate, suggesting that a model based on cortical mechanisms is necessary [Lingelbach et al, 1985 *Perception* **14**(1) A7; Spillmann, 1994 *Perception* **23** 691–708; Geier et al, 2004 *Perception* **33** Supplement, 53; Westheimer, 2004 *Vision Research* **44** 2457–2465]. We present in this paper the following evidence to show that the retinal ganglion cell theory is untenable: (i) varying the makeup of the grid in a manner that does not materially affect the putative differential responses of the ganglion cells can reduce or eliminate the illusory effect; (ii) varying the grid such as to affect the putative differential responses of the ganglion cells does not eliminate the illusory effect; and (iii) the actual spatial layout of the retinal ganglion cell receptive fields is other than that assumed by the theory. To account for the Hermann grid illusion we propose an alternative theory according to which the illusory effect is brought about by the manner in which S1 type simple cells (as defined by Schiller et al, 1976 *Journal of Neurophysiology* **39** 1320–1333) in primary visual cortex respond to the grid. This theory adequately handles many of the facts delineated in this paper.

1 Introduction

The Hermann grid illusion (1870) in its best-known form consists of intersecting vertical and horizontal white bars superimposed on a black background, thereby forming an array of evenly spaced black squares. At the intersection of the bars, ghostly gray smudges are perceived comprising the illusion. The grid in this form is displayed in figure 1a. The smudges are seen everywhere except at the center of gaze. In figure 1b, the grid is displayed in reverse contrast; in this case white smudges are perceived at the intersections.

Over the years, the Hermann grid illusion has received considerable attention (for examples see Hering 1920; Baumgartner 1960; Spillmann and Levine 1971; Spillmann 1994; Ninio and Stevens 2000; De Lafuente and Ruiz 2004). Interest in the illusion was heightened when a clever hypothesis was advanced to explain the perception of the phantasmal smudges (Baumgartner 1960). We shall refer to this hypothesis as the retinal ganglion cell theory. As cited in several publications, the theory is laid out in figures 1c and 1d (Wolfe 1984; Sekuler and Blake 1994; Spillmann 1994). The explanation suggested is based on the findings made by neurophysiologists demonstrating that retinal ganglion cells have antagonistic center/surround organization (Kuffler 1953; Werblin and Dowling 1969; Schiller 1996). Consequently, when the grid consists of black squares and white bars, an ON-center retinal ganglion cell responds much more vigorously to a small bright spot placed into its receptive field center than to a large bright spot that activates both the center and the surround of the receptive field. The argument advanced was that smaller responses are elicited in the ON-center retinal ganglion cells whose receptive field centers fall into the intersections of the white bars than in cells whose receptive fields fall along non-intersecting regions of the bars.

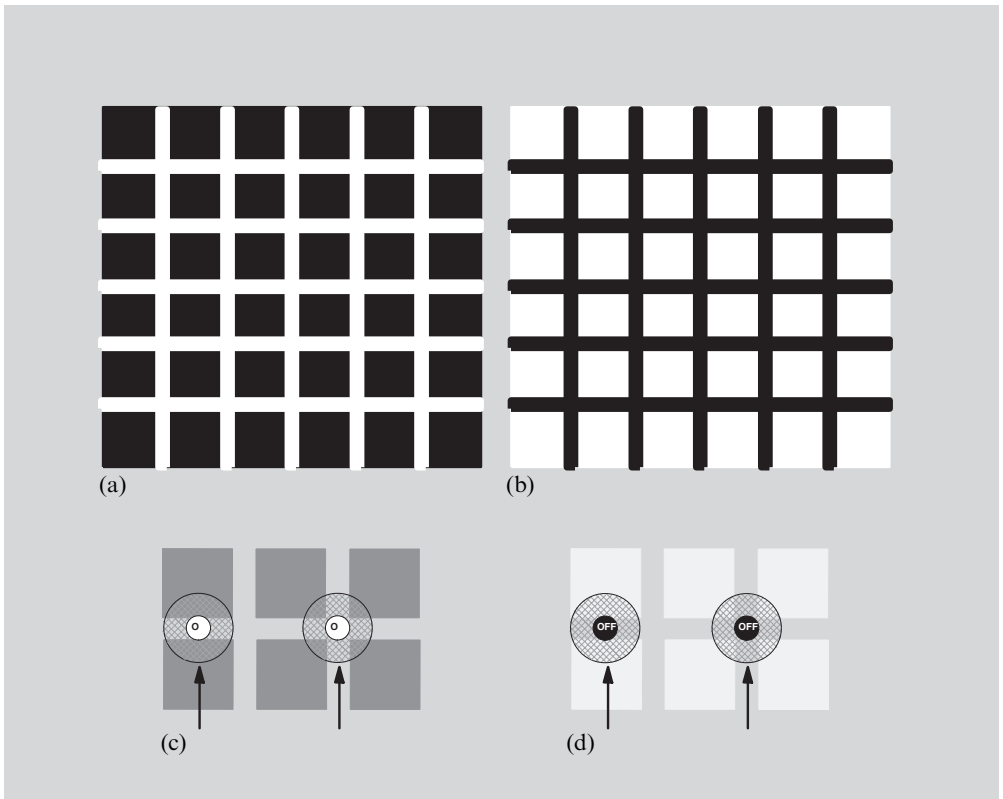


Figure 1. (a) Classic Hermann grid. Smudges seen at the intersections constitute the illusory effect. (b) The illusory effect occurs with both signs of contrast. (c) The theory proposed by Baumgartner to explain the illusion. (d) Baumgartner's OFF-center retinal ganglion cell explanation.

This difference in activity is due to the fact that at the intersections more surround inhibition is produced in ON-center retinal ganglion cells than at other sites. The same considerations apply to OFF-center ganglion cells when contrast is reversed, as in figure 1b.

The fact that in the center of gaze the smudges are not perceived was attributed to the much smaller size of receptive fields in the foveal representation. As a result, the entire receptive field (center plus surround) may fall within one of the white bars, thereby eliminating the response differential between retinal ganglion cells positioned at the intersections as compared to those positioned at non-intersecting regions.

Although this is an appealing hypothesis, it has been pointed out that the explanation may be oversimplified (Spillmann 1971, 1981, 1994; Wolfe 1984). In spite of these observations, the theory has persisted over the years unchanged. It is widely accepted, and continues to appear in textbooks as *the explanation* (Sekuler and Blake 1994).

The purpose of this paper is threefold. First, facts and figures are presented that establish that the retinal ganglion cell theory is untenable. Second, alternative ideas about the Hermann grid illusion are considered and evaluated. Third, a new theory is proposed to explain the Hermann grid illusory effect. Rather than reporting on experiments conducted in a small population of subjects, this paper consists of a series of demonstrations that allow the reader to serve as subject as well as judge. The demonstrations are compelling and we are confident they will convince the readers of the validity of the claims made.

2 Why the retinal ganglion cell theory is untenable

In this section seven points are advanced leading to the conclusion that the retinal ganglion cell theory cannot appropriately explain the Hermann grid illusion. Each point is backed up by the figures that will convince the reader of the validity of the arguments. The seven points are as follows.

2.1 *The illusion is perceived over a large range of sizes*

In the retina, several classes of retinal ganglion cells have been identified (Watanabe and Rodieck 1989; Schiller and Logothetis 1990; Wässle and Boycott 1991; Hendry and Yoshioka 1994). In the primate, these include the midget, parasol, and konio-cellular cells. The layout of the first two, the midget and parasol, will be discussed in more detail in section 2.7. The size of receptive fields in the retina is fixed and is defined by the size of the receptors and their convergence onto the retinal ganglion cells. This being the case, according to the retinal ganglion cell theory one would expect that the illusory effect produced by the Hermann grid would be sharply confined to a specific size of the intersecting bar widths. Figure 2 shows that this is not the case. Here, two widely different size grids are shown in (a) and (b). The ghostly smudges can be seen in both displays. Also, the illusion persists over quite a range when viewing distance is altered. This can, of course, be readily done by the reader by looking at figure 2 from different distances.

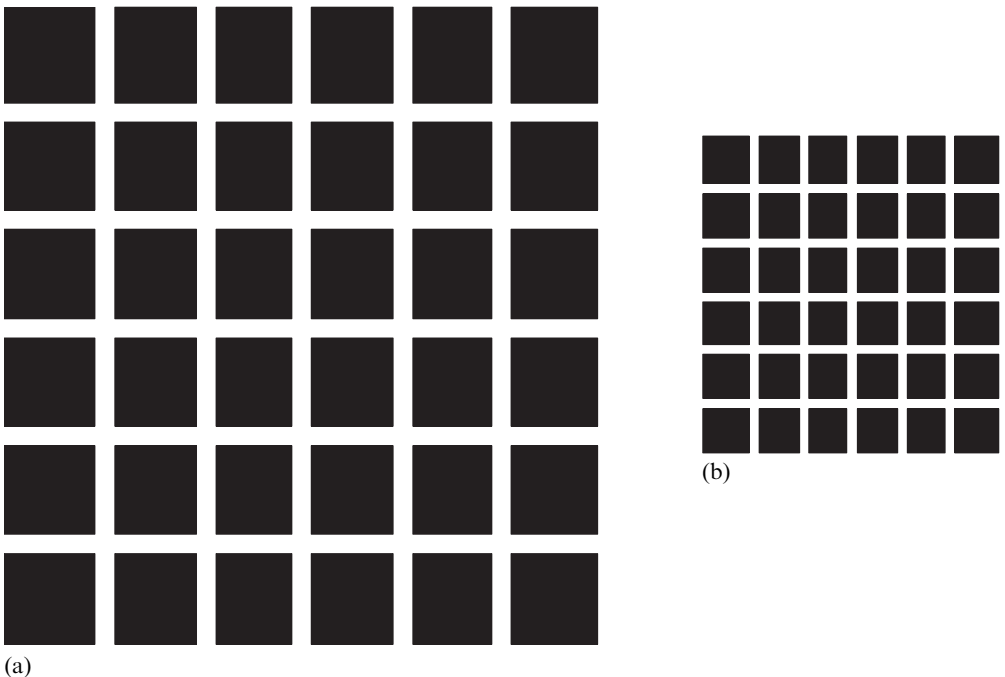


Figure 2. The illusory effect can be obtained over a large range of sizes. Smudges can be perceived in both (a) and (b) and also when viewed at various distances.

2.2 *The illusion is reduced when the grid is rotated by 45°*

Although it has been known for years by aficionados of the Hermann grid illusion that when the grid is rotated by 45° the illusory effect is reduced in a majority of viewers (Spillmann 1971, 1994; Spillmann and Levine 1971; Levine et al 1980), only recently has a study been published in which this has been quantitatively examined by a clever cancellation method (De Lafuente and Ruiz 2004). Figure 3b provides an example of the grid rotated by 45°, with figure 3a showing the classic grid for comparison.

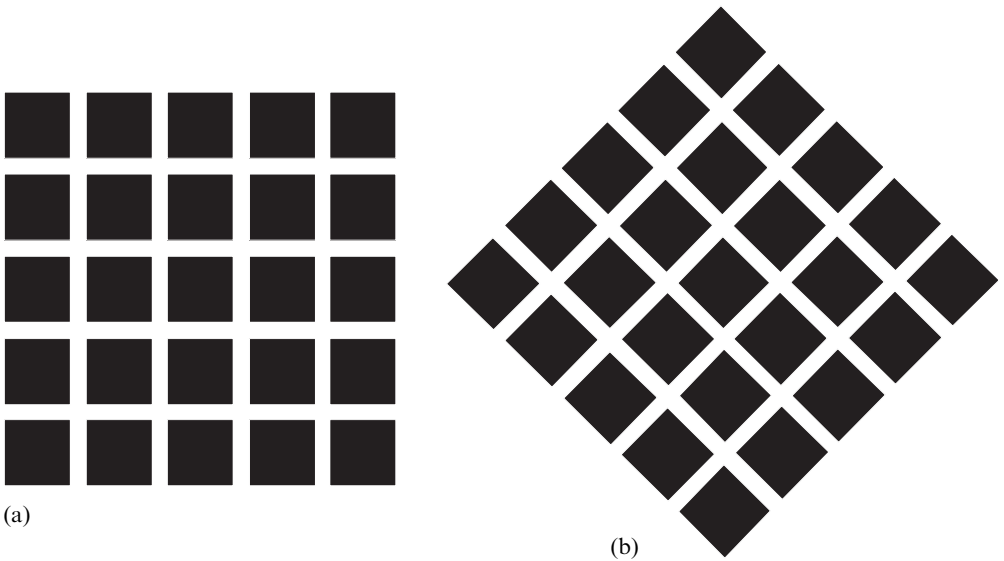


Figure 3. (a) Classic Hermann grid. (b) The illusory effect is reduced when the grid is rotated by 45° .

The retinal ganglion cell theory does not readily explain the reduction in the illusory effect with the 45° rotation. Numerous studies have, however, shown that there is an ‘oblique effect’ according to which acuity and sensitivity is lower for oblique lines and grids than it is for horizontal and vertical lines (Campbell et al 1966; Campbell and Maffei 1971; Appelle 1972, 1975; Westheimer 2001, 2003). Although debated, this effect has been attributed to an anisotropy in the representation of orientation specificity in the visual cortex; in central vision there may be a greater representation of neurons with horizontal and vertical orientation specificities than diagonal ones (Mansfield 1974; Finlay et al 1976).

2.3 The illusion can be reduced or eliminated by manipulations that do not alter the antagonistic center/surround activation of retinal ganglion cells

Here, several manipulations will establish that major variations in the illusory effect arise when the display is manipulated in such a fashion as to have only minor effects on the presumed activation of the center and surround mechanism of the retinal ganglion cells.

In figure 4 the standard Hermann grid is shown along with five manipulations: figure 4a once again shows the standard grid for comparison. In 4b the horizontal bars are straight but the vertical bars zigzag. The illusory effect is reduced. In figure 4c both the horizontal and vertical bars zigzag; the illusory effect appears greatly reduced. The effects produced by these figures suggest that having straight bars without change in the orientation of the bars across intersections is important in giving rise to the illusory effect. For further examples of grid manipulation and the consequential effects on the illusion, see Spillmann (1994, figure 3, page 701), Lingelbach and Ehrenstein (2002), and <http://web.mit.edu/bcs/schillerlab/research/A-Vision/A15-1.html>.

In figures 4d and 4e, another set of manipulations is shown that address the same point. In these figures, instead of straight lines the black squares have serrated edges. Those in figure 4d are at a higher spatial frequency than those in figure 4e. When viewed at normal reading distance, the illusory effect is greatly reduced, more so for figure 4e than for figure 4d. When viewing distance is increased, the illusory effect can be re-established once the serrations can no longer be resolved. This suggests that having straight edges is indeed an important factor in giving rise to the Hermann grid illusion. These observations play a central role in the theory we shall propose in which orientation selectivity of neurons is a central feature.

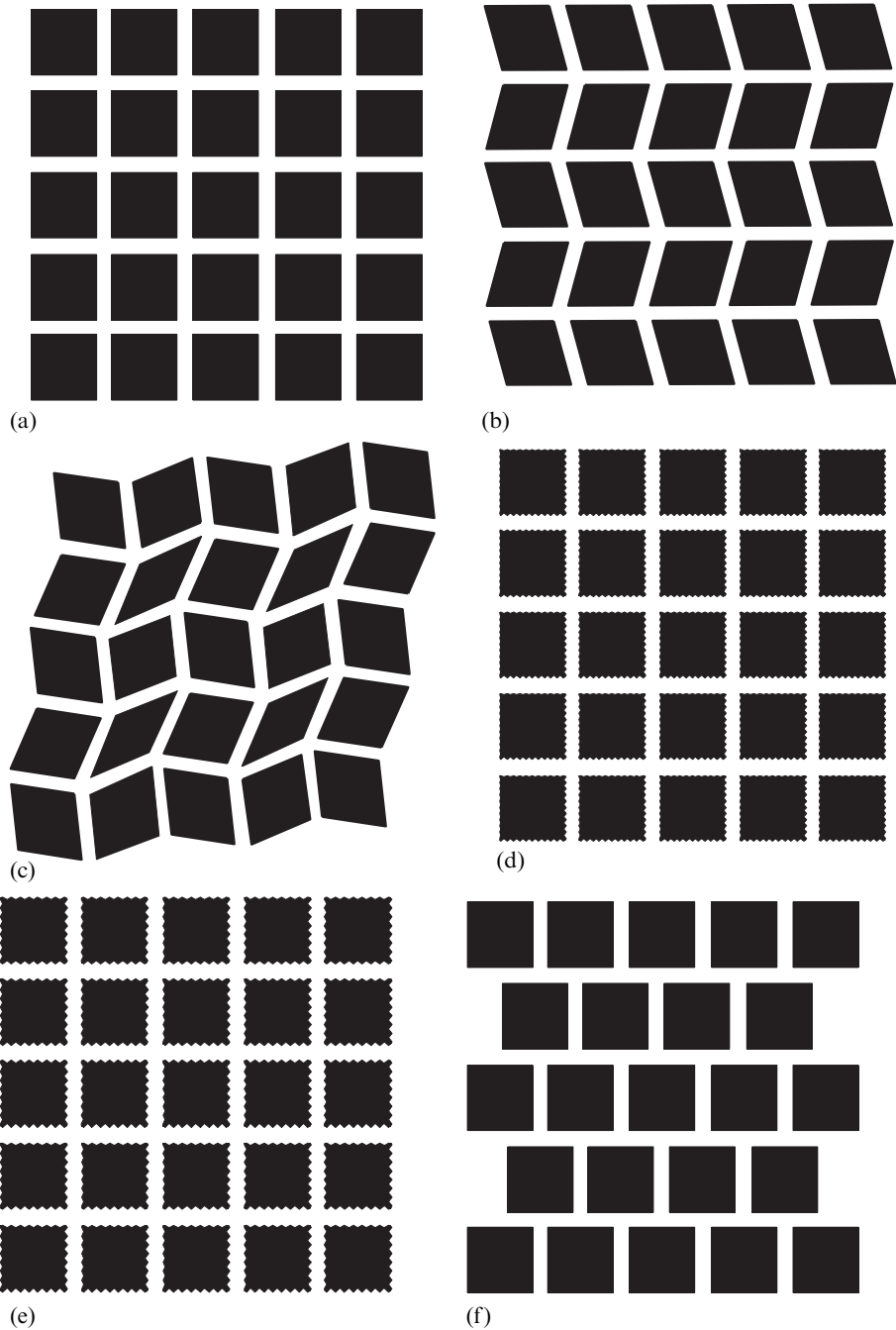


Figure 4. The illusory effect is reduced when bar orientations are discontinuous. (a) The classic illusion with straight, continuous bars. (b) Vertical bars are discontinuous. (c) Both vertical and horizontal bars are discontinuous. (d) and (e) Serrated bar edges shown for two spatial frequencies. Viewing (d) and (e) at a greater distance reinstates the illusion when the serrations can no longer be resolved. (f) Vertical bars are offset. For further examples of grid manipulation see Spillmann (1994, figure 3, page 701), Lingelbach and Ehrenstein (2002), and <http://web.mit.edu/bcs/schillerlab/research/A-Vision/A15-1.html>.

Figure 4f demonstrates that the illusory effect does not occur when alternate rows of squares are shifted, thereby eliminating four-way orthogonal intersections.

2.4 The ratio of square size to the width of the intersecting bars is an important factor in producing the illusory effect

In figure 5, the ratio of the black square size and the white bar diameter is varied. Figure 5a shows the standard grid with a roughly 3 to 1 ratio. In figure 5c a 1 to 1 ratio is shown. Under this latter condition there is very little, if any, illusory effect.

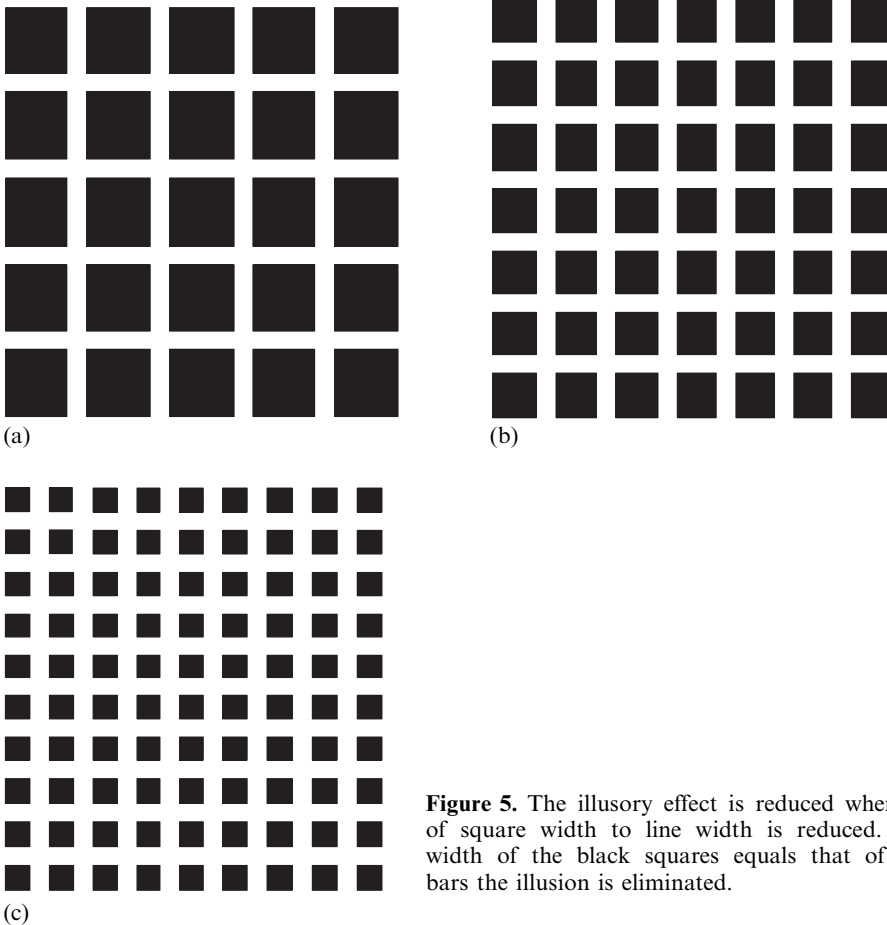


Figure 5. The illusory effect is reduced when the ratio of square width to line width is reduced. When the width of the black squares equals that of the white bars the illusion is eliminated.

2.5 Enhancing center/surround antagonism at the intersections of bars does not enhance the illusory effect

Figure 6a shows the standard Hermann grid on the left. Below appears the essence of the retinal ganglion cell theory as already described. According to this theory, if the center/surround antagonism for the putative cells that fall into the intersections were increased, the illusory effect should become greater. The center/surround antagonism can be increased by providing additional bars with various orientations at each intersection as shown in figure 6b (Lingelbach et al 1985; Spillmann 1994, figure 4a). Doing so results in having four bars intersect instead of just two. The presumed layout according to the retinal ganglion cell theory appears below the figure. Instead of even darker smudges, however, as would be predicted by the theory, the illusory effect is greatly reduced if not eliminated in figure 6b. These observations therefore raise further questions about the validity of the retinal ganglion cell theory.

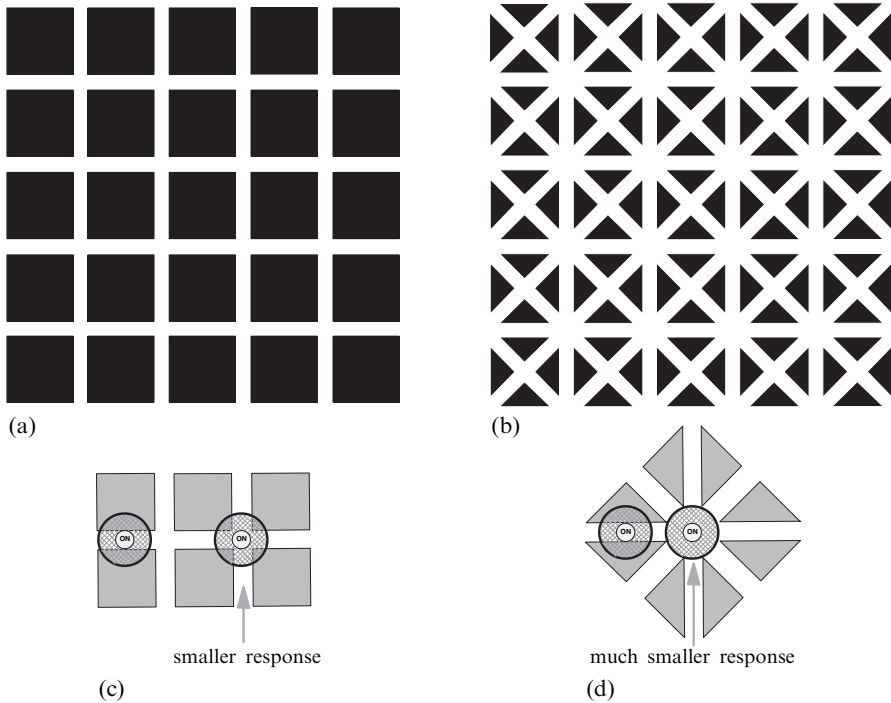


Figure 6. According to the Baumgartner theory, increasing center/surround antagonism at the intersections by adding diagonal bars as shown in (b) (similar to Lingelbach et al 1985) should increase the illusory effect compared with the classic illusory effect as presented in (a). This is not the case.

2.6 Varying the contrast and color in the Hermann grid produces illusory effects not readily handled by the theory

In this section, we shall examine what happens when the contrast and color of the elements in the Hermann grid are manipulated. In figure 7, the contrast and color of the bars is varied. In figures 7a and 7b, two modified grids are shown that raise interesting questions about the nature of the illusion. In this figure, the vertical set of bars has a lower contrast than the white horizontal bars. They may be described as having a light shade of gray. In figure 7a, the vertical gray bars are in front thereby rendering the horizontal white bars discontinuous. The illusory effect appears more pronounced than when all the bars have the same contrast as in the standard Hermann grid displays shown in previous figures. This observation is similar to that reported by Spillmann and Levine (1971). By contrast, in figure 7b the horizontal white bars are placed in front. As a result the horizontal white bars are continuous and the vertical gray bars are discontinuous. Under these conditions, the illusory effect is not obtained. Similar effects can be obtained with displays in which the contrast is reversed under which conditions the illusory effects are also reversed.

Thus, it appears that to obtain the illusory effect with different contrasts and colors, the lower contrast bars and the color bars have to be in front so they are continuous. The color of the smudges also depends on which set of bars is in front (see figures 7c and 7d). Similar observations had been reported by Spillmann and Levine (1971, see their figures 1a and 1b) and by Oehler and Spillmann (1981).

What happens when the situation is reversed and the color of the squares is varied while keeping the bars white? This is shown in figures 8a and 8b where the squares are, respectively, red and green, and the intersecting bars white. The smudges seen at the intersections have the color of the squares, with faint red smudges in

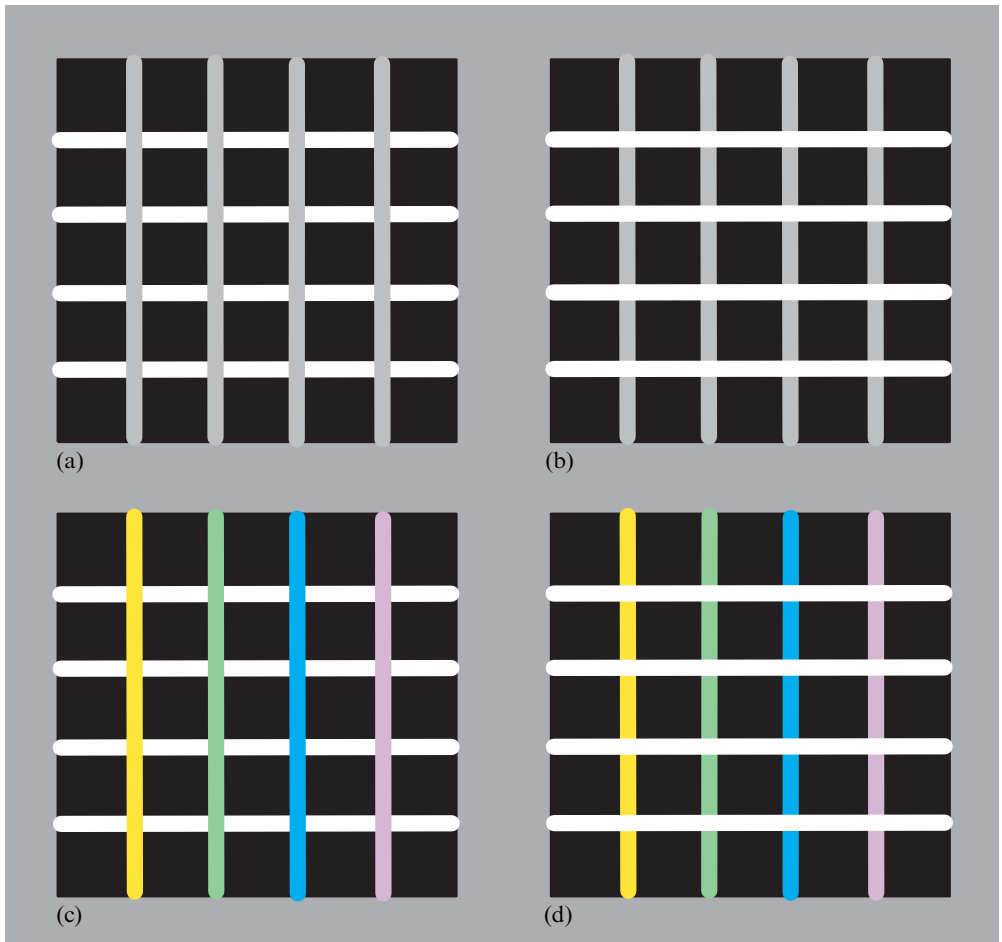


Figure 7. Using gray and white bars enhances the illusion but only when the gray bars are placed in front of the white bars (a); when the white bars are in front there is no illusory effect (b). When various color bars are used at the intersections with the white bars, homonymous color patches are seen but only when the color bars are in front (c); when the white bars are in front the illusory effect is greatly reduced (d). This effect has previously been reported by Spillmann and Levine (1971).

figure 8a and faint green smudges in figure 8b. Thus the color of the perceived smudges is defined by the color of the squares (Levine et al 1980). It does not appear that the retinal ganglion cell theory can readily explain this effect.

What happens under isoluminant conditions? This is depicted in figures 8c and 8d. All the elements of these figures are near isoluminance. The overall brightness is higher for figure 8c than for figure 8d. As reported by Oehler and Spillmann (1981), the illusory effect is minimal under both of these conditions.

The theory to be presented in the third section of this paper endeavors to explain the effects noted here.

2.7 The spatial arrangement of retinal ganglion cell receptive fields is not what has been assumed by the theory

We shall now proceed to examine the manner in which the receptive fields of retinal ganglion cells are laid out relative to the Hermann grid in the primate retina. Examination of this will establish that the inferences made by the retinal ganglion cell theory regarding the spatial arrangement of receptive fields relative to the Hermann grid are incorrect.

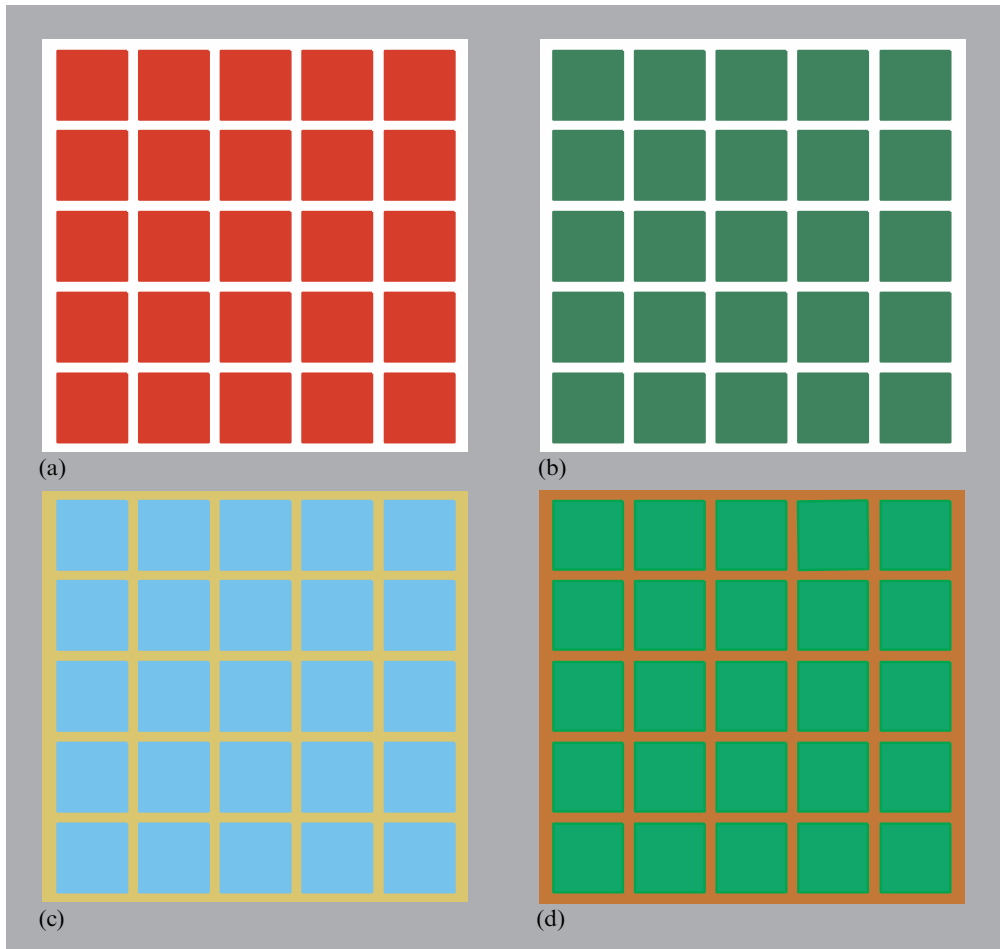


Figure 8. When the squares are colored, the smudges seen at the intersections have homonymous colors [(a) and (b)]. When the squares and bars are isoluminant, the illusory effect is greatly reduced [(c) and (d)].

In the retina, several different classes of retinal ganglion cells have been identified. Two of these classes, the midget and the parasol, most likely play a significant role in the Hermann grid illusion. In central retina, the ratio of midget and parasol cells is about 9 to 1, whereas in peripheral retina the ratio is near 1 to 1 (Dacey and Petersen 1992). This arrangement can be seen in the lateral geniculate nucleus where for central representation this structure has six layers, four of which are parvocellular that receive input from the midget system and two of which are magnocellular that receive input from the parasol system (Malpeli and Baker 1975; Schiller and Logothetis 1990). By contrast, in the peripheral retina the layers are reduced to four, of which two are parvocellular and two are magnocellular with close to equal number of cells within each pair of layers. Seven other facts are noteworthy: (i) the receptive field size of cells increases with increasing eccentricity from the fovea; (ii) overall, the receptive field sizes of the parasol cells are three times the diameter of the receptive field sizes of the midget cells (Watanabe and Rodieck 1989); (iii) in the central retina the receptive field center of midget cells consists of input from a single cone; (iv) the size of cones increases dramatically with increasing eccentricity; (v) there are few, if any, parasol cells with the foveola; (vi) there are no rods in the fovea; and (vii) in the central retina the number

of retinal ganglion cells outnumbers the cone photoreceptors by a factor of 2 to 4 (Williams and Coletta 1987; Rodieck 1988; Williams 1988; Curcio et al 1990; Wässle et al 1990; Wässle and Boycott 1991; Dacey 1994; Masland 2001).

Figure 9 shows schematically some of these points. In figure 9a the size and layout of the photoreceptors in the primate retina is shown as arranged in the fovea and 5 deg out. In the fovea the diameter of the cones is about $2.4 \mu\text{m}$ (0.7 min of arc).

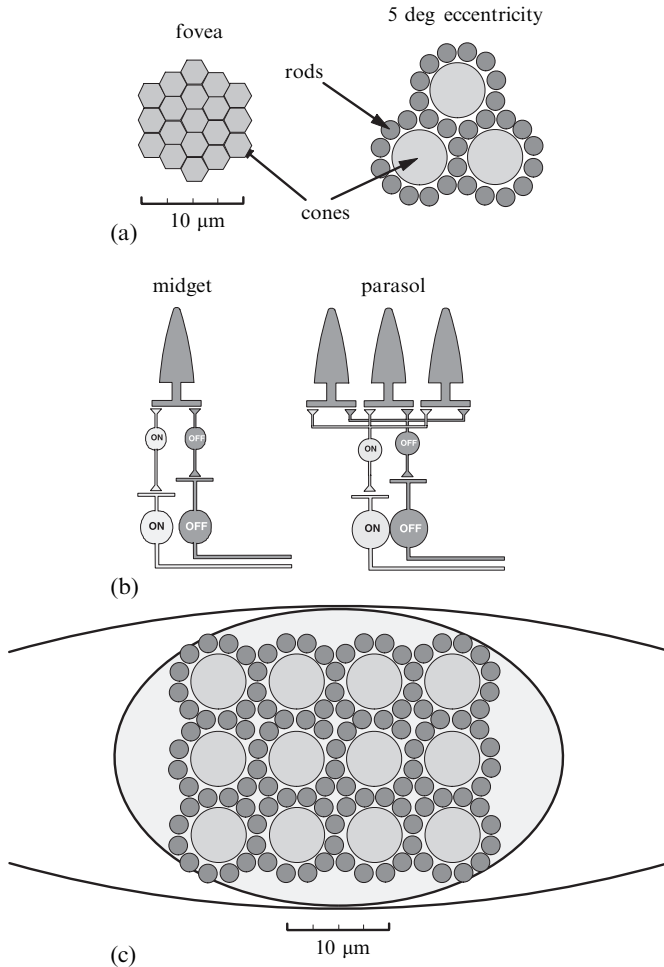


Figure 9. (a) Shown is the primate photoreceptor layout in the fovea and at 5 deg eccentricity for rods and cones. Foveal cone diameter is $2.4 \mu\text{m}$ (0.7 min of arc); intercone distance is the same. At an eccentricity of 5 deg cone diameter is $5.8 \mu\text{m}$ (1.7 min of arc); intercone distance is $7.5 \mu\text{m}$ (2.2 min of arc). Rods are interspersed between the cones. (b) In central retina, the receptive field center of each midget ganglion cell is comprised of input from a single cone via either ON or OFF midget bipolar. Several cones comprise the receptive field center of parasol cells via parasol bipolar cells. Most cones outside the fovea connect with both midget and parasol bipolars and ganglion cells. The cones also connect with several other classes of ganglion cells. Thus, there are more than three times as many bipolar cells in the retina as there are cones. In addition there is the rod system that connects with the ganglion cells via rod bipolars and amacrine cells. These and the horizontal cells of the retina are not shown. (c) Composition of an S1 simple cell receptive field center at an eccentricity of 5 deg. The smallest S1 cell receiving input from the midget system is estimated to be comprised of 9–12 cones that would cover an area of about $24 \mu\text{m}$ by $32 \mu\text{m}$ that equals 0.16 deg by 0.12 deg. The largest S1 cell receptive field center at this eccentricity that receives input from the parasol system is approximately 0.35 deg by 0.46 deg.

The intercone distance is the same, owing to the hexagonal nature of the receptor array. Five degrees out, the cones are more than twice the diameter (about $5.8 \mu\text{m} = 1.7 \text{ min of arc}$), rods are interspersed between cones; as a result, the intercone distance is approximately $7.5 \mu\text{m}$ (2.2 min of arc). As shown in figure 9b, the receptive field center of midget retinal ganglion cells is comprised of a single cone in the central retina. A single cone gives rise to both an ON and OFF retinal ganglion cell via ON and OFF bipolar cells. As a result of this arrangement, in the central retina there are more bipolar cells and retinal ganglion cells than there are cone photoreceptors. In contrast with the midget cells, the receptive field center of parasol cells is comprised of several cones of various types, thereby rendering this system unable to process specific wavelength information for color vision (De Valois and Jacobs 1968; Gouras 1968; De Monasterio and Gouras 1975; Rodieck 1988; Kaplan et al 1990; Kolb 1991; Lee 1996). Not shown are the horizontal and amacrine cells that make lateral connections in the retina.

Figure 9c shows the presumed convergence of input to S1 type simple cells in the cortex at an eccentricity of 5 deg. The nature of this arrangement is discussed in more detail in the section below that provides an alternative theory explaining the Hermann grid illusion.

Given the known size and distribution of midget and parasol retinal ganglion cells, let us now examine how their receptive fields are laid out in relation to the Hermann grid. In figure 10a a section of the Hermann grid is shown. When set up in such a manner as to make the width of the white bars 5 mm and the viewing distance 57.3 cm, which is approximately arm's length, the area indicated by the black square is 5 deg from the black cross, which is where the viewer should fixate. At that eccentricity the smudges are typically well perceived. At the noted viewing distance this area represents 0.5 deg by 0.5 deg of visual angle. The distribution of ON-center midget and parasol cell receptive fields at the eccentricity of 5 deg is depicted in figures 10b and 10c. A similar number of OFF-center cells cover this area (not shown), making for a total of 365 midget and 50 parasol cells in this 0.5 deg by 0.5 deg area 5 deg from the fovea. This number is much higher in the fovea where 3700 midget ganglion cells cover a 0.5 deg by 0.5 deg region. At higher eccentricities there is a progressively greater decline in the number of ganglion cells that cover the same-size area. Coverage at an eccentricity of 10 deg is approximately half of what it is at 5 deg (Dow et al 1981; Wässle and Boycott 1991; Dacey 1994). Yet the illusory effect remains constant.

These observations suggest that the manner in which the receptive fields of retinal ganglion cells cover the visual field is not at all like that proposed by the retinal ganglion cell theory.

3 Alternative ideas about the Hermann grid illusion

Several other possibilities as to what gives rise to the Hermann grid illusion merit brief consideration.

3.1 *Eye tremor*

The illusory effect could be due to eye tremor and the resultant smearing of after-images that occurs more dramatically at the intersections of the Hermann grid than at non-intersecting sites. This idea can be readily dispelled by examining the condition in which the image is presented extremely briefly. This can be accomplished by either taking very short glimpses or by covering figure 1 with a plain sheet of paper and uncovering the image very briefly. Doing so shows that the illusory effect is just as pronounced, if not more so, under brief exposures. This suggests that the effects may be attributed to simultaneous processing of images, or, to put it differently, to simultaneous contrast as first suggested by Hering (1920).

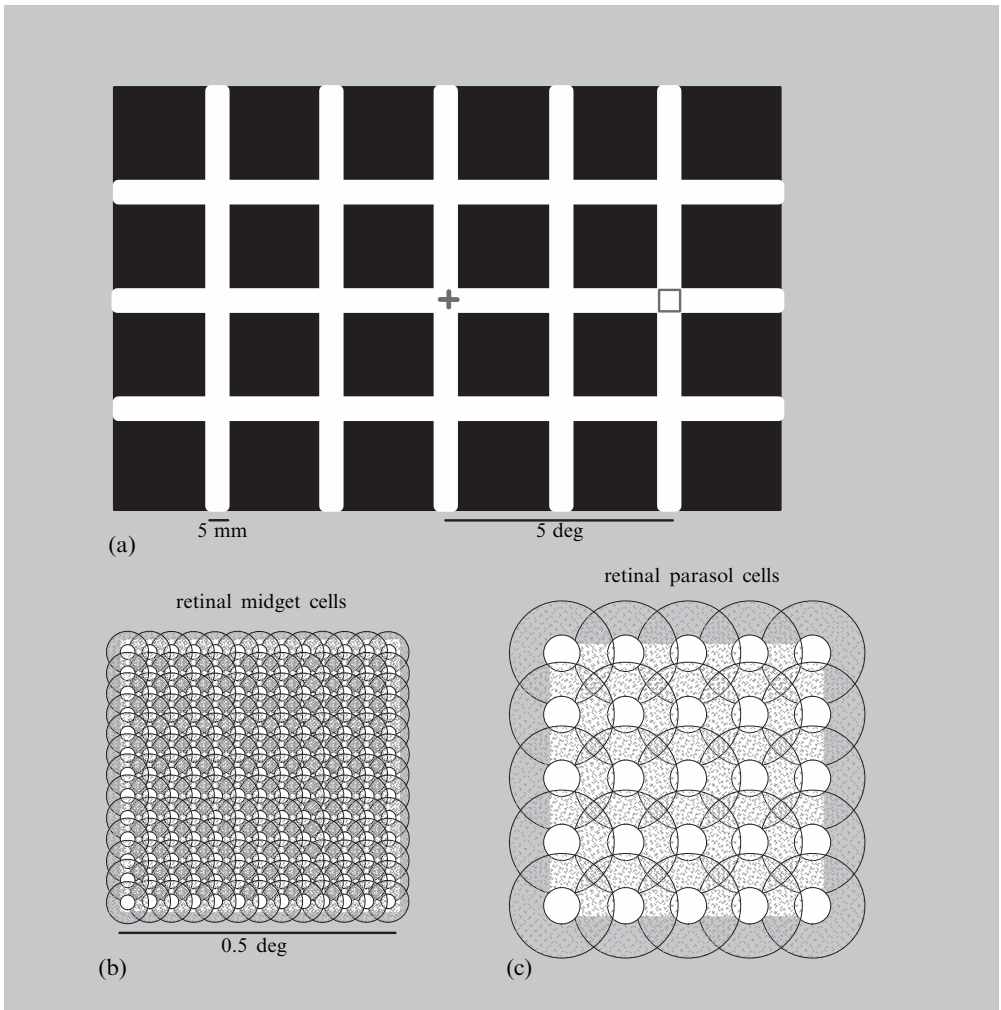


Figure 10. (a) If the white bar width of this grid is set to be equal to 5 mm, when viewed at a distance of 57.3 cm, this equals 0.5 deg of visual angle; under these conditions, the intersection outlined by the black square is 0.5 deg by 0.5 deg in size and sits 5 deg from the central fixation point. The actual layout of the receptive fields in this area is shown in (b) for midget retinal ganglion cells and in (c) for parasol retinal ganglion cells. The 0.5 deg by 0.5 deg area is covered by 365 midget and 50 parasol cells, half of which are ON and half OFF as indicated in the figure.

3.2 Rod/cone interaction

Since the illusory effect is not obtained in foveal vision where there are no rods, and occurs in peripheral vision where the rods and cones are intermingled, it is conceivable that the illusion is the product of rod/cone interactions. This can be tested by examining the grid under brightly illuminated conditions when rods are largely bleached and therefore are not activated by the display. When this is done, the illusory effect persists, suggesting that the effect is not due to rod/cone interactions. The reader can verify this by looking at the Hermann grid in bright sunshine. In some studies it has been reported that the illusory effect does occur in foveal vision when the bars are sufficiently narrow—approximately 5 min of arc (Spillmann 1994). Since the fovea is rod-free this observation further discounts the idea that the illusion is attributable to rod/cone interactions.

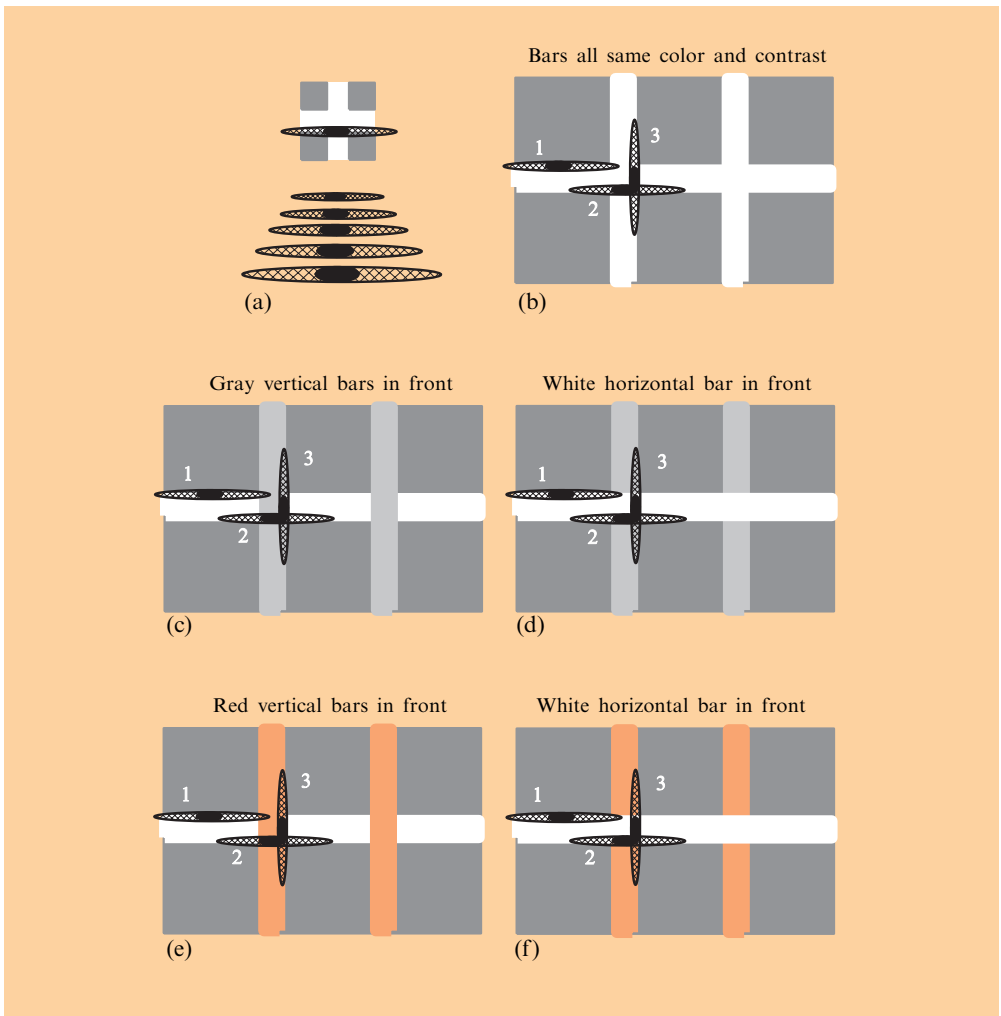


Figure 11. S1 receptive fields cover a range of sizes, permitting the persistence of the Hermann illusion as the grid is enlarged or reduced. (a) Illustration of the range of S1 cell sizes at the Hermann grid intersections. (b), (c), and (d) The responses of ON and OFF horizontally and vertically oriented S1 cells are considered at three locations on the Hermann grid for three variations of bar contrast. The presumed responses are summarized in figure 12. (e) and (f) Where bar color was manipulated, we also considered the responses of S1 color-selective cells. In all of the grid variations shown, the ON and the OFF horizontal S1 cells fire equally at location 1. At locations 2 and 3 in (b), activity is greatly reduced owing to the lack of an edge in the receptive field center; this leads to the perception of dark smudges. In (c) the contrast between the squares and the vertical bars is less than in (b); thus, at these locations the S1 response is even lower than in (b) due to the reduction in the residual flank activity and consequently, the smudges are perceived to be even darker. In (d), location 2, the horizontal ON S1 cells fire vigorously, easily overpowering the reduction in response from both the OFF cells at this location and both the ON and OFF cells at location 3; this strong 'light' signal eliminates the illusion. For (e) and (f), we additionally consider the activation of vertically oriented red-selective S1 cells. The lack of a line through the horizontally oriented ON and OFF S1 receptive fields at the intersections in (e) leads to a reduced response from these cells. All vertically oriented ON and OFF S1 cells fire less owing to the lower contrast difference between the vertical bars and the squares (as compared to the standard grid). However, red-selective vertically oriented S1 cells fire vigorously. The robust red cell response, in combination with the moderate response from the non-color selective vertical cells produces the perceived dark smudges. When the white bars are superimposed on the red bars (f), the strong response from the horizontal ON S1 cells eliminates the illusory effect.

3.3 *Differential contribution of the midget and parasol systems*

Although still under debate, it is believed that parasol retinal ganglion cells are rare or nonexistent in the foveola, where the illusory effect is reduced even with very thin bars (Dacey 1994; Masland 2001). This consideration raises two possibilities. (i) The illusory effect is produced by the parasol system, and (ii) the effect is due to an interaction between these midget and parasol systems. At this stage, noninvasive methods have not yet been devised that would make it possible to selectively activate either of these systems with displays that give rise to the Hermann grid illusion. Hence further work will need to be undertaken to examine this possibility.

4 **A new theory accounting for the Hermann grid illusion**

As derived from the displays shown so far, it appears that the Hermann grid illusion cannot be uniquely attributed to the events occurring at the level of the retina and the lateral geniculate nucleus. Figure 4 suggests that cells selective for oriented line segments may be involved in giving rise to the illusion. It is well known that the majority of cells in area V1 are orientation-specific (Hubel and Wiesel 1959, 1962, 1965, 1968).

The theory presented here is based on two central premises. The first is that orientation-selective neurons play a central role in the Hermann grid illusory effect. The second is that the perception of lightness and darkness is the product of the relative activity of neurons driven by the ON and by the OFF systems. The ON retinal ganglion cells are excited by light increment, whereas the OFF cells are excited by light decrement (Hartline 1938; Kuffler 1953; Rodieck 1973; Schiller et al 1986; Schiller 1996). Increased activity in ON cells produces a greater sense of lightness, and increased activity in OFF cells produces a greater sense of darkness (Jung 1961). The overall sense of lightness and darkness is the product of the relative activity of these two systems. This sense is produced by neurons in the cortex that receive selective input from each of these systems. Some of these cortical neurons lack orientation selectivity and some are selective for orientation.

In area V1, several different classes of cells have been identified (Hubel and Wiesel 1965; Kato et al 1978; Orban et al 1979). Neurons that lack orientation specificity and receive input selectively from either the ON or the OFF system probably make a significant contribution to the perception of lightness and darkness as well as to the perception of color. Among the orientation-specific neurons, most notable are the simple and complex cells (Hubel and Wiesel 1965; Mullikin et al 1984). Complex cells receive a convergent input from the ON and OFF systems that is spatially intermingled in their receptive fields. It appears that such cells are unlikely to convey information about sign of contrast specifying lightness and darkness. Several subclasses of orientation-specific simple cells have been identified that may have one or more subfields, where each subfield is either ON or OFF. The cells with just one subfield that are either ON or OFF may be well suited to contribute to the perception of lightness and darkness, in addition to the contribution made by unoriented cells. Simple cells with just one subfield have been called the S1 type; approximately 27% of the simple cells (67 out of 245) fell into this category in a study by Schiller et al (1976a). The excitatory input to these cells comes from either ON or OFF retinal ganglion cells via the LGN (Schiller 1996). The ON S1 cells are excited by light edges that fall into their receptive fields, whereas the OFF S1 type cells are excited by dark edges (Schiller et al 1976b; Schiller and Malpeli 1978; Malpeli et al 1981).

The receptive fields of neurons in V1 are larger than those seen in retinal ganglion cells and the LGN. It has been estimated that neurons with the smallest receptive field centers in the fovea represent 0.2 deg of visual angle and receive input from 12–13 cones as depicted in figure 9c (Dow et al 1981). Extrapolating this to an eccentricity of 5 deg, the smallest receptive field center comprised of 12 cones makes for a

receptive field center diameter of approximately 10 min of arc. It is notable that there is considerable variation in receptive field size among cortical cells at every eccentricity, which depends in part on whether the input is from midget or from parasol cells and in part on the degree of convergence. These physiological data are comparable to those obtained in psychometric studies by Troscianko (1982a), Koenderink (1977), Wilson and Bergen (1979), and Berbaum and Chung (1981) (see also Jung and Spillmann 1970).

The overall configuration of simple-cell receptive fields is believed to be elongated along their axis of orientation; this is reflected in the fact that their responses tend to increase when the length of an optimally oriented bar in the receptive fields is expanded over a moderate range. There is considerable variation among cells in the degree of summation as a function of line length (Schiller et al 1976a); some in fact show a decrease in responses with increasing length akin to what has been shown in hypercomplex cells (Hubel and Wiesel 1965; Henry et al 1978; Orban et al 1979). In those cells that show summation with increasing length, one may surmise that discontinuous line segments, such as those that are formed at the intersections of the Hermann grid, would elicit a small response in these neurons even when their receptive field centers fall into the region of the intersections. Figure 11 depicts this arrangement.

Figure 11 shows several variations of the Hermann grid, each of which presents three S1 cells representative of the types that would be activated by the grid stimuli, namely horizontally oriented ON, horizontally oriented OFF, vertically oriented ON, vertically oriented OFF, and horizontally and vertically oriented color-selective S1 cells (as described below).

We propose that the illusory smudges are the result of the relative degree of activity of the ON and OFF S1 cells at the intersections, as compared with activity at non-intersecting locations.

The degree of variation in S1 receptive field size is illustrated in figure 11a. The fact that receptive field coverage is not limited to only one size can explain why, for a given retinal eccentricity, the illusion persists when the size of the grid is varied.

In figure 11b, where the bars are all the same color and contrast, we consider the cells activated at the three numbered regions. At location 1, horizontally oriented ON and OFF S1 cells are activated equally (this is also the case for figures 11c to 11f). At locations 2 and 3, where the receptive field centers fall along the intersections and hence are not activated by a continuous edge, the horizontally and vertically oriented ON and OFF S1 cells produce a decreased response compared with the responses elicited along the edges of the non-intersecting regions (such as location 1) thereby leading to the perception of the smudges. These cells do retain some activity owing to the activation of their flanks that fall along the dark edges of the figure, but since the overall firing at these locations is less than in the bar regions immediately adjacent to the intersections, the intersections themselves are perceived as dark smudges.

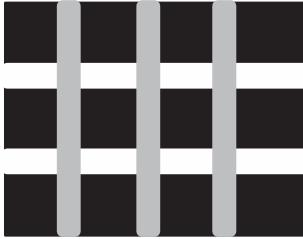
Presumably, the perception of lightness and darkness in those regions of the figure that contain no edges is produced largely by the responses elicited in unoriented cells in V1 that receive either ON or OFF inputs as already noted.

In figure 7 we have examined the effect of bar contrast and color on the Hermann grid illusion. When vertical gray bars are laid on top of horizontal white bars, the illusion remains, and is perhaps even stronger than when all the bars are white. On the other hand, when the horizontal white bars are on top, as in figure 7b, smudges are virtually nonexistent.

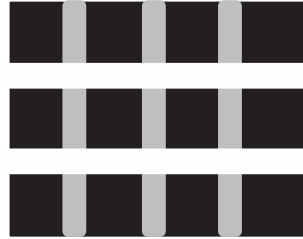
These results can be explained by the S1 theory as illustrated in figures 11c and 11d. In 11c, position 2, ON and OFF cell activity will be reduced substantially because there is no edge in the RF center. At position 3, activity is diminished even further owing to the decrease in bar/square contrast (as compared with the standard grid)

and a mismatch between the center and surround sign of contrast. Since activity at bar intersections is so much less than at non-intersections, very dark smudges are observed. To clarify this, the presumed magnitude of the responses of horizontally and vertically oriented S1 cells falling into the intersections and non-intersections of the displays shown in figures 11c and 11d is illustrated in figure 12.

Activity level, vertical gray bars in front



Activity level, horizontal white bars in front



	very high	high	medium	low	very high	high	medium	low
At intersections								
horizontally oriented ON S1 cell				✓		✓		
horizontally oriented OFF S1 cell				✓		✓		
vertically oriented ON S1 cell		✓	✓					✓
vertically oriented OFF S1 cell								✓
At non-intersections								
horizontally oriented ON S1 cell	✓				✓			
horizontally oriented OFF S1 cell	✓				✓			
vertically oriented ON S1 cell				✓				✓
vertically oriented OFF S1 cell				✓				✓

Figure 12. This table provides an estimate, based on what we know about the response characteristics of S1 cells, of how they respond when two of the conditions shown in figure 11 are presented.

In figure 11d, position 2, both ON and OFF horizontal S1 cells will fire; the ON cells will fire much more vigorously than the OFF cells owing to the comparably higher activation of their RF centers. At position 3, the ON and the OFF cells will respond minimally, if at all, owing to the lack of an edge in their receptive field center; residual flank activity which accounted for the effect in figure 11b is diminished owing to the lower contrast differential along this edge. The horizontal ON cell activity overrides any other signal, and therefore no smudges are seen.

Next one needs to examine the extent to which this S1 theory can explain the illusory effects obtained with different colors.

Research has established that there is considerable variation of input to V1 cells from the various classes of retinal ganglion cells. Some cortical cells receive selective input from the ON and OFF systems as had already been noted, while many receive convergent input from these systems (Schiller and Logothetis 1990). Some V1 cells receive selective input from either the midget and parasol retinal ganglion cells via the LGN, while some receive convergent input from these two systems (Schiller and Logothetis 1990). Last, it has recently been established that the koniocellular system terminates predominantly in the upper layers of V1. Some of these cells process color along the blue/yellow axis (Chatterjee and Callaway 2003; Doi et al 2003).

To explain the smudges obtained when either the squares or the bars have different colors, we propose that the S1 type simple cells come not only as ON and OFF, but as red and green and blue/yellow by virtue of the specificity of input from color-selective

midget cells and koniocellular neurons (some of which mediate blue/yellow) coursing through the LGN to V1 (Chatterjee and Callaway 2003; Doi et al 2003). Making these assumptions can explain the results obtained. We propose that the illusory effects seen—and not seen—are a product of the co-activation of color-selective S1 cells, ON-selective S1 cells, and OFF-selective S1 cells.

Figure 11e shows representative horizontally and vertically oriented receptive field locations for S1 cells activated at various portions of the Hermann grid. The co-activation of the OFF, the ON, and the red-selective cells needs to be considered for each of these locations. Activated at the intersections (locations 2 and 3) are vertically oriented red-selective S1 cells, vertically and horizontally oriented OFF S1 cells, and horizontally oriented ON S1 cells. Of these the vertically oriented red cells are activated vigorously, the vertically oriented OFF cells are activated moderately, and the horizontally oriented ON and OFF S1 cells are activated only weakly. The vertical red S1 cells are activated vigorously because the red line segment extends throughout the receptive field. OFF S1 cells are activated moderately because of the extended dark edges and the red line in the center of the receptive fields that is darker than the horizontal white bar. As a result of this, dark reddish smudges are perceived at the intersections.

By contrast, in figure 11f, the horizontally oriented ON cells are activated much more vigorously than other cells. This is because the appropriately oriented white line segments pass through the center of their receptive fields at the intersections. Hence these vigorous responses override the weak responses elicited by the other vertically and horizontally oriented cells. Consequently no illusory effect is obtained.

The S1 theory may also explain why the Hermann grid illusion in the original stimulus pattern is round and extends slightly beyond the confines of the square area. Adjacent to and at an intersection, the total S1 response is a product of the co-activation of horizontally and vertically oriented cells; the magnitude of combined response depends on the exact location relative to the corners of the four squares comprising the intersection. The circular shape may be due to a gradual decrease in the total response from S1 cells as the intersections are approached and fewer of the flanks are stimulated by edge. Since we propose that the illusion is due to the comparatively different firing levels, this could result in the perception of circular spots slightly larger than the area of the intersection, calculated by Troscianko (1982a) to be equal to 1.4 times the bar width.

The S1 theory can also explain many of the other facts noted in the demonstrations.

4.1 *The illusion persists over a range of grid sizes*

In figure 2 it has been shown that the illusion is effective over a range of sizes which is problematic for the retinal ganglion cell theory. The S1 theory is less affected by this observation for the following reasons: (i) the receptive fields of cortical cells are larger and more variable in size (Gilbert 1977; Dow et al 1981), (ii) their responses are largely controlled by the orientation of edges (Hubel and Wiesel 1959), and (iii) responses in many cells summate as the length of the line segment is extended (Gilbert 1977; Hammond and Ahmed 1985).

4.2 *Rotating the grid by 45° reduces the magnitude of the illusion*

The essential feature of the S1 theory is that the illusion is a product of activity in orientation-selective V1 neurons. Several lines of evidence indicate that our sensitivity and acuity for horizontal and vertical line segments and gratings are better than for diagonal ones, referred to as the 'oblique effect' (Appelle 1972, 1975; Westheimer and Beard 1998). This effect may be due to a higher proportion of neurons with horizontal and vertical orientations in V1, compared to diagonal orientations (Mansfield 1974).

4.3 *Discontinuities in the orientation of line segments reduce the illusory effect*

This has been shown in figure 4. Such discontinuities greatly reduce the responses of orientation-specific neurons but do not affect the responses of neurons in the retina and LGN that have circular receptive fields. This finding strongly supports the idea that it is the activity of orientation-selective neurons that gives rise to the illusory effect.

4.4 *Adding line segments diagonally across the squares in the grid reduces the illusory effect*

This has been shown in figure 6. Under these conditions, ON and OFF S1 cells with many different orientations are activated. Additionally, owing to the larger separation at the intersections between line segments of the same orientation, the degree of activation is greatly reduced. Hence, according to the S1 theory, under these conditions (figure 6b) the illusory effect should be diminished.

4.5 *The smudges seen at the intersections retain the color of the squares in the grid*

As first reported by Preyer (1897/98), when colored squares are used to construct the grid, the perceived smudges are of that color. According to the S1 theory, activation of the oriented S1 cells is primarily dependent on their color selectivity. The smudges generated have homonymous color to that of the squares since the edges of the squares co-activate two types of neurons: the S1 cells that are selective for the colors represented, and either the OFF S1 cells when the squares are dark relative to background or the ON S1 cells when contrast conditions are reversed. It is this co-activation that gives rise to the appropriately colored smudges.

4.6 *The illusion is minimal at isoluminance*

The premise is that the illusion depends on the co-activation of both color-selective S1 cells and ON and OFF S1 cells. Under isoluminant conditions, it is presumed that the ON and OFF S1 cells are minimally activated. Activating color-selective cells alone is insufficient to produce the smudges, given that the prime factor in the illusion is perception of contrast differences dependent on the relative activity of the ON and OFF system.

4.7 *The illusion is greatly reduced under interocular viewing conditions*

In an attempt to determine whether the Hermann grid illusion is a product of peripheral or central mechanisms, a few researchers have attempted to assess the illusory effect under dichoptic viewing conditions (Lavin and Costall 1978; Troscianko 1982b). The elements of the display presented to each eye are such that they do not elicit an illusory effect under monocular viewing conditions but, when fused, can produce the grid. The inference is that, if the mechanisms that give rise to the illusory effect occur centrally, interocular presentation should be as effective as monocular or binocular. Two of the studies using this kind of procedure showed that interocular presentation largely negated the illusory effect and hence peripheral mechanisms were implicated. The third study, on the other hand (Lavin and Costall 1978), found an interocular effect and concluded that central mechanisms are involved. Unfortunately all of these studies are seriously flawed; none of them presents compelling evidence for or against central mechanisms, primarily because the conditions of interocular presentation that were used produce rather pronounced binocular rivalry which cannot be overcome [see discussion by Spillmann (1994, page 697)], even with the outline forms used by Troscianko (1982b).

In the attempt to minimize interocular rivalry, we have created a number of different figures for viewing through a stereoscope. Previous work has established that under brief presentation conditions (less than 100 ms duration) binocular rivalry is minimized; studies have also shown that stereoscopic vision is effective with brief stimulus presentations (Hering 1920; Schiller and Wiener 1963; Uttal et al 1994).

Providing ample identical contours for each eye also reduces rivalry. With these facts in mind, we constructed a number of displays from modified versions of the Hermann grid to be viewed through a stereoscope. The figures were constructed and presented in Microsoft PowerPoint, thereby allowing us to control the length of time each image was shown. First, the viewer would be presented with a fixation display (figure 13 or figure 14, top panels). This display could be viewed for as long as necessary for the viewer to comfortably fuse the identical images. Once he had fused the fixation display, the viewer pressed a button, causing the pair of interocular Hermann grid images (figure 13 or figure 14, bottom panels) to be presented briefly [50 or 66.7 ms (2 or 3 frames)]. At the same time as the Hermann grid images were extinguished, the fixation display reappeared.

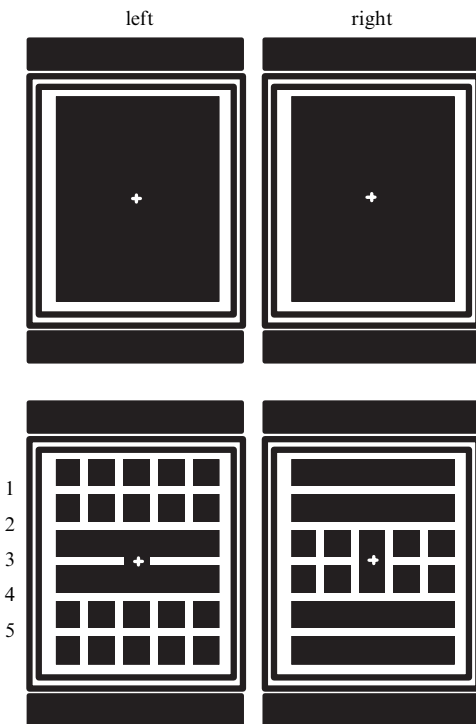


Figure 13. Display created to minimize interocular rivalry. When scanned and presented in Microsoft PowerPoint, or downloaded from the *Perception* website, the top panel serves as a fixation display. Using a stereoscope, the viewer should first fuse the identical images and then press a button causing the bottom display to flash on briefly. When the image to the left eye or the image to the right eye is presented singly, smudges are perceived along bars 1 and 5 (left eye), or along bar 3 (right eye). Brief interocular presentation leads to the perception of smudges along bars 1, 3, and 5 but not along bars 2 and 4.

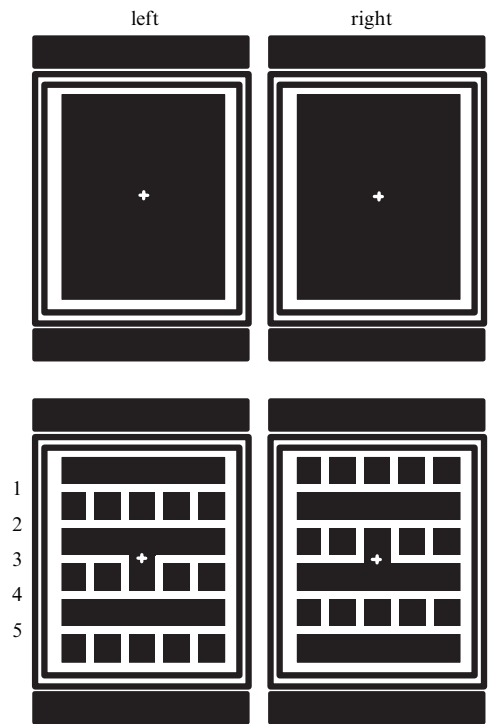


Figure 14. As in figure 13, this display was created to minimize interocular rivalry. The top panel serves as a fixation display. The pair of grids shown in the bottom half of the figure is arranged such that with either monocular or interocular viewing for either brief or prolonged exposure minimal illusory effects arise. This suggests that the Hermann illusory effect occurs before input from the two eyes converges in the cortex.

The pair of Hermann grids shown in the bottom of figure 13 causes different perceptions of smudge patterns depending on how the grids are presented. When the pair is briefly viewed monocularly through the scope, smudges are apparent along bars 1 and 5 for the left eye and along bar 3 for the right eye. Brief interocular presentation leads to the perception of smudges along bars 1, 3, and 5. In both cases,

smudges are minimal or not seen at all for bars 2 and 4, where intersecting bars exist only as a product of interocular image fusion.

The displays in figure 14 serve as controls. This set was designed such that viewing either grid individually and without the scope produces little illusory effect. This is also the case for monocular viewing through the scope for both prolonged and brief presentations. When the pair of grids is briefly viewed dichoptically through the scope, little or no illusory effect is obtained even though binocular rivalry is minimal.

The reader can readily verify these observations by scanning these and presenting them in PowerPoint or by obtaining them on the *Perception* website. The images can readily be set up for rapid presentation, but a stereoscope such as the Stereopticon 707 by Taylor–Merchant is required for proper viewing. The size of the images may need to be scaled down for comfortable viewing.

The demonstrations shown in figures 13 and figure 14 establish that when the Hermann grid is modified and shown such that intersections are provided only interocularly, the illusion is greatly diminished or is eliminated. This suggests therefore that the illusory effect is one that occurs mostly before the input from the two eyes converges on single neurons in the visual system. It has been established that the first station in the geniculo-striate system at which convergent input from the two eyes is seen is in area V1. However, it appears that V1 is only the first stage in a gradual progression from monocularly driven neurons to binocularly driven ones; furthermore it appears that in V1 binocularity is more prevalent in complex cells than in simple cells. In one study, Hubel and Wiesel (1968) found that, although 60% of the cells in monkey V1 receive binocular input, only 12% of the tested population of simple cells was binocular; Poggio (1972) found only 43% binocularity; and in a sample of 636 V1 cells, Schiller et al (1976b) found binocularity in 49% of the simple cells and 88% of the complex cells studied. Given the above, and the finding that the percentage of monocularly and binocularly driven cells in S1 is similar to the rest of the simple cell population (Schiller et al 1976b), it is reasonable to assume that monocularly driven S1 cells play a significant role in giving rise to the smudges in the Hermann grid.

References

- Appelle S, 1972 "Perception and discrimination as a function of stimulus orientation: the 'oblique effect' in man and animals" *Psychological Bulletin* **18** 266–278
- Appelle S, 1975 "The effect of stimulus duration and monocular viewing on the 'oblique effect' in peripheral vision" *American Journal of Optometry and Physiological Optics* **52** 263–266
- Baumgartner G, 1960 "Indirekte Größenbestimmung der rezeptiven Felder der Retina beim Menschen mittels der Hermannschen Gittertäuschung" *Pflügers Archiv für die gesamte Physiologie* **272** 21–22 (Abstract)
- Berbaum K, Chung C S, 1981 "Perceptive field sizes and a new version of the Hermann grid" *Perception* **10** 85–89
- Campbell F W, Kulikowski J J, Levinson J, 1966 "The effect of orientation on the visual resolution of gratings" *Journal of Physiology* **187** 427–436
- Campbell F W, Maffei L, 1971 "The tilt after-effect: a fresh look" *Vision Research* **11** 833–840
- Chatterjee S, Callaway E M, 2003 "Parallel colour-opponent pathways to primary visual cortex" *Nature* **426** 668–671
- Curcio C A, Sloan K R, Kalina R E, Hendrickson A E, 1990 "Human photoreceptor topography" *Journal of Comparative Neurology* **292** 497–523
- Dacey D M, 1994 "Physiology, morphology and spatial densities of identified ganglion cell types in primate retina" *Ciba Foundation Symposium* **184** 12–28; discussion 28–34, 63–70
- Dacey D M, Petersen M R, 1992 "Dendritic field size and morphology of midsize and parasol ganglion cells of the human retina" *Proceedings of the National Academy of Sciences of the USA* **89** 9666–9670
- De Lafuente V, Ruiz O, 2004 "The orientation dependence of the Hermann grid illusion" *Experimental Brain Research* **154** 255–260
- De Monasterio F M, Gouras P, 1975 "Functional properties of ganglion cells of the rhesus monkey retina" *Journal of Physiology* **251** 167–195

- De Valois R L, Jacobs G H, 1968 "Primate color vision" *Science* **162** 533–540
- Doi E, Inui T, Lee T W, Wachtler T, Sejnowski T J, 2003 "Spatiochromatic receptive field properties derived from information-theoretic analyses of cone mosaic responses to natural scenes" *Neural Computation* **15** 397–417
- Dow B M, Snyder A Z, Vautin R G, Bauer R, 1981 "Magnification factor and receptive field size in foveal striate cortex of the monkey" *Experimental Brain Research* **44** 213–228
- Finlay B L, Schiller P H, Volman S F, 1976 "Meridional differences in orientation sensitivity in monkey striate cortex" *Brain Research* **105** 350–352
- Geier J, Sera L, Bernath L, 2004 "Stopping the Hermann grid illusion by simple sine distortion" *Perception* **33** Supplement, 53
- Gilbert C D, 1977 "Laminar differences in receptive field properties of cells in cat primary visual cortex" *Journal of Physiology* **268** 391–421
- Gouras P, 1968 "Identification of cone mechanisms in monkey ganglion cells" *Journal of Physiology* **199** 533–547
- Hammond P, Ahmed B, 1985 "Length summation of complex cells in cat striate cortex: a reappraisal of the 'special/standard' classification" *Neuroscience* **15** 639–649
- Hartline H K, 1938 "The responses of single optic nerve fibers of the vertebrate eye to illumination of the retina" *American Journal of Physiology* **121** 400–415
- Hendry S H, Yoshioka T, 1994 "A neurochemically distinct third channel in the macaque dorsal lateral geniculate nucleus" *Science* **264** 575–577
- Henry G H, Goodwin A W, Bishop P O, 1978 "Spatial summation of responses in receptive fields of single cells in cat striate cortex" *Experimental Brain Research* **32** 245–266
- Hering E, 1920 "Vom simultanen Grenzkontrast", in *Grundzüge der Lehre vom Lichtsinne* chapter 32 (Berlin: Springer) [*Outlines of the Theory of the Light Sense*; translation by L M Hurvich, D Jamieson (1964, Cambridge, MA: Harvard University Press)]
- Hermann L, 1870 "Eine Erscheinung des simultanen Contrastes" *Pflügers Archiv für die gesamte Physiologie* **3** 13–15
- Hubel D H, Wiesel T N, 1959 "Receptive fields of single neurones in the cat's striate cortex" *Journal of Physiology* **148** 574–591
- Hubel D H, Wiesel T N, 1962 "Receptive fields, binocular interaction and functional architecture in the cat's visual cortex" *Journal of Physiology* **160** 106–154
- Hubel D H, Wiesel T N, 1965 "Receptive fields and functional architecture in two nonstriate visual areas (18 and 19) of the cat" *Journal of Neurophysiology* **28** 229–289
- Hubel D H, Wiesel T N, 1968 "Receptive fields and functional architecture of monkey striate cortex" *Journal of Physiology* **195** 215–243
- Jung R, 1961 "Korrelationen von Neuronentätigkeit und Sehen", in *Neurophysiologie und Psychophysik des visuellen Systems* Eds R Jung, H H Kornhuber (Berlin: Springer) pp 410–435
- Jung R, Spillmann L, 1970 "Receptive-field estimation and perceptual integration in human vision", in *Early Experience and Visual Information Processing in Perceptual and Reading Disorders* Eds F A Young, D B Lindsay (Washington, DC: National Academy of Sciences) pp 181–197
- Kaplan E, Lee B B, Shapley R M, 1990 "New views of primate retinal function" *Progress in Retinal Research* **9** 273–336
- Kato H, Bishop P O, Orban G A, 1978 "Hypercomplex and simple/complex cell classifications in cat striate cortex" *Journal of Neurophysiology* **41** 1071–1095
- Koenderink J, 1977 "Current models of contrast processing", in *Spatial Contrast* Eds H Spekreijse, L H van der Tweel (Amsterdam: North-Holland) pp 116–119
- Kolb H, 1991 "Anatomical pathways for color vision in the human retina" *Visual Neuroscience* **7** 61–74
- Kuffler S W, 1953 "Discharge patterns and functional organization of mammalian retina" *Journal of Neurophysiology* **16** 37–68
- Lavin E, Costall A, 1978 "Detection thresholds of the Hermann grid illusion" *Vision Research* **18** 1061–1062
- Lee B B, 1996 "Receptive field structure in the primate retina" *Vision Research* **36** 631–644
- Levine J, Spillmann L, Wolf E, 1980 "Saturation enhancement in colored Hermann grids varying only in chroma" *Vision Research* **20** 307–313
- Lingelbach B, Block B, Hatzky B, Reisinger E, 1985 "The Hermann grid illusion—retinal or cortical?" *Perception* **14**(1) A7 (abstract)
- Lingelbach B, Ehrenstein W H, 2002 "Das Hermann Gitter und die Folgen" *Deutsche Optikerzeitung* **5** 14–20
- Malpeli J G, Baker F H, 1975 "The representation of the visual field in the lateral geniculate nucleus of *Macaca mulatta*" *Journal of Comparative Neurology* **161** 569–594

- Malpeli J G, Schiller P H, Colby C L, 1981 "Response properties of single cells in monkey striate cortex during reversible inactivation of individual lateral geniculate laminae" *Journal of Neurophysiology* **46** 1102–1119
- Mansfield R J, 1974 "Neural basis of orientation perception in primate vision" *Science* **186** 1133–1135
- Masland R H, 2001 "The fundamental plan of the retina" *Nature Neuroscience* **4** 877–886
- Mullikin W H, Jones J P, Palmer L A, 1984 "Periodic simple cells in cat area 17" *Journal of Neurophysiology* **52** 372–387
- Ninio J, Stevens K A, 2000 "Variations on the Hermann grid: an extinction illusion" *Perception* **29** 1209–1217
- Oehler R, Spillmann L, 1981 "Illusory colour changes in Hermann grids varying only in hue" *Vision Research* **21** 527–541
- Orban G A, Kato H, Bishop P O, 1979 "Dimensions and properties of end-zone inhibitory areas in receptive fields of hypercomplex cells in cat striate cortex" *Journal of Neurophysiology* **42** 833–849
- Poggio G F, 1972 "Spatial properties of neurons in striate cortex of unanesthetized macaque monkey" *Investigative Ophthalmology* **11** 368–377
- Preyer W, 1897/98 "On certain optical phenomena. Letter to Professor E C Sanford" *American Journal of Psychology* **9** 42–44
- Rodieck R W, 1973 *The Vertebrate Retina; Principles of Structure and Function* (San Francisco, CA: W H Freeman)
- Rodieck R W, 1988 "The primate retina" *Comparative Primate Biology* **4** 203–278
- Schiller P H, 1996 "The ON and OFF channels of the mammalian visual system", in *Progress in Retinal and Eye Research* Eds N N Osborne, G J Chader (Oxford: Pergamon Press) pp 173–195
- Schiller P H, Finlay B L, Volman S F, 1976a "Quantitative studies of single-cell properties in monkey striate cortex. I. Spatiotemporal organization of receptive fields" *Journal of Neurophysiology* **39** 1288–1319
- Schiller P H, Finlay B L, Volman S F, 1976b "Quantitative studies of single-cell properties in monkey striate cortex. II. Orientation specificity and ocular dominance" *Journal of Neurophysiology* **39** 1320–1333
- Schiller P H, Logothetis N K, 1990 "The color-opponent and broad-band channels of the primate visual system" *Trends in Neuroscience* **13** 392–398
- Schiller P H, Malpeli J G, 1978 "Functional specificity of lateral geniculate nucleus laminae of the rhesus monkey" *Journal of Neurophysiology* **41** 788–797
- Schiller P H, Sandell J H, Maunsell J H, 1986 "Functions of the ON and OFF channels of the visual system" *Nature* **322** 824–825
- Schiller P H, Wiener M, 1963 "Monoptic and dichoptic visual masking" *Journal of Experimental Psychology* **66** 386–393
- Sekuler R, Blake R, 1994 *Perception* (New York: McGraw-Hill)
- Spillmann L, 1971 "Foveal perceptive fields in the human visual system measured with simultaneous contrast in grids and bars" *Pflügers Archiv für die gesamte Physiologie* **326** 281–299
- Spillmann L, 1981 "Illusions of contrast, brightness, color, and motion and their neurophysiological interpretation" *Freiburger Universitätsblätter* **74** 73–77
- Spillmann L, 1994 "The Hermann grid illusion: a tool for studying human perspective field organization" *Perception* **23** 691–708
- Spillmann L, Levine J, 1971 "Contrast enhancement in a Hermann grid with variable figure–ground ratio" *Experimental Brain Research* **13** 547–559
- Troscianko T, 1982a "A given visual field location has a wide range of perceptive field sizes" *Vision Research* **22** 1363–1369
- Troscianko T, 1982b "A stereoscopic presentation of the Hermann grid" *Vision Research* **22** 485–489
- Uttal W R, Davis N S, Welke C, 1994 "Stereoscopic perception with brief exposures" *Perception & Psychophysics* **56** 599–604
- Wässle H, Boycott B B, 1991 "Functional architecture of the mammalian retina" *Physiological Review* **71** 447–480
- Wässle H, Grunert U, Röhrenbeck J, Boycott B B, 1990 "Retinal ganglion cell density and cortical magnification factor in the primate" *Vision Research* **30** 1897–1911
- Watanabe M, Rodieck R W, 1989 "Parasol and midget ganglion cells of the primate retina" *Journal of Comparative Neurology* **289** 434–454
- Werblin F S, Dowling J E, 1969 "Organization of the retina of the mudpuppy, *Necturus maculosus*. II. Intracellular recording" *Journal of Neurophysiology* **32** 339–355

-
- Westheimer G, 2001 "Relative localization in the human fovea: radial-tangential anisotropy" *Proceedings of the Royal Society of London, Series B* **268** 995-999
- Westheimer G, 2003 "Meridional anisotropy in visual processing: implications for the neural site of the oblique effect" *Vision Research* **43** 2281-2289
- Westheimer G, 2004 "Center-surround antagonism in spatial vision: retinal or cortical locus?" *Vision Research* **44** 2457-2465
- Westheimer G, Beard B L, 1998 "Orientation dependency for foveal line stimuli: detection and intensity discrimination, resolution, orientation discrimination and vernier acuity" *Vision Research* **38** 1097-1103
- Williams D R, 1988 "Topography of the foveal cone mosaic in the living human eye" *Vision Research* **28** 433-454
- Williams D R, Coletta N J, 1987 "Cone spacing and the visual resolution limit" *Journal of the Optical Society of America A* **4** 1514-1523
- Wilson H R, Bergen J R, 1979 "A four mechanism model for threshold spatial vision" *Vision Research* **19** 19-32
- Wolfe J M, 1984 "Global factors in the Hermann grid illusion" *Perception* **13** 33-40

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