VISUAL ILLUSIONS:

PERCEPTION OF LUMINANCE, COLOR, AND MOTION IN HUMANS

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To my grandfather Heinrich,

my parents Elke and Rainer,

my brother Sven,

and

to my fiancée Sandra.

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Zusammenfassung

In den vergangenen Jahrhunderten haben Studien mit und über visuelle Illusionen zu einem besseren Verständnis des menschlichen visuellen Systems beigetragen. Ziel dieser Dissertation ist es nun, einen Beitrag zu diesem Forschungsgebiet mittels visueller Illusionen als Untersuchungsgegenstand zu leisten. In mehreren psychophysischen Experimenten und qualitativen Herangehensweisen habe ich versucht, dieses Ziel zu erreichen. Da es sich bei dem menschlichen visuellen System um ein überaus komplexes System handelt, dessen Verarbeitungsmechanismen sehr stark vernetzt und interaktiv sind, konzentriere ich mich in meiner Arbeit nicht ausschließlich auf ein einzelnes Forschungsgebiet bei visuellen Illusionen, sondern untersuche eine ganze Serie von Täuschungsphänomenen. Die vorliegende Dissertation ist in drei Hauptteile untergliedert: 1. Assimilationsphänomene und Filling-in (perzeptuelle Einfüllung); 2. geometrisch-optische Illusionen, Helligkeitsillusionen und Farbtäuschungen (diese werden unter Bedingungen mit Helligkeitskontrast und Isoluminanz – Helligkeitsgleichheit – mit chromatischem Kontrast untersucht); 3. Scheinbewegung in statischen Mustern. Diese Untersuchungen erweitern unser Wissen über verschiedenste Verarbeitungsmechanismen, beginnend bei den niedrigen Verarbeitungsstufen (Retina) bis hin zu den höheren Arealen im visuellen Kortex (V5/MT, MST). Die Untersuchungsergebnisse werden im Kontext aktueller Forschungsarbeiten im Bereich der Sehforschung interpretiert und diskutiert. Darüber hinaus präsentiere ich neuartige visuelle Phänomene (Illusionen), welche einen wertvollen Beitrag für zukünftige Forschung in den Bereichen Psychophysik, Physiologie und bildgebenden Verfahren zur Erforschung des Gehirns leisten können.

Abstract

Over the past centuries studies on visual illusions have provided us with a better understanding of the human visual system. The aim of this thesis is to contribute to this research field by utilizing visual illusions as research tools. In several psychophysical experiments and qualitative approaches I try to realize this aim. Since the human visual system is complex and processing mechanisms are highly interactive in networks, I will not focus on a single field but rather investigate a whole series of visual illusions. The thesis is divided into three major threads: 1. phenomena of fading and filling-in; 2. geometric-optical illusions, luminance illusions, and color illusions at conditions of luminance contrast and isoluminance with chromatic contrast; 3. apparent motion illusions. These studies expand our knowledge on various processing mechanisms from low-level (retina) to higher-levels of the visual cortex (V5/MT, MST). The results of the studies are interpreted and discussed within the context of current research work in the field of Vision Sciences. Furthermore, I present some new visual (illusory) phenomena, which could serve as valuable tools for future research in psychophysical, physiological, or brain imaging studies.

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Erklärung
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“The complex structure of the visual system is sometimes exposed by its illusions.”

D.M. Eagleman (2001, p920)

I Introduction

Visual Illusions and why we study them

“The act of ‘seeing’ seems so effortless that it is difficult to appreciate the vastly sophisticated – and poorly understood – machinery that underlies the process” (Eagleman, 2001, p920). Visual illusions exist at the extremes of what our system has evolved to handle. They are neither just entertaining misperceptions nor “subjective perversions of the contents of objective perceptions” (Külpe, 1893), even though they sometimes stem from assumptions made by the visual system. For instance, Gregory (2001) regards perceptions as guesses or predictive hypotheses by the visual system of what may be out there in the visual scene, whereas in other situations they represent an active recalibration. Optical illusions represent good adaptations of the visual system to standard viewing situations (Bach & Poloschek, 2006). They serve as a powerful window into the neurobiology of vision, and may help to unravel the processes underlying visual perception (Eagleman, 2001). Furthermore, they have led to new experimental techniques. Over the past two centuries, studies on visual illusions have provided us with a better understanding of the human visual system, but we are still far away from an overarching understanding. However, recently the general public –and not just the scientific community– has gained interest in visual illusions, which is reflected in a rising number of basic scientific and popular scientific books on visual illusions (e.g. Block & Yuker, 1996; Ditzinger, 2006; Ernst, 1998; Robinson, 1972; Sarcone & Waeber, 2005; Seckel, 2003, 2004, 2005, 2006). They try to assign the scientific fascination into everyday life perception. To the Gestaltists mismatches between stimulus and percept serve as evidence of how the brain processes visual information (e.g., Wertheimer, 1912; Köhler, 1920, 1923, 1947; for overview see Spillmann & Ehrenstein, 2004). Illusory phenomena may in this sense serve as noninvasive tools for studying the neural mechanisms underlying visual perception and can thus reveal the limitations as well as creative abilities of the visual system (Spillmann & Ehrenstein, 2004). Robinson (1972) takes this a step further by pointing out that it is rather easy to formulate a theory, which is consistent with correct perception, but more challenging to produce a theory capable of predicting the failures as well as the successes of the perceptual system. But, he also addresses the issue that the practical importance of visual illusions should not be overestimated, since most perceptual environments are too rich to give rise to the percept of illusions. Thus, visual illusions occur as the extremes of visual perception.

Outline of the thesis

This thesis augments the understanding of the human visual system by using a variety of illusory phenomena in several psychophysical experiments. Moreover, we introduce new visual phenomena that could be valuable tools for future research in the field of Vision Sciences to increase our knowledge about the visual system even more.

The thesis follows three main threads, by investigating: 1. the phenomena of assimilation, fading and filling-in; 2. geometric-optical-, luminance-, and color illusions at conditions of luminance contrast and isoluminance with pure chromatic contrast; 3. apparent motion illusions.

In the first part the classical phenomena of color assimilation (e.g., von Bezold, 1874), fading and filling-in (e.g., Troxler, 1804; Krauskopf, 1963) are investigated. Chapter 1 introduces color assimilation effects and shows their strong influence on grouping effects in dot lattices (*Color assimilation as a grouping factor*). In Chapter 2 (*Filling-in with color: different modes of surface completion*) five experiments investigate filling-in of disk-ring patterns with isoluminant colors (blue, green, red, and yellow) and the influence of achromatic (black) borders. Chapter 3 (*Perceptual filling-in from the edge of the blind spot*) shows that only a minimal amount of information at the edge of the blind spot is needed to fill in this receptor free area of the retina to make up a complete percept. This accounts for color (0.05 deg of visual angle) as well as for texture (0.2 deg of visual angle). The final chapter of this section (Chapter 4: *Filling-in with texture: uniform vs. random orientation*) deals with the issue of texture filling-in at different texture orientations. We could show that the same patterns, center and surround texture just inverted in the second pattern, with the same amount of texture information cause different filling-in latencies. Salience of different textures is important for filling-in latencies. The results obtained in this psychophysical study get support from neurophysiological single cell recording studies in terms of center-surround activation and inhibition. All studies reported here support the assumption that filling-in is an active process instead of a passive tagging. This accounts for color as well as for texture in ‘normal’ perception and natural scotomas.

Part two addresses, amongst other issues, the assumption by Livingstone and Hubel (1987, 1988) that many visual illusions disappear under conditions of isoluminance and suggest that they are mediated solely by the magnocellular system. Since luminance and color processing in the retina and LGN are separated, one could expect that processing mechanisms work largely independent for different features and that therefore some visual illusions break down under conditions of isoluminance. In an experiment on geometric-optical illusions (Chapter 5: *Geometric-optical illusions at isoluminance*) we show that 9 geometric-optical illusions occur at same strength independent of the mode of presentation (luminance, low luminance contrast, isoluminance). Thus, certain visual illusions do not break down when presented at isoluminance as suggested by Livingstone and Hubel. It seems as if illusions, which do not break down, are rather processed by neurons sensitive for color *and* luminance information. Furthermore, we introduce a new effect which we refer to as 'weaves' (Chapter 6: *Weaves and the Hermann grid*). In weaves light horizontal and dark vertical lines are intertwined. Depending on the background luminance, light perceptual smudges are perceived where light gray lines cross in front of dark gray lines (with a white background) or dark smudges where dark lines cross in front of light gray lines (with black background). This effect is compared with the classical Hermann grid illusion minutiously -since it appears to be quite similar at first glance, but it is much stronger and less sensitive- and its relevance for the Vision Sciences is pointed out. Our conclusion there is that the classical Hermann grid is a sub-phenomenon of the weaves. In the final chapter of this section we take a closer look at contrast asynchronies and the resulting grouping effects. It is demonstrated that apparent motion due to contrast modulation (2nd order motion) can also lead to strong grouping effects (Chapter 7: *Grouping by contrast—figure-ground segregation is not fundamental*).

During the third and final part of this thesis, static motion illusions are investigated and eventually a new motion illusion is introduced. Chapter 8 (*Apparent rotation and jazzing in Leviant's Enigma illusion*) attempts to uncover the critical factors that elicit the streaming motion in the Enigma-figure. Orthogonality of the abutting lines is demonstrated to be an important factor for this illusion. However, this factor is primarily responsible for the strength of the illusory effect. But it is not a crucial factor for it, since patterns were generated lacking orthogonality or junctions, which still show a reduced illusory streaming motion on the rings. In this experiment accommodation and eye movements were excluded as possible factors eliciting the effect. In a subsequent study (Chapter 9: *Reversal of apparent rotation in the Enigma-figure with and without motion adaptation and the effect of T-junctions*) we investigated the time course of reversals in motion direction in the Enigma-figure and found a similar pattern as obtained for classical bistable figures. This indicates that this motion illusion shares some properties with non-motion illusions which has not been shown or expected before. The different experiments on the Enigma-figure resulted in a new motion illusion (Chapter 10: *A new motion illusion – The Rotating-Tilted-Lines illusion*) which is introduced in the final chapter. The rotary motion seen is this figure is reminiscent of the motion perceived in the Pinna-Brelstaff-Illusion (Pinna & Brelstaff, 2000). They both rely on changes in retinal image size. However, our new illusion is much simpler than the Pinna-Brelstaff-Illusion and it could be a useful tool in the future for continued investigation (single cell recordings, functional imaging techniques, etc.) of this class of motion illusions to find a neural correlate and finally an explanation for them.

In summary, we present a whole variety of studies on visual illusions and we make a step towards understanding visual processes and explaining these illusions. We find further pieces of knowledge for how the human visual system deals with these kinds of stimuli to process them in an appropriate manner. Apart our findings we hope that future research will make use of our data and new visual illusions.

Reading advice

Every chapter of this thesis is written as a separate scientific study. Therefore, it is possible for the reader to read only those chapters he or she is mainly interested to find valuable methods, data or interpretations he or she is concerned with. The disadvantage of this writing style is that those who aim at reading the whole work might find repeating information in some of the introductory sections. However, it helps to focus on each scientific problem/question that is dealt with in detail. Since every chapter has its own Discussion and Conclusion (or both combined), the Conclusion at the end of the thesis will be rather recapitulated.

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II Research work

Part 1 –

Assimilation and filling-in

Chapter 1 –

Color assimilation as a grouping factor[1]

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[1] This work was published in a slightly different form: Hamburger, K. (2005). Color assimilation as a Grouping Factor. *Gestalt Theory, 27 (2)*, 155-163.

A color assimilation pattern devised by Golomb (1962) and several new variants of it were studied. The pattern consists of 4 columns of 3 x 12 black disks. The disks in each column are surrounded by either a red, yellow, or blue ring; rings in the fourth column are of mixed color. The rings produce a veil of subtle color emanating onto (filling) the white background (into the white interspaces). The influence of this color assimilation on perceptual grouping and the impact of color shifts on grouping are described. Grouping even persists at observation distances too large to still perceive the color of the inducing annuli. Furthermore, depth effects and apparent motion due to grouping are shown. Similarities and differences between this and other color spreading phenomena are discussed.

Introduction

In the last 25 years, the Freiburg psychophysics laboratory has reported on two kinds of chromatic assimilation, Van Tuijl's (1975) *neon color effect* and Pinna's (Pinna, 1987) *watercolor effect.* Both effects are long-range effects. The former is characterized by filling-in an illusory surface area with color, such as the central gap of the Ehrenstein figure (Redies & Spillmann, 1981) or the region inside the Kanizsa triangle (Varin, 1971). The latter stands out by imparting its color uniformly onto a surface area delineated by a dark/bright chromatic double contour. While the illusory coloration in both cases is similar, the way in which it is induced is not. Filling-in of neon color requires end-points ("terminators") that are connected by an illusory contour running *at right angles* to the tips of the inducing lines (see, however, the flank effect; Redies &

Spillmann, 1981). In comparison, propagation of watercolor depends on the presence of two colored borders, flanking each other, and originates *in parallel* to those contours. This difference suggests two mechanisms. Both effects have in common that they are immediately visible and both effects have strong figure-ground properties. In fact, Pinna, Werner, and Spillmann (2003) demonstrated that the watercolor effect overrules all the classical Gestalt factors such as proximity, good continuation, closure and surroundedness, symmetry, convexity, amodal completion, and past experience. Furthermore, neon color spreading is characterized by perceptual transparency, whereas the watercolor effect is not. The assumed correlation between perceptual transparency and color spreading has recently been investigated by Wollschläger (2002).

Here, I deal with a phenomenon of color assimilation discovered in 1962 by the artist Louis Golomb under the supervision of his teacher William S. Huff at the *Hochschule für Gestaltung* in Ulm (Germany). In fact, it was Professor Huff who communicated Golomb's figure to us. The effect is apparent in Figure 1a, which shows an array of black disks that are surrounded by very thin colored rings. Although the rings are barely perceptible, the veil of color emanating from them is very clear, especially as it groups the black disks into three vertical columns of red, yellow, and blue. There is also a fourth column (on the right) that has no uniform color and that looks less distinct. We suggest that this effect must be due to neural "bleeding", quite different from the neon color and watercolor effects.

In this paper, I will demonstrate how this assimilative color affects perceptual grouping. Furthermore, I will point out similarities as well as differences between Golomb's effect and the neon color and watercolor effects.

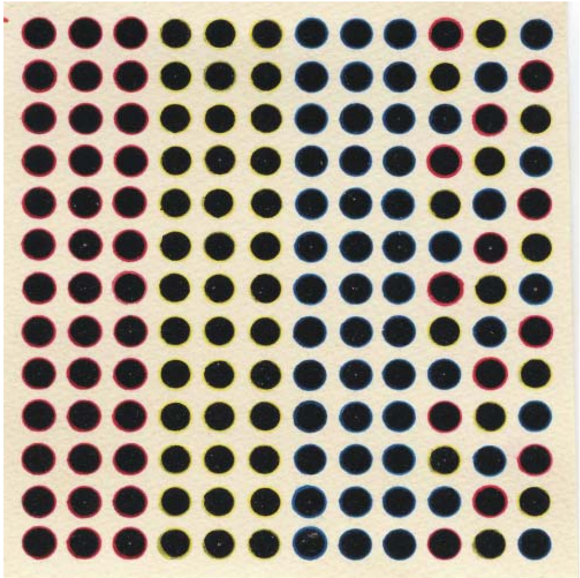

Figure 1a: Louis Golomb's assimilation pattern (1962).

Methods

Stimuli and procedure

Stimuli similar to Golombs's original figure were designed and presented on a Fujitsu Siemens Amilo-A laptop computer to explore how color assimilation and grouping is affected by manipulating different parameters. Stimuli were created in CorelDraw 12 and shown once in random order. The black disks had a diameter of 0.95 deg while the surrounding colored rings had a width of 0.19 deg. In variants of this pattern thin colored annuli (Figures 6 and 7) were inserted inbetween the black disk and the colored ring or between the colored ring and the white background. The width of these annuli was a mere 0.03 deg. The whole stimulus pattern subtended 18.43 deg. Observation distance was 60 cm. Subjects viewed the patterns with freely moving eyes in a dark room. There was no time limit for the inspection of each stimulus, but subjects responded on average within 20 s. Altogether, there was a total of 9 stimulus arrays.

Subjects

Seventeen undergraduate students, aged 21 to 27 years, from the University of Freiburg participated in the experiment. They had normal or corrected-to-normal visual acuity and normal color vision (tested with the Ishihara pseudoisochromatic plates; Ishihara, 1982). All subjects were naïve with regard to the purpose of the study.

Task

Subjects familiarized themselves with the effect under consideration by viewing the original Golomb figure. Thereafter they were asked to rate the strength of color assimilation for the red, yellow, and blue columns using a scale ranging from 0 – 10 (anchors: only black disks = 0; original Golomb pattern = 10). They were instructed to also comment on the salience of perceptual grouping as well as on perceived depth and apparent motion.

Results

All subjects reported seeing color assimilation in the original stimulus pattern and its computerized version, although to a slightly weaker extent in the computer version.

In the first variant (Figure 1b) of the Golomb pattern yellow was described as the most conspicuous color by 9 subjects, followed by red (6 subjects) and blue (2 subjects). In contrast, when colored disks were used in conjunction with thick black rings, to test for black rings as a barrier preventing assimilation, the color never spread onto the background (Figure 2). A small black annulus in conjunction with a colored ring prevents assimilation onto the disk but enhances color spreading onto the interspaces (Figure 3). In this stimulus the hierarchy of color strength persisted (yellow being reported as strongest by 8 subjects, red by 7 subjects, and blue by 2 subjects). Furthermore, little or no color spreading was reported if the ring surrounding the disk had the same color and could not be perceptually segregated from it (see the third column in Figure 4).

In addition to color assimilation, Figure 5 frequently elicited a depth percept (10 subjects). The yellow disks surrounded by blue rings were reported as lying in front, whereas the blue disks surrounded by yellow rings were reported as lying in the back. In this pattern, subjects also reported sliding motion of the columns in a vertical or horizontal direction when they moved their eyes.

While color assimilation was a strong factor for grouping, shifts in color appearance in conjunction with assimilation led to even more striking perceptual grouping. Figures 6 and 7 elicit different colors within a single column although the colors of the wider rings were physically identical, representing the same red, yellow, and blue as in the stimuli used before. Only the small annuli between disk and ring and between ring and surround were added. Figure 8 illustrates how many subjects perceived Figure 6 and 7 as subdivided into 6 or 3 sections, respectively, due to the color mixture from the combination of ring and annuli. All subjects reporting about a subdivision (10 subjects) perceived Figure 6 as 6 subfields, whereas for Figure 7 5 subjects reported about seeing 6 subfields, 4 perceived three subfields and a single subject 4 subfields. In Figure 9, where the width of the ring and the surrounding ring was identical (0.19 deg), all subjects reported six sections. Color spreading was strongest for yellow (11 subjects), followed by red (4 subjects) and blue (2 subjects).

For Figure 10, 16 subjects reported yellow assimilation as strongest, followed by red (1 subject) and blue (none). Strong outward color assimilation was reported by 14 subjects, when the yellow ring was on the outside and strong inward assimilation when yellow was located on the inside. Three subjects did not report any direction of color spreading. The darker borders (blue, red) prevented color assimilation onto the white area next to their own position when combined with yellow.

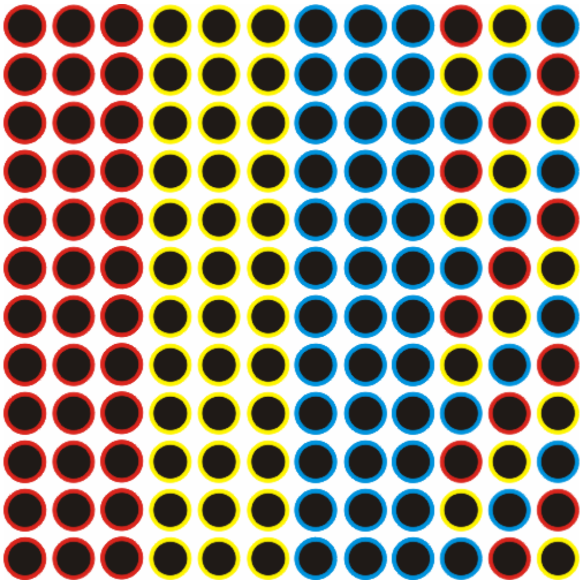

Figure 1b: Computerized version of the Golomb assimilation pattern. The black disks had a diameter of 0.95 deg while the colored rings had a width of 0.19 deg. The whole stimulus pattern subtended 18.43 deg.

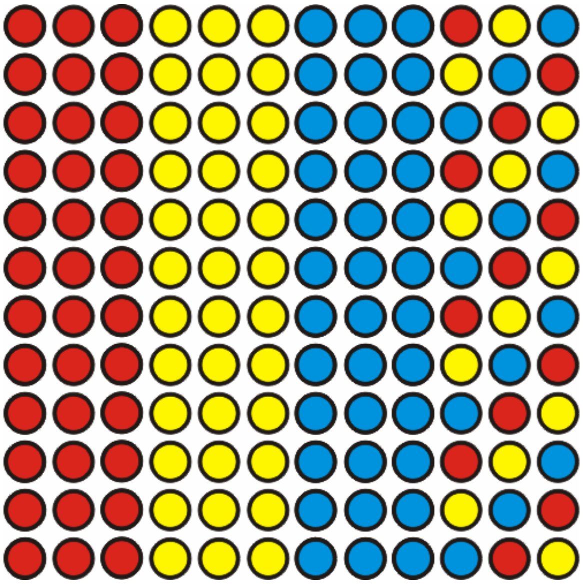

Figure 2: Inversion of the Golomb pattern (Figure 1b).

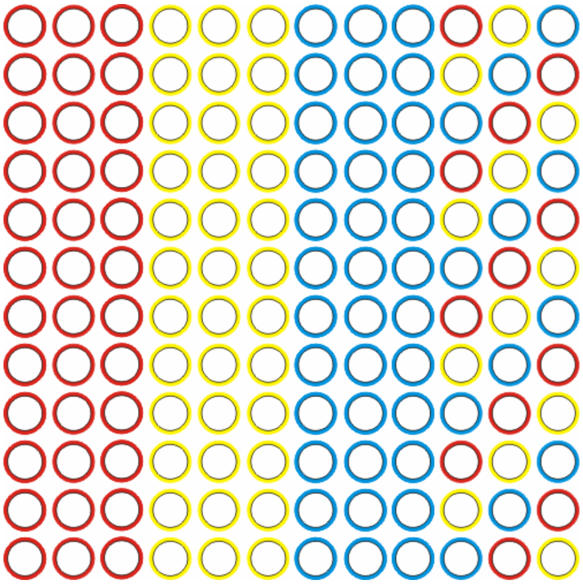

Figure 3: The black disks were replaced by black annuli of 0.03 deg on the inside of the colored rings.

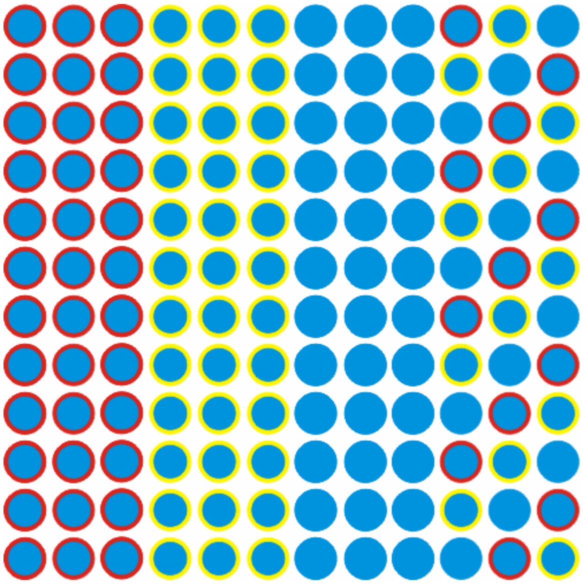

Figure 4: The black disks were replaced by colored disks (here blue). Thus, the disk-ring hierarchy disappeared in one column (here in the blue column).

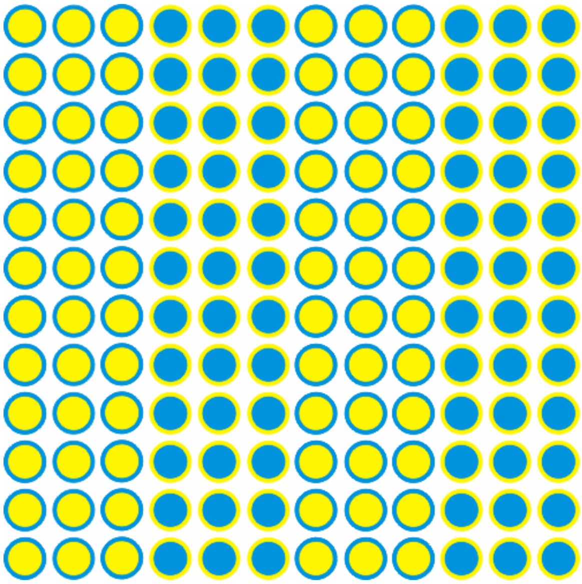

Figure 5: Yellow disks were surrounded by blue rings and blue disks were surrounded by yellow disks.

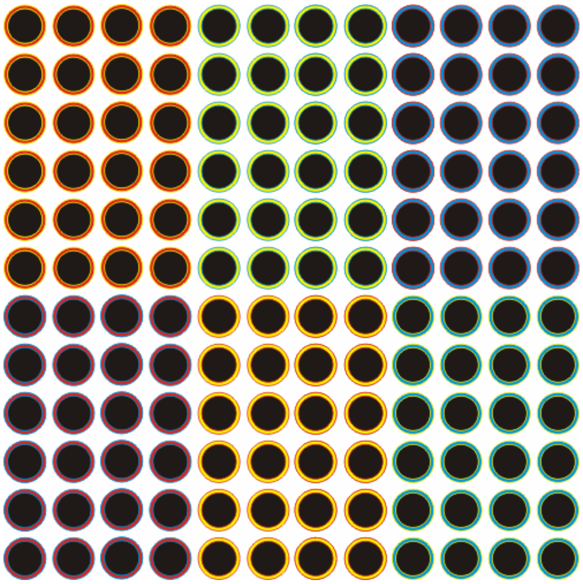

Figure 6: Colored annuli of 0.03 deg in width were added on the inside and outside of the colored rings of Figure 1. Physically, the ring colors (yellow, red, and blue) were identical in each column. Perceptual shifts in ring color appear due to the small annuli.

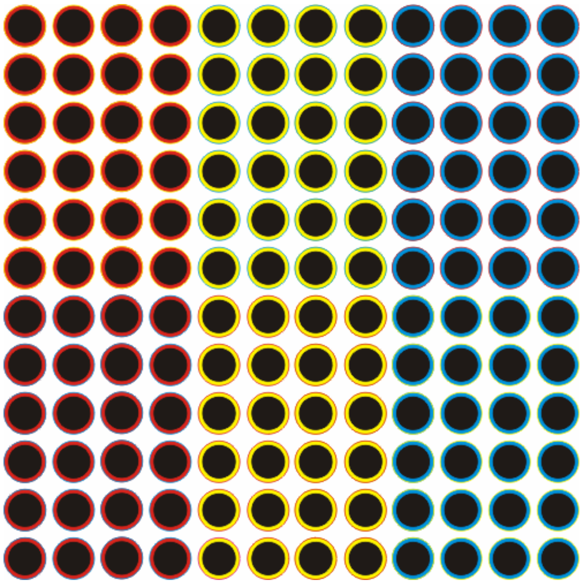

Figure 7: Similar pattern as shown in Figure 6 except that this time the annuli between disks and colored rings were removed.

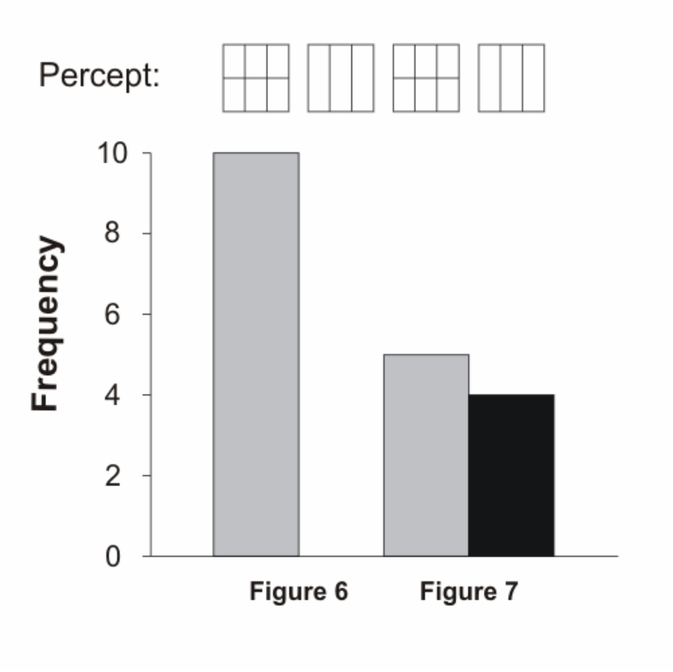

Figure 8: Perception of figures with small colored annuli surrounding the rings. The percept differed when there was no second annulus on the inside. Figure 6 was always perceived as 6 sections, whereas Figure 7 was seen as 6 sections as well as 3 sections.

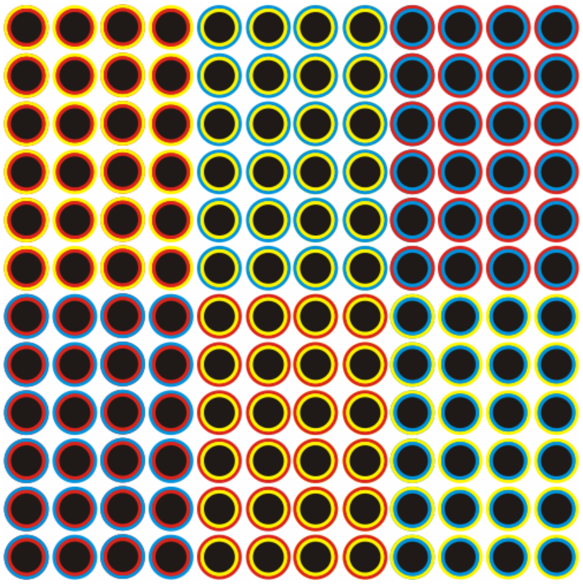

Figure 9: Black disks were surrounded by two colored rings of same width (0.19 deg).

Figure 10: Similar pattern as shown in Figure 9 except that this time the black disks were removed.

Discussion

What I can state from these results obtained is:

(i) The induced effect of color assimilation typically was more salient than the inducing effect, although it was less saturated.

(ii) Color assimilation produced perceptual grouping of the individual elements within a column. Grouping in differently colored columns was usually reported first, suggesting that the global color perceived on the background was stronger than the local color perceived on the rings. In this sense one may say that the whole is more than just the sum of its parts. This is clearly shown by the right column in Figure 1a and 1b which consists of differently colored elements and exhibits grouping only along the diagonals, if at all.

(iii) The darker contour defines what is perceived as figure and what as ground, showing that color assimilation is not only a strong factor for grouping, but also for figure-ground-organization. In the Golomb patterns the darker contour always belongs to the figure, thus, creating different percepts depending on the position of the dark contour. Rubin (1921) called this principle belongingness (Zusammengehörigkeit) nowadays known as border ownership (Nakayama & Shimojo, 1990). The direction of assimilation follows the direction of the double contour, meaning that assimilation depends on the law of the lowest contrast. If the stimulus consists of two colored rings (of equal width plus a white disk), color spreading depends on the location of the yellow ring. When placed on the inside, subjects perceived inward color spreading (filling-in), and when placed on the outside outward color spreading. However, the black disks are essential for inducing the strongest color assimilation on the background for the Golomb figures.

(iv) Assimilation is stopped at an apparent edge and no color mixtures in the assimilated surfaces emerge, which is in line with the characteristics of the watercolor effect (Pinna, Brelstaff & Spillmann, 2001). So, the color seems to propagate from the contour onto the area.

(v) Strong color shifts occurred in the combination of disk, ring, and annuli, which depended on ring color as well as on the color of the annuli. When the observation distance was increased to the point where the narrow annuli could no longer be identified, assimilation and grouping in different subfields still prevailed. Thus, we do not need to consciously see the small annuli to perceive color shifts and the resulting grouping. Paradoxically, the annulus between the black disk and the colored ring seems to play a very important role for grouping. However, the hue of the rings (and additionally the assimilative color) perceptually shifts as a function of the color of the annuli. Likewise, in the von Bezold spreading effect (Seitz, 1921) colored elements show a color shift (assimilation) towards the hue of the adjacent area. Thus, the von Bezold effect and the color spreading in these Golomb patterns are quite similar, but in the Golomb patterns we additionally see a strong color spreading onto the white interspaces which depends on the perceived color shift. Thin lines resulted in color shifts, whereas with thick lines no color shifts occurred. Larger shifts in color appearance with a patterned chromatic background than with a uniform background have recently been reported by Monnier and Shevell (2003, 2004) and Shevell and Monnier (2005). They assume that an S-cone spatially antagonistic receptive field might be a neural substrate mediating the large color shifts. Stronger assimilation for thinner lines was also reported by Cao and Shevell (2004).

(vi) Both the neon color effect and the watercolor effect are more salient with thin inducing lines. Similarly, in Golomb patterns narrow rings surrounding the black disks and additional thin annuli yield the strongest color assimilation. Furthermore, as in the watercolor effect, color assimilation in Golomb patterns requires a luminance hierarchy proceeding from low to high.

Conclusion

This work shows that colored rings although quite narrow can spread their color onto the white background, thereby enabling perceptual grouping. Phenomenologically, this kind of assimilation is similar to the *neon color* and *watercolor effects*. However, it differs from these phenomena by being limited in the presented stimuli to a short-range (about 1 deg). The mechanism underlying assimilative color spreading is still unknown, although chromatic aberration may play a role. Further experimentation using an achromatizing lens is thus suggested.

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Chapter 2 –

Filling-in with color: different modes of surface completion[2]

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[2] This work was published in a slightly different form: Hamburger, K., Prior, H., Sarris, V., & Spillmann, L. (2006). Filling-in with colour: Different modes of surface completion. *Vision Research, 46 (6-7),* 1029-1038.

We investigated the figural dynamics of filling-in processes in figures with more than one possible figure-ground organisation. Using a central disk and two concentric rings as well as similar stimuli consisting of three nested squares or parallel stripes, we tested for filling-in with different equiluminant color combinations. We observed four modes of filling-in: First, in most of the cases, the inner ring assumed the color of the central disk and outer ring (M1). Second, the central disk became filled-in with the color of the inner ring, without any color change on the outer ring (M2). Third, in a first step, the color of the inner ring spread onto the central disk; then, in a second step, the color of the outer ring spread over the whole stimulus (M3). This two step filling-in process has not been reported so far. Fourth, a mode (M4) was sometimes observed that was characterised by the central disk and outer ring assuming the color of the inner ring. Thus, color filling-in or color spreading proceeded both in a centripetal (periphery to fovea) as well as a centrifugal direction. The colors red and yellow proved to be stronger inducers than blue and green. Conversely, the latter colors became filled-in more easily than the former. The filled-in color was always that of the inducing stimulus, i.e., there was no color mixture. This suggests a long-range, neural process underlying filling-in under these conditions.

Introduction

Troxler (1804) observed that with strict fixation a small, low-contrast stimulus presented in the periphery of the visual field quickly fades into the background and becomes invisible. This phenomenon is known as Troxler-effect (Pirenne, 1962). Fading also occurs with large, centrally fixated targets that assume the brightness and color of the surrounding background (Krauskopf, 1963; Spillmann, Neumeyer & Hunzelmann, 1984). This adaptation has been attributed to *filling-in*, a neural process involving active propagation of surround features into the target area (Gerrits, De Haan & Vendrik, 1966; Gerrits & Vendrik, 1970; DeWeerd, Gattass, Desimone & Ungerleider, 1995). While Troxler used static stimuli, later studies have shown that even slowly rotating or flickering objects fade into the background (Spillmann et al., 1984).

The present study aims at a deeper understanding of the figural dynamics of the Troxler-effect. To this end, we studied fading and filling-in of color in compound stimuli that consisted of a central disk, a concentric “inner” ring, and a surrounding “outer” ring (Figure 1A). In hierarchical stimulus patterns of this kind, figure-ground segregation can take different forms. For example, if the small disk in the center were perceived as figure, filling-in would be expected to proceed from the outside to the inside (centripetal). On the other hand, if the inner ring were perceived as figure and the central disk and outer ring as ground, filling-in would be expected to proceed in two directions (centripetal and centrifugal). In this case the notion that Troxler-type fading and filling-in typically proceed from the outer edge of a surface towards the center (Paradiso & Nakayama, 1991) may not hold.

Our first question, therefore, was whether filling-in would proceed in one or two directions, and how often each of these two modes would occur. A second question was whether filling-in would affect only part of the stimulus, e.g., the central disk being filled-in by the color of the inner ring, or whether it would lead to surface uniformity of the entire stimulus, including the outer ring. A third question was whether the individual colors of the compound stimulus had an influence on the filling-in process. Would some colors be stronger inducers or more susceptible to filling-in than others? Concentric disk-ring stimuli were used throughout. However, in order to assess the possible role of stimulus shape on Troxler fading, we also used two other stimulus patterns in Experiment 1, “nested squares” and triplets of parallel vertical stripes.

Experiment 1

In this experiment, we presented a ring of a given color on a background of a different color. The ring was expected to be filled-in by the color of the surround in accordance with earlier findings, suggesting that the figure becomes assimilated by the ground, not vice versa (Spillmann et al., 1984).

Methods

Stimuli

Figure 1 depicts the stimuli used. Stimulus pattern A consisted of a gray central disk surrounded by a colored inner ring and a gray outer ring. The diameter of the disk was 7.0 deg while the width of the two surrounding rings subtended 3.5 deg each. The overall stimulus diameter was 21.0 deg. Stimulus pattern B consisted of a gray central square surrounded by a colored inner frame which in turn was enclosed by a gray outer frame. Angular sizes were the same as for the disk-ring condition (A). Stimulus C was composed of a vertical colored stripe of 3.5 deg in the center flanked by gray stripes of 5.2 deg on the left and right.

Stimuli were made from equiluminant matte Munsell papers having the notations: 5B 7/8, 5G 7/8, 5Y 7/8, 5R 7/8, and a neutral gray N8. Thus, hue varied whereas value and chroma were held constant. Stimuli were pasted on white poster cardboard and illuminated by four OSRAM© 860 LUMILUX daylight fluorescent lamps (470 Lux at presentation level). The following color combinations were used: gray-blue-gray, gray-green-gray, gray-yellow-gray, gray-red-gray. Stimuli were presented 12 times in a random order; they were shown at eye level and at right angles to the line of sight.

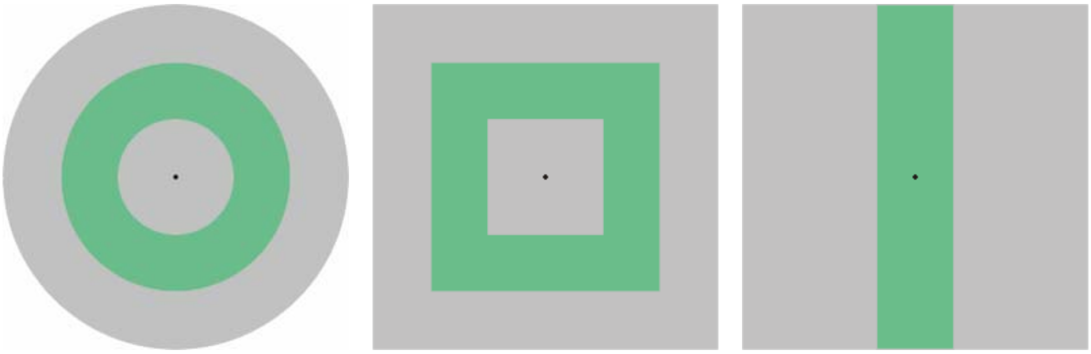

Figure 1: Sample stimuli used in Experiment 1. The inner ring, inner square and inner stripe had the colors blue, green, yellow, and red, whereas the other stimulus parts were gray. All colors and gray were equiluminant.

Subjects

Six observers participated (mean age 25.2 years, SD = 4.4). All of them had normal or corrected-to-normal visual acuity and normal color vision (tested with the Ishihara pseudoisochromatic plates; Ishihara, 1982). Prior to the actual experiment each subject had at least 5 hours of practice using stimuli that were similar to, but different from, the ones used in the experiments reported here. While three subjects had pre-experience with filling-in experiments, the other ones were inexperienced. All subjects were naïve with regard to the purpose of the study.

Procedure

Subjects fixated a black fixation point (0.18 deg) in the center of the stimulus using both eyes. They were seated on an adjustable chair resting their head on a chin- and forehead-rest to keep head position and observation distance (65 cm) constant. Subjects were instructed to maintain fixation, while keeping their attention evenly distributed over the stimulus pattern. Blinking was discouraged, as it is known to make the target reappear after it has faded (c.f. Gerrits, Stassen & van Erning, 1984). After a fixation period of 20 s, a trial was terminated and subjects were asked to report whether fading had occurred and how it had proceeded. We only used the first change of color for data analysis and ignored subsequent changes even if they constituted a different mode. Subjects were also instructed to describe whether the filled-in color was one of the stimulus colors or whether it was mixed; and whether the mode of filling-in corresponded to M1, M2, M3, M4 or M0 (no or partial filling-in such as a moon-shaped color change). Finally, they were asked which stimulus part had been perceived as figure and which as ground. The experimenter noted down subjects' responses after each trial. There was at least a 1 min-break between trials. An experimental session took about 2 hrs.

Results

Five of six subjects reported filling-in. One observer did not perceive filling-in due to poor fixation and frequent blinking; this subject was therefore excluded from the data analysis.

Filling-in effects occurred in 95.1% of the trials. Four modes were reported. *Mode 1*: The inner ring assumed the color of the central disk and outer ring. *Mode 2:* The central disk changed its color to that of the inner ring resulting in a larger, perceptually uniform surface enclosed by the unchanged outer ring. *Mode 3:* In a first step the central disk adopted the color of the inner ring (as in M2), and in a second step the combined area of disk and inner ring took on the color of the outer ring. *Mode 4*: The inner ring imparted its color both on the enclosed disk (*filling-in*) and the surrounding outer ring (*filling-out*). As our study aimed at the figural dynamics of filling-in, we do not report the frequency for partial filling-in (M0) in detail. Results for M0 are shown in Table 1. The distribution of the four response modes over all stimulus patterns was similar across all 5 subjects. In individual observers the perceived mode could vary among repeated presentations of the same stimulus. The hue of the filled-in color was always that of the inducing stimulus part. No color mixture in the filled-in areas was perceived in this or any of the following experiments. Within the observation period of 20 s stimulus and induced colors did not change.

Results for the stimulus pattern A (disk-ring arrangement) are shown in Figure 2. In 38.5% of the trials, the colored inner ring changed its color to that (gray) of the central disk and outer ring (M1). Induced coloration was sudden and uniform and subjects could not tell whether filling-in had proceeded from one or the other direction. However, preliminary studies showed that without the outer ring, the gray center assumed the color of the inner ring from the outside to the inside, suggesting that these new, more complex stimuli are treated in a different manner by the visual system. Alternatively, in 34.4% of the trials the central disk became filled-in by the color of the inner ring, while the outer ring remained unchanged (M2). In 20.6% of the trials, two-step filling-in occurred, where the central disk first assumed the color of the inner ring and thereafter the whole stimulus appeared in the same color as the outer surround (M3). Only in 6.5% of the trials did the inner ring spread its color equally onto the central disk as well as the outer ring (M4). The difference in occurrence of the four response modes was highly significant (X2 = 25.61, p < 0.0001).

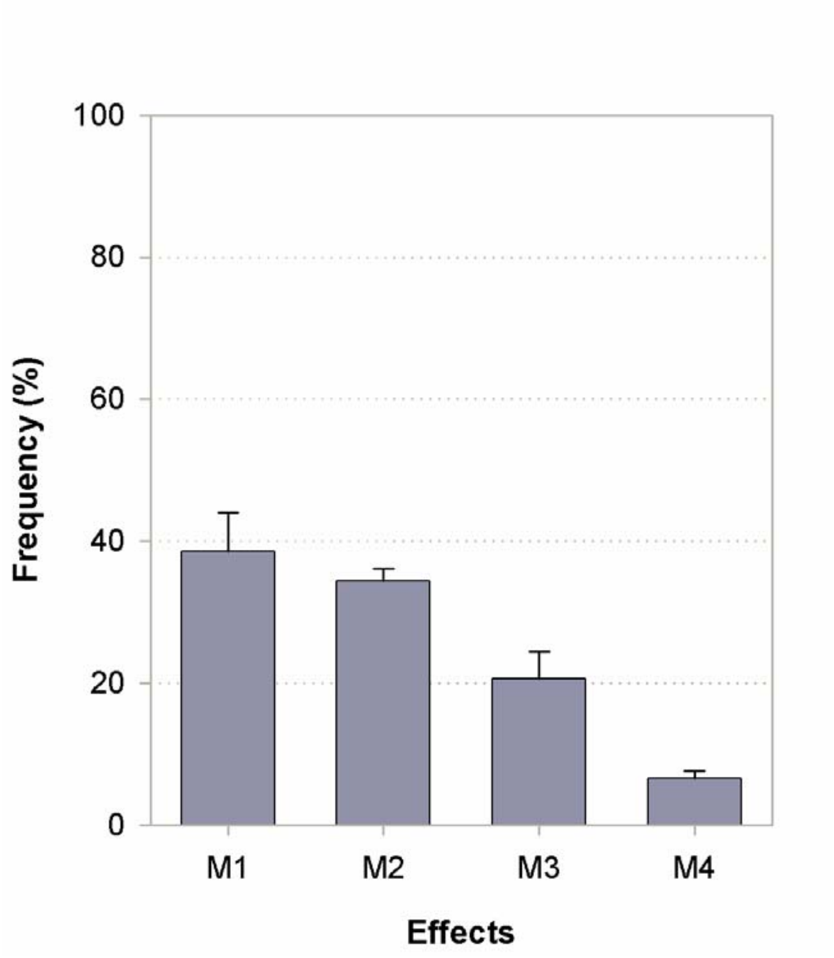

Figure 2: Relative frequency of filling-in plotted for each of Modes 1 – 4. Group mean and SEM (N = 5) based on each subject's averaged responses over all four colors (58 ± 10 responses per subject).

Although equiluminant, the four colors did not behave in the same way: This is shown in Figure 3. Blue and green inner rings were filled-in more often by the gray surround of the outer ring and central disk (M1) than were red and yellow inner rings.

These latter rings, in turn, imparted their color more often onto the central disk than the former (M2). The difference in response frequency between these two color pairs is again highly significant (Fisher’s exact test, $P < 0.0001$). No remarkable differences for the colors could be found in M3 and M4.

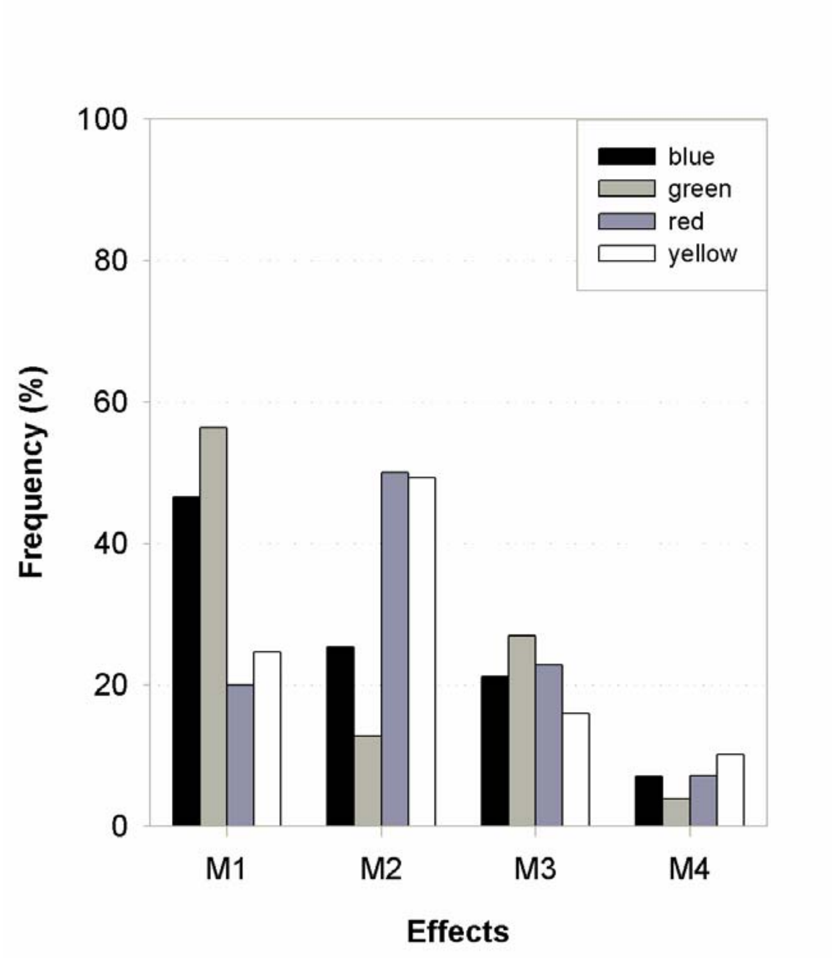

Figure 3: Relative frequency of filling-in plotted for each of Modes 1 – 4. The parameter is the color of the inner ring.

The same four response (or filling-in) modes as for stimulus pattern A were observed for stimulus patterns B (nested squares) and C (triplet of stripes) with the same order of relative frequencies. As in the disk-ring stimulus, the four modes differed in frequency (nested squares: X2 = 31.24, p < 0.0001; stripes: X2 = 113.55, p < 0.0001). However, filling-in of the inner frame by the identical colors of the central square and the outer frame (M1) was more frequent (49.8%) than with stimulus pattern A, while filling-in of the central square by the color of the inner frame (M2) was less frequent (22.2%). Two-step filling-in (M3) was perceived in 17.9% of the trials and filling-out (M4) in 10.1%.

With the striped stimulus pattern (C), the overall order of response (filling-in) modes was also similar. However, here filling-in of the colored stripe in the middle by the gray flanks was the most frequent mode by far (M1=68.0%). The other effects ranged from 14.9 to 6.7% (M2: filling-in of one of the two flanking bars with the color of the central stripe; M3: filling-in of one of the flanking bars by the color of the central stripe (first step), followed by the uniform filling-in with the gray of the other flanking bar (second step); M4: filling-out from the colored stripe onto the whole stimulus). The proportion of M1 with regard to the total number of effects was higher than for the disk-ring pattern and the nested squares (Friedman ANOVA: X2 = 8.40, p < 0.02).

Discussion

When presented with stimulus pattern A, subjects predominantly reported perceiving the inner ring as figure and the central disk and outer ring as ground. Rather than seeing three individual stimulus components, they perceived a colored figure on a gray background. Under these conditions the ring faded into the background. This mode of fading and filling-in (M1) is consistent with observations by Spillmann et al. (1984) who found that what is perceived as figure assumes the brightness of the ground, not vice versa. These results then suggest that filling-in does not necessarily start at the outermost edge and proceed towards the fovea (centripetal), but may actually proceed in both directions. In addition, filling-in frequently also started from the edge separating the inner ring and central disk, resulting in a perceptually enlarged, central area in the color of the inner ring (M2). Similar results were obtained with stimulus pattern B (squares).

In a substantial number of trials, the central disk first assumed the color of the inner ring, and thereafter the combined area (disk and inner ring) became filled-in by the color of the outer ring. This two-step filling-in-process (M3) was unexpected and constitutes a new finding. It is interesting for two reasons. First, it shows that filling-in does not always originate from what is perceived as ground, i.e., the central disk in conjunction with the outer ring. Second, it demonstrates that the uniform surface that emerges after step 1 fading becomes a victim of a more unitary color due to step 2 fading. In other words, a percept that has no physical correlate becomes replaced by another percept which also lacks a physical correlate.

In this experiment, red and yellow showed themselves as strong inducers whereas blue and green were more susceptible to becoming filled-in. A possible interpretation for the different strength of colors is that blue and green usually resemble background colors in natural scenes, whereas red and yellow are typically associated with properties of objects (foreground), such as the ripeness of fruits. Therefore, they would be expected to have a higher perceptual salience. In evolutionary terms it would not be useful if fruits tended to fade into the background and thereby became invisible.

As the same modes of filling-in occurred with all three stimulus patterns (A-C), we decided to use only stimulus pattern A in the following experiments.

Experiment 2

Here we asked what would happen if the colors used in stimulus pattern A were switched around among the stimulus components: i.e., colored disk - gray inner ring - colored outer ring (Figure 4, left). In Experiment 1, the colored inner ring was seen as a figure in front of a gray background. We now tested whether the same regularities of filling-in would obtain when color and gray were exchanged and whether the inner ring would again be perceived as figure or not.

Methods

Stimuli

Colors and stimulus presentation were the same as before (blue-gray-blue, green-gray-green, yellow-gray-yellow, and red-gray-red). Each stimulus was presented 8 times in a random order. Three of the six previous subjects participated (mean age 23.7, SD = 2.1).

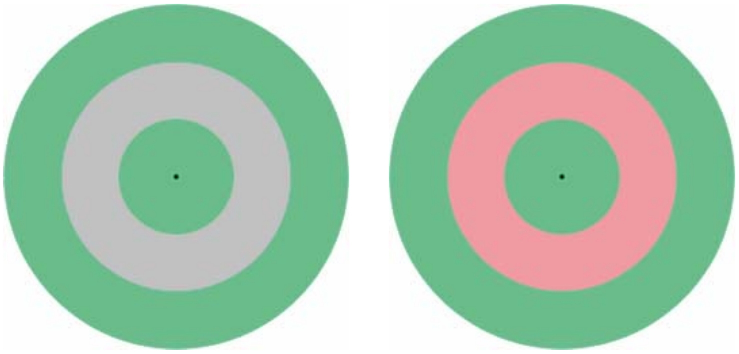

Figure 4: Sample stimuli used in Experiment 2 (left) and Experiment 3 (right). In both stimulus patterns the central disk and the outer ring were of the same color, but in the left pattern the inner ring was gray, whereas in the right pattern it was colored.

Results

Results are shown in Figure 5. All three subjects reported seeing filling-in (87.4%). The predominant effect again was M1: filling-in of the inner gray ring by the color of the central disk and outer ring now occurred in an overwhelming 75% of all trials. In comparison, M2 and M3 occurred in only 10.6% and 12.5%, respectively. M4 occurred very rarely (1.9%). The difference in occurrence of the four response modes was highly significant (X2 = 133.76, p < 0.0001). Again, the colors red and yellow induced filling-in more often than did blue and green.

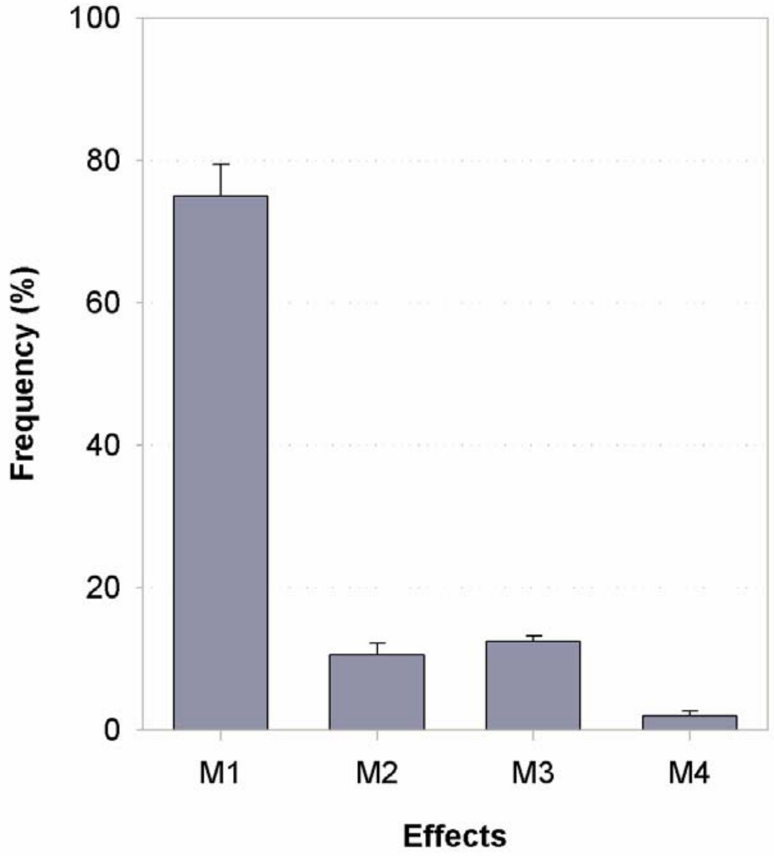

Figure 5: Relative frequency of filling-in plotted for each of Modes 1 – 4. The stimulus consisted of a colored disk, gray inner ring and colored outer ring. Group mean and SEM (N = 3) based on each subject's averaged responses over all four colors (35 ± 6 responses per subject).

Discussion

Compared with Experiment 1, the gray inner ring became much more frequently filled-in by the color of the perceived background (central disk and outer ring) than the colored inner ring before. It thus appears that gray is not only a weaker inducer than each of the four colors tested in Experiment 1, but is also more susceptible to filling-in. This assumption is consistent with the results showing that all subjects perceived the gray inner ring as figure and the equally colored disk and outer ring as ground.

Experiment 3

Here, we replaced the gray inner ring by a colored ring. This was done because the results of the two previous experiments had shown that filling-in for chromatic and achromatic inner rings occurred with different frequencies. In particular, we wanted to find out what would happen if we used two different colors and no gray (Figure 4, right).

Methods

The color combinations used in this experiment for the central disk, inner ring and outer ring were as follows: blue-green-blue, blue-red-blue, green-blue-green, green-red-green, red-blue-red, and red-green-red. Stimulus presentation, experimental conditions, and subjects (N = 3) were the same as in Experiment 2.

Results

Results are shown in Figure 6. All three subjects perceived filling-in effects (94.4%). Filling-in of the inner ring (M1) again represented the main effect (44.7%). Filling-in of the central disk by the inner ring (M2) occurred in 24.1% of the cases. So did the two-step filling-in process M3 (24.1%). M4 represented 7.1% of the responses. The difference in occurrence of the four response modes was highly significant (X2 = 29.44, $p < 0.0001$).

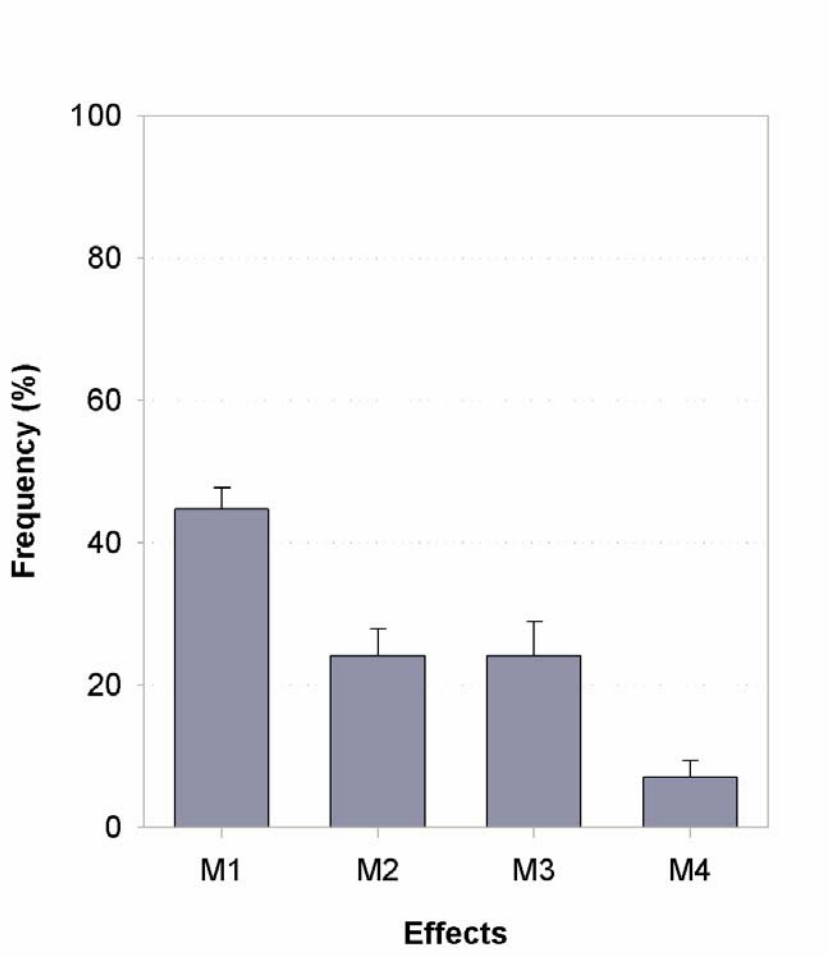

Figure 6: Relative frequency of filling-in plotted for each of Modes 1 – 4. Responses are averaged over 6 sets of colored stimuli used each consisting of two different colors. Group mean and SEM (N = 3) based on each subject's averaged responses over all four colors (57 ± 8 responses per subject).

Discussion

Again, the inner ring, no matter what color, was perceived as a figure on a uniformly colored background. The fact that the frequencies for M2 and M3 increased when two colors were used instead of only one color and gray confirms our earlier finding that gray is a weak inducer.

Experiment 4

Classical filling-in studies predominantly dealt with a single object on a uniform background. Here, more complex stimuli were used. They consisted of a central disk, surrounded by an inner ring that in turn was surrounded by an outer ring. All stimulus components had different colors and there was no bias that would have imparted any of them the status of figure or background. As a result, the stimulus pattern looked perfectly flat as compared to the previous experiments where the figure on the background perceptually appeared to lie slightly in front. In Experiment 1, we had already seen that filling-in need not necessarily start from the outer edge. Thus, with the more complex stimulus configuration, we expected Modes 2 and 3 to occur more often than Mode 1. In order to keep the duration of the experiment within reasonable limits, we used a strong inducer (red) together with two weak inducers (green and gray).

Methods

We used the following 6 color combinations for the central disk, inner ring, and outer ring: gray-red-green, gray-green-red, green-gray-red, green-red-gray, red-green-gray, and red-gray-green. A sample stimulus is shown in Figure 7. Stimulus presentation, experimental conditions, and observers (N = 3) were the same as in Experiment 2.

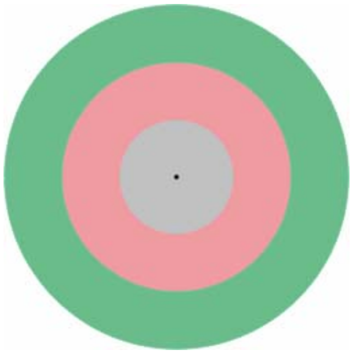

Figure 7: Sample stimulus used in Experiment 4. The central disk is gray, the inner ring red, and the outer ring green. All combinations of these three colors were used in this experiment.

Results

Results are shown in Figure 8. All three subjects reported filling-in (93.8%). However, this time the frequency for M1 decreased to 33.4%. In comparison, M2 increased to 39.1%, while the two-step filling-in process M3 fell to 19.7%. The percentage for M4 was 7.8%. Again, the difference in occurrence of the four response modes was highly significant (X2 = 28.39, $p < 0.0001$). As in Experiments 1 – 3, red was a stronger inducer than gray and green. For response mode M1, 90 % of the cases occurred when the central disk or outer ring were red and the inner ring green or gray; only 10 % when the colors were reversed (random expectation 66:33 %). This difference was significant for each individual participant (binomial tests, all $p < 0.01$). In 50 % of M2 responses, the inner ring was red and the central disk gray or green, in 13 % of the cases the order was reversed (random expectation 50:50 %). Again this difference was significant for each individual subject (binomial tests, all $p < 0.01$).

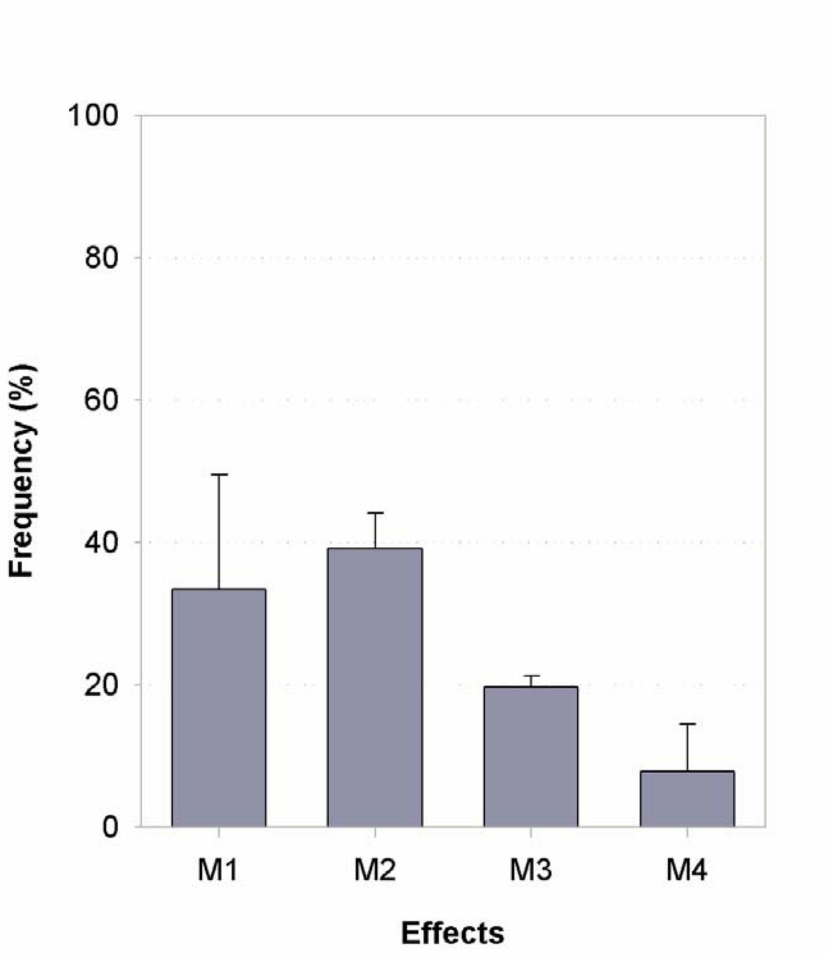

Figure 8: Relative frequency of filling-in plotted for each of Modes 1 – 4. Responses are averaged over 6 sets of colored stimuli used each consisting of two different colors and gray. Group mean and SEM (N = 3) based on each subject's averaged responses over all colors (112 ± 25 responses per subject).

Discussion

In this experiment, subjects did not always see a figure on a ground. Rather they reported seeing either three different stimulus components (disk and two rings) or two components on a background (disk and inner ring as figure, outer ring as ground). Our prediction that Mode 2 would occur more often in this experiment as before was confirmed by the data, but not the prediction for Mode 3. This might be due to the different inducing properties of the colors used. On the other hand, filling-in of the whole stimulus in a single step becomes reduced as expected.

Experiment 5

The final question was whether a black annulus separating the central disk from the inner ring or the inner ring from the outer ring would act as a perceptual barrier and prevent filling-in from occurring. This experiment was done to test the hypothesis that the border surrounding a target first needs to be cancelled ("broken down") before the enclosed surface area can be filled-in (Paradiso & Nakayama, 1991; Spillmann & DeWeerd, 2003). To test for the influence of the width of the barrier on filling-in, we compared the effects of a wide and a narrow black annulus.

Methods

We tested all 6 patterns of Experiment 4 in conjunction with a narrow annulus of 0.18 deg inserted in-between the central disk and inner ring, or between the inner ring and outer ring; and a wider annulus of 1.76 deg placed in the same locations (Figure 9). Each stimulus combination was presented only once, resulting in a total of 24 trials. The same six observers as in Experiment 1 participated.

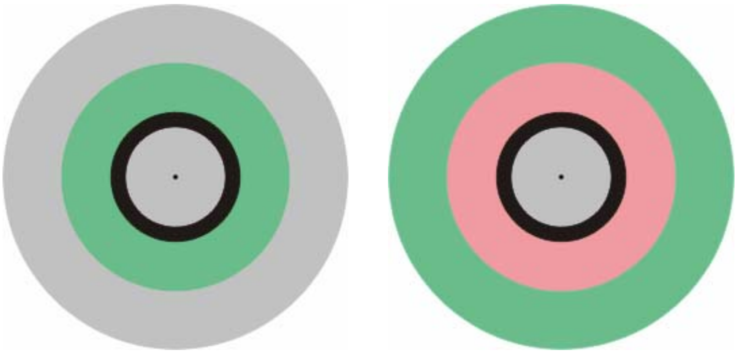

Figure 9: Sample stimuli used in Experiment 5. A wide annulus always prevented the enclosed area from filling-in (N = 102). But in about 70% of the trials, the black annulus became an inducer itself by spreading blackness inward onto the inner ring or central disk, respectively.

Results

Whereas the narrow annulus did not prevent the enclosed surface area from becoming filled-in in any of the trials, the wider annulus always did. Filling-in of color occurred from the outer ring onto the inner ring and also proceeded from the inner ring onto the disk, but in no instance did it “jump” the black annulus. Furthermore, in 68.6% of the trials, the wide black annulus became an inducer itself by spreading blackness inward onto the inner ring or central disk.

Discussion

A wide black annulus not only prevents filling-in; it also acts as an inducer by itself. Compared with the other colors tested, black as an inducer was even stronger than red and yellow.

General Discussion and Conclusions

Based on the results of Experiments 1 – 5 we can state:

(i) In a compound stimulus consisting of a central disk, an inner ring and an outer ring filling-in was perceived by 5 out of 6 observers. The filled-in color was always that of the inducing stimulus. Color mixtures due to a negative afterimage were not observed, suggesting that filling-in of color was based exclusively on the induction from the surround. It would thus qualify as a long-range neural process.

(ii) Four modes of filling-in and surface completion were found. First, the inner ring became filled-in with the gray (or color) of the central disk and outer ring (M1). Second, the central disk became filled-in with the color (or gray) of the inner ring, without any color change on the outer ring (M2). Third, in a first step, the inner ring imparted its color (or gray) onto the central disk, while in a second step the color of the outer ring took possession of the inner ring and central disk (M3). Fourth, the central disk and outer ring assumed the color of the inner ring (M4), i.e., *filling-out* (in case of color spreading onto the outer ring). Table 1 summarizes the response frequencies (in percent) for each of the four filling-in modes.

Table 1: Response frequencies of filling-in (in percent). The number of subjects and the number of stimulus presentations varied for the different experiments. Trials in which no or partial filling-in occurred (M0) were omitted from the analysis and data presentation.

Stimulus pattern		**M1**	**M2**	**M3**	**M4**	**(M0)**
		(inner ring)	(central disk)	(two-steps)	(filling-out)	
Exp. 1	**A**	38.5	34.4	20.6	6.5	(4.9)
	B	49.8	22.2	17.9	10.1	(11.4)
	C	68.0	14.9	10.4	6.7	(5.6)
Exp. 2	**A**	75.0	10.6	12.5	1.9	(12.6)
Exp. 3	**A**	44.7	24.1	24.1	7.1	(5.6)
Exp. 4	**A**	33.4	39.1	19.7	7.8	(6.2)

(iii) Filling-in typically was completed in one step, but in a good number of cases also occurred in two steps. This latter condition (M3) is interesting inasmuch as it shows a sequential propagation of color spreading. It thereby demonstrates that a perceptually filled-in color may give way to another color due to a second filling-in process occurring after the first has been completed. This stepwise filling-in process appears to be a new phenomenon, which hitherto has not been reported and thus deserves further investigation.

The observed sequence (already true for M1) is not consistent with a unidirectional progression of color spreading from the periphery towards the fovea such as may be surmised from Troxler’s (1804) or Krauskopf’s (1963) original studies. Instead, it suggests that filling-in under certain conditions originates at the edge closest to the fovea, before it starts anew from the outer border of the stimulus to produce the final percept. It remains to be seen whether this observation is consistent with the ideas of Grossberg (1994) and DeWeerd, Desimone and Ungerleider (1998) according to which a shorter contour representation in the visual cortex breaks down more rapidly and therefore filling-in from this location should occur earlier. In their study DeWeerd et al. (1998) found a limit of 6 deg in size for filling-in from the surround. Thereupon, they suggested that these findings supported the involvement of horizontal connections in perceptual filling-in. Unlike, target sizes in our experiment clearly exceeded that limit by more than a factor 2 (up to 14 deg here).

Our results clearly suggest a relationship between the dynamics of filling-in (spatial propagation) and figure-ground organization. Filling-in in monkeys with steady fixation (Zhang & Von der Heydt, 1995; Friedman, Zhou & Von der Heydt, 1999) has been linked to that found with artificial image stabilization in human observers (Ditchburn & Ginsborg, 1952; Riggs, Ratliff, Cornsweet & Cornsweet,1953; Yarbus, 1967). Thus, we would expect similar modes of filling-in as reported for stabilized images, just less pronounced. In particular, blurred edges instead of sharp contours (Krauskopf, 1963) are known to facilitate fading. Indeed, Friedman at al. (1999) found in trained monkeys that blurred disks produced filling-in more rapidly than sharp edges. One may therefore speculate as to whether the two-step filling-in process (M3) as well as the filling-out process (M4) would occur faster and as a consequence thereof more often with blurry edges (Shimojo, Wu & Kanai, 2003).

(iv) As a rule, stimulus parts that were perceived as figure became embedded in the ground *(filling-in)* much more often than parts that were perceived as ground *(filling-out*). This shows that figure-ground organisation is an important factor in filling-in.

Filling-out or color spreading from the figure onto the ground did occur in all experiments, but only in very few instances. This finding differs from the results of Shimojo et al. (2003), who found that for certain stimulus arrangements and with strict fixation the center almost always spread its color onto the surrounding area.

(v) Areas having colors that commonly represent backgrounds in natural scenes (e.g., blue, green) tended to become filled-in more often than typical foreground colors (e.g., red, yellow), even if all colors had the same luminance (value) and spectral purity (chroma). Conversely, the latter colors were more effective as inducers. One reason might be that some colors are more salient than others. For example, DeWeerd et al. (1998) found that the time required for filling-in of a red (perceptually more salient) square was longer than for an equiluminant gray square. Another possibility would be that colors that typically represent background colors in natural scenes (blue, green) are more easily filled-in than colors that commonly represent the foreground (red, yellow). Informal observations in trained monkeys (Von der Heydt, Friedman & Zhou, 2003) suggest similar filling-in phenomena irrespective of color (e.g., a gray patch surrounded by a colored ring and vice versa.). Our findings suggest that all four response modes occur with all color combinations of the stimulus, however, with different frequencies depending on the colors of the disk and rings. The strong inducing properties of some colors in our study are consistent with the hypothesis that color filling-in depends on an active propagation of surround features (Gerrits et al., 1966; Gerrits & Vendrik, 1970; DeWeerd et al., 1995), rather than merely by passive “tagging” (Dennett, 1991). Furthermore, the two-step filling-in process found here seems to be incompatible with "tagging", because it shows that the intermediate percept which itself is an illusion changes again by virtue of a subsequent, higher-order illusion.

(vi) With a wide black annulus separating the central disk from the inner ring or the inner ring from the outer one, color filling-in was no longer perceived. Instead, the enclosed surface area assumed the blackness of the barrier. This result is new and further supports the idea of an active filling-in process. Obviously, a wide annulus acts as an inducer just as other colors. A possible reason for the ineffectiveness of the narrow annulus in this regard is that it is perceived as a boundary of either the inner ring or central disk due to 'border-ownership' (Nakayama & Shimojo, 1990). This latter result does not support theories in which contours are barriers for color spreading.

(vii) There were slight differences in the frequency of filling-in between the disk-ring (A), nested squares (B) and striped stimulus (C) patterns. However, the dominance of the inner ring in inducing its color onto the central disk was greater in stimulus pattern A than in B.

(viii) Overall, the observed effects are consistent with the two-stage model by Spillmann and DeWeerd (2003) according to which there is a 'slow' degradation of boundaries due to adaptation (cancellation) followed by a 'fast' spreading of surface features (substitution). The nature of these processes will be subject to future investigation. The perception of filling-in by monkeys with steady fixation may be based on a gradual decay of color border signals (Von der Heydt et al., 2003) which may explain the slow time course of filling-in. In primate visual areas V1 and V2 these authors found no evidence for surface filling-in. Thus, they concluded that their physiological results were incompatible with an isomorphic filling-in which postulates color signals spreading from the border onto uniform regions. Therefore, they suggested symbolic filling-in for an explanation. Since the great majority of color-sensitive cells are edge-selective, they propose that the visual system computes surface color from orientation-selective border responses.

Further analysis of the stepwise filling-in process (M3) may yield a better understanding of the neuronal basis of color filling-in. Following Von der Heydt et al. (2003), information about the perceived color of a surface is represented in two ways in the visual cortex: first, by the activity of neurons whose receptive fields represent surfaces and, second, by neurons whose receptive fields include borders. We suggest that two-step filling-in involves either way of processing. Follow-up studies with complex color compounds as used here will help to better understand the dynamics of color filling-in as well as the neuronal processes underlying the Troxler effect.

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Chapter 3 –

Perceptual filling-in from the edge of the blind spot[3]

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[3] This work was published in a slightly different form: Spillmann, L., Otte, T., Hamburger, K., & Magnussen, S. (2006). Perceptual Filling-in From the Edge of the Blind Spot. *Vision Research, 46*, 4252-4257.

Looking at the world with one eye, we do not notice a scotoma in the receptor-free area of the visual field where the optic nerve leaves the eye. Rather we perceive the brightness, color, and texture of the adjacent area as if they were actually there. The mechanisms underlying this kind of perceptual filling-in remain controversial. To better understand these processes, we determined the minimum region around the blind spot that needs to be stimulated for filling-in by carefully mapping the blind spot and presenting individually fitted stimulus frames of different width around it. Uniform filling-in was observed with frame widths as narrow as 0.05 deg visual angle for color and 0.2 deg for texture. Filling-in was incomplete, when the frame was no longer contiguous with the blind spot border due to an eye movement. These results are consistent with the idea that perceptual filling-in of the blind spot depends on local processes generated at the physiological edge of the cortical representation.

Introduction

The blind spot in human vision refers to the receptor-free area of the retina where the optic nerve leaves the eye. This part of the visual field, subtending 5 x 7 deg visual angle and centered about 15° temporally, is perimetrically blind in monocular vision, but is hardly ever "seen" because of normal retinal and cortical representation of the corresponding region in the fellow eye. However, even in monocular vision the blind spot is generally not noticed because of perceptual filling-in of color and texture from the surround (Walls, 1954; Ramachandran, 1992a).

Filling-in of color is observed for another naturally occurring scotoma, the foveal blue scotoma (Magnussen, Spillmann, Stürzel & Werner, 2001; Magnussen, Spillmann, Stürzel & Werner, 2004); and filling-in of color, brightness and texture also occurs in cases of scotomas caused by retinal lesions (Safran & Landis, 1996; Zur & Ullmann, 2003). Similar effects are observed during figural fading due to stimulus stabilization on the retina (Gerrits & Vendrik, 1970) or prolonged steady fixation of a target (Krauskopf, 1963; Ramachandran & Gregory, 1991; Spillmann & DeWeerd, 2003; Hamburger, Prior, Sarris & Spillmann, 2006); and a number of visual illusions demonstrate that color and brightness generated at contours, invade empty fields under ordinary viewing conditions. Well-known examples are the Craik-O'Brien-Cornsweet illusion (Cornsweet, 1970; Davey, Maddess & Srinivasan, 1998), the neon-color effect (van Tuijl & Leeuwenberg, 1979; Bressan, Mingolla, Spillmann & Watanabe, 1997), the watercolor effect (Pinna, Brelstaff & Spillmann, 2001), and the moving (Tynan & Sekuler, 1975; Menees, Stürzel & Spillmann, 2002) and stationary (Gyoba, 1983) phantom illusions. Most current explanations of perceptual filling-in phenomena are based on the idea of an active physiological process, a lateral spreading of information generated at contours (e.g. Gerrits & Vendrik, 1970; Ramachandran, 1992a; Spillmann & Werner, 1996; Spillmann & DeWeerd, 2003; Sasaki & Watanabe, 2004); in the case of the blind spot, completion is assumed to result from a process whereby a representation of the missing information is created in the non-stimulated cortical area by signals from the surround. Komatsu (2006) recently proposed a neurophysiological model where signals from oriented contrast-sensitive cells along the edge of the blind spot representation spread across a two-dimensional array of feature sensitive cells and color sensitive surface cells, regenerating the missing information.

The results of psychophysical and neurophysiological experiments are consistent with the idea of active information processing in the cortical region corresponding to a scotoma, when the surround is stimulated. With flickering monochromatic blue backgrounds, Magnussen et al. (2001) observed that the foveal blue-scotoma was visible as a dark spot in the center of the visual field, and in a subsequent paper (Magnussen et al., 2004) these same authors showed that the scotoma was visible as a hole in the rapidly fading negative afterimage of the monochromatic background. Presumably in both cases filling-in was counteracted by creating differential activity at the border between the blue-insensitive scotoma and the blue-sensitive retinal surround. Likewise, several studies have shown that scotomas resulting from lesions to the visual pathway may be made visible on dynamic textured backgrounds (Aulhorn & Köst, 1988; Aulhorn, Schiefer & Herzau, 1990; Churchland & Ramachandran, 1996; Bachmann & Fahle, 2000). In studies of the blind spot, Tripathy and Levi (1994) found that the detection of a test letter "T", presented monocularly within the area corresponding to the blind spot of the fellow eye, was impaired by presenting flanking masker T's around the blind spot of that eye. Furthermore, Murakami (1995) adapted monocularly the retinal region surrounding the blind spot to a drifting grating, and observed a motion aftereffect in the fellow eye, in the region corresponding to the blind spot of the adapted eye. He and Davis (2001) showed that a large radial grating stimulus, centered on the blind spot, produced binocular rivalry in competition with a small stimulus presented to the corresponding monocular region of the fellow eye.

Similar results were obtained by Tong and Engel (2001), who used functional magnetic resonance imaging (fMRI) and found that the BOLD-response to a stimulus rivaling with a stimulus presented to the blind spot of the contralateral eye was similar to the rivalry response obtained when both stimuli fell on corresponding, but functional retinal loci. More recently, functional imaging experiments by Meng, Remus and Tong (2005) demonstrated physiological filling-in activity in areas corresponding to moving visual phantoms in visual areas V1 and V2. With single-cell recording in the monkey, DeWeerd, Gattass, Desimone and Ungerleider (1995) found that when the receptive field was entirely enclosed within a gray square presented on a dynamic noise background, the response of the cell to the artificial scotoma first dropped, but then recovered, indicating neural filling-in; this happened at about the same time when perceptual filling-in occurred also for human observers. This filling-in response was particularly prominent in visual area V3.

Most experiments and demonstrations of perceptual filling-in of natural scotomas, including the blind spot, have used stimuli that covered larger regions of the surround, or extended well into the surround of the blind spot (Kawabata, 1983; Andrews & Campbell, 1991; Ramachandran, 1992a; Zur & Ullman, 2003; Magnussen et al., 2001; 2004), one exception being a brief report by Ramachandran (1992b), who observed that with a distribution of rings in the visual field, the ring covering the blind spot “popped out” in perception as a uniform disk. Thus, it is not known whether the mechanism of filling-in depends upon activity along the physiological edge of the blind spot representation or whether the effect depends upon processes that recruit a wider region of the surround. We here show that filling-in of color and texture depends upon a border region of just a few min of arc of visual angle surrounding the blind spot, consistent with an edge account of perceptual filling-in.

Methods

The blind spot was mapped with observers positioned on a chin-and-forehead rest fixating a cross with the left eye; their right eye was covered. The cross was presented straight ahead at a distance of 100 cm while a 21“ Phillips 201B monitor was positioned to the left such that the blind spot fell onto the computer screen with fixation of the cross. Four OSRAM L36W/25 universal-white fluorescent tubes produced a room illumination of 95 LUX at eye level. To determine the exact shape and position of the blind spot, subjects slowly moved a dim, red laser point across the monitor while fixating the cross, and the positions where the laser point disappeared or reappeared on the screen where marked by the experimenter. The results for these two criteria were averaged and used as coordinates for blind spot testing. We took approximately 60 values depending on each subject’s accuracy. This detailed mapping revealed that the borders of the blind spot might be quite irregular, as illustrated in Figure 1, and varied somewhat between subjects. Thus individual adjustments of the stimulus conditions were necessary.

Based on each observer’s blind spot, stimulus frames were generated on a computer, and displayed on the monitor. To test for filling-in of color, frames were prepared in red (CIE: $X = 0.54$, $Y = 0.32$), green ($X = 0.3$, $Y = 0.56$) and blue ($X = 0.14$, $Y = 0.14$), with their width ranging from 0.05 - 0.33 deg visual angle. Preliminary observations showed that on a black background filling-in was perceived more easily than on a white background for identical contrasts, but opposite polarities, between stimulus frame and background. For the actual experiment, we therefore used a luminance of 35 cd/m^2 for the frame and of 4 cd/m^2 for the background (C = 0.79).

To test for filling-in of texture, we used black-and-white square-wave gratings of comparable contrast with a spatial frequency of 2 and 3 c/deg oriented either horizontally or vertically. In addition, we presented white-on-black dot patterns of identical figure-ground contrast with dot sizes of 0.17 and 0.25 deg and an inter-dot distance equaling dot diameter. The width for these frames ranged from 0.17 – 0.66 deg; with narrower frame widths, texture was not discernible at this retinal eccentricity and hence no filling-in of pattern could be observed. Examples of stimulus frames drawn to scale are shown in Figure. 1. Texture frames had to be wider than color frames to ensure discriminability of the textures. Discriminability was ascertained by repeatedly and randomly presenting each frame at the same retinal eccentricity as the blind spot and asking subjects to report the kind of texture seen.

Observers were instructed to specify whether filling-in of the blind spot was complete or incomplete. In addition, they were asked to rate the amount of filled-in area in steps of 10%. To prevent Troxler-type fading of the frame, observers covered and uncovered the stimulus periodically with their hand. On average subjects took 15 s to perform the task, but there was no time limit. Six trained observers (aged between 20 – 30 yrs) with normal or corrected-to-normal visual acuity and normal color vision participated, each completing 12 trials with colored and 18 trials with textured frames. Informed written consent to participate in this study was obtained from all observers.

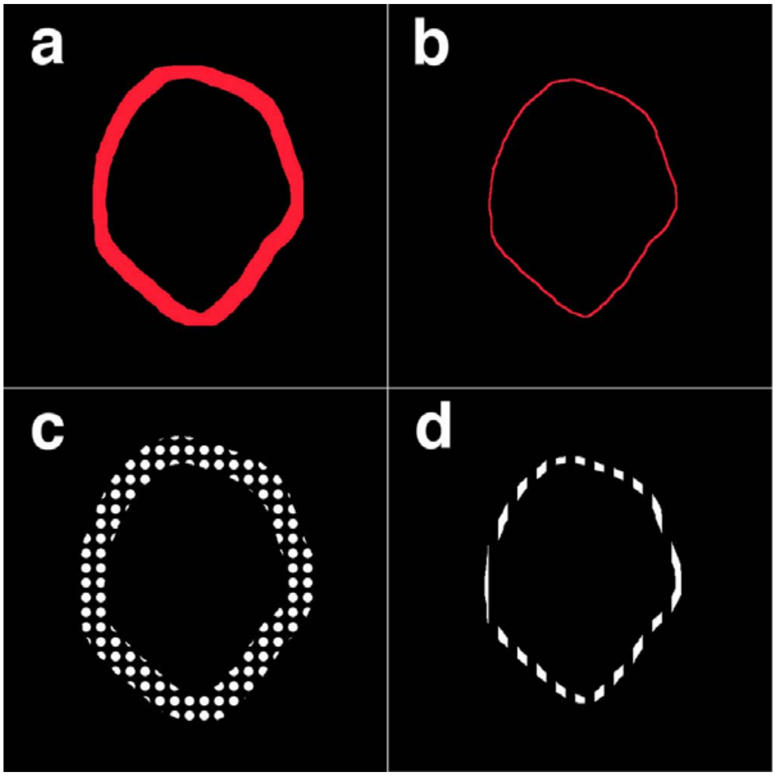

Figure 1: Examples of individually fitted stimulus frames, drawn to scale. (a) Colored frame of 0.33 deg width. (b) Colored frame of 0.05 deg width. (c) Dotted frame of 0.66 deg width and 0.25 deg dot diameter. (d) Striped frame of 0.17 deg width and 2 c/deg spatial frequency.

Results

We determined the minimum region around the blind spot that needs to be stimulated for perceptual filling-in by detailed mapping of the blind spot and subsequent placing of individually fitted stimulus frames of different width around the edge. The task was to report all observations pertinent to filling-in of the blind spot.

Qualitative observations

In the majority of cases observers reported complete filling-in, implying that the color or pattern of the frame perceptually had invaded the blind spot area and filled it uniformly (i.e., 100%), so that it was indistinguishable from the frame. In these cases filling-in was instantaneous, but often lasted less than a second, especially with narrow frames. These short-lived effects may be attributed, in part, to two factors: first, Troxler-type fading which tended to "wash out" the stimulus frame, thereby preventing filling-in of surround properties into the blind spot area; second, involuntary eye movements that displaced the frame relative to the blind spot, thus breaking overall adjacency and resulting in partial filling-in.

In these latter cases, the induced color or pattern still filled most of the blind spot, but left parts of the field empty or foggy. Notably, with improper fixation, one could actually see two dark "shadows", one on the side where the frame had invaded the blind spot and the other on the opposite side, where the frame had moved away from the blind spot border. Examples of partial filling-in are illustrated in Figure 2 (a, c) for colored and patterned frames, respectively. To express this aspect of filling-in quantitatively, observers estimated the filled-in area as a percentage of the total.

Quantitative measurements

Figure 2 shows the results for the six observers obtained with colored (panel b) and patterned (panel d) stimulus frames. The results are presented in terms of the proportion of the blind spot area that was reported as perceptually filled-in. Since we observed no differences between colors, results for red, green, and blue frames were collapsed. Each symbol in Figure 2b represents the results from one observer (median of the three colors) and the large circles represent the median of the 18 values measured per frame size (6 subjects x 3 colors). The median starts at 80% for a frame width of 0.05 deg, increasing to nearly 100% with the frame width rising to 0.33 deg. A closer look at the original data reveals that for colored frames subtending as little as 0.05 deg, complete (i.e. 100%) filling-in was still observed in 40% of the trials (not shown).

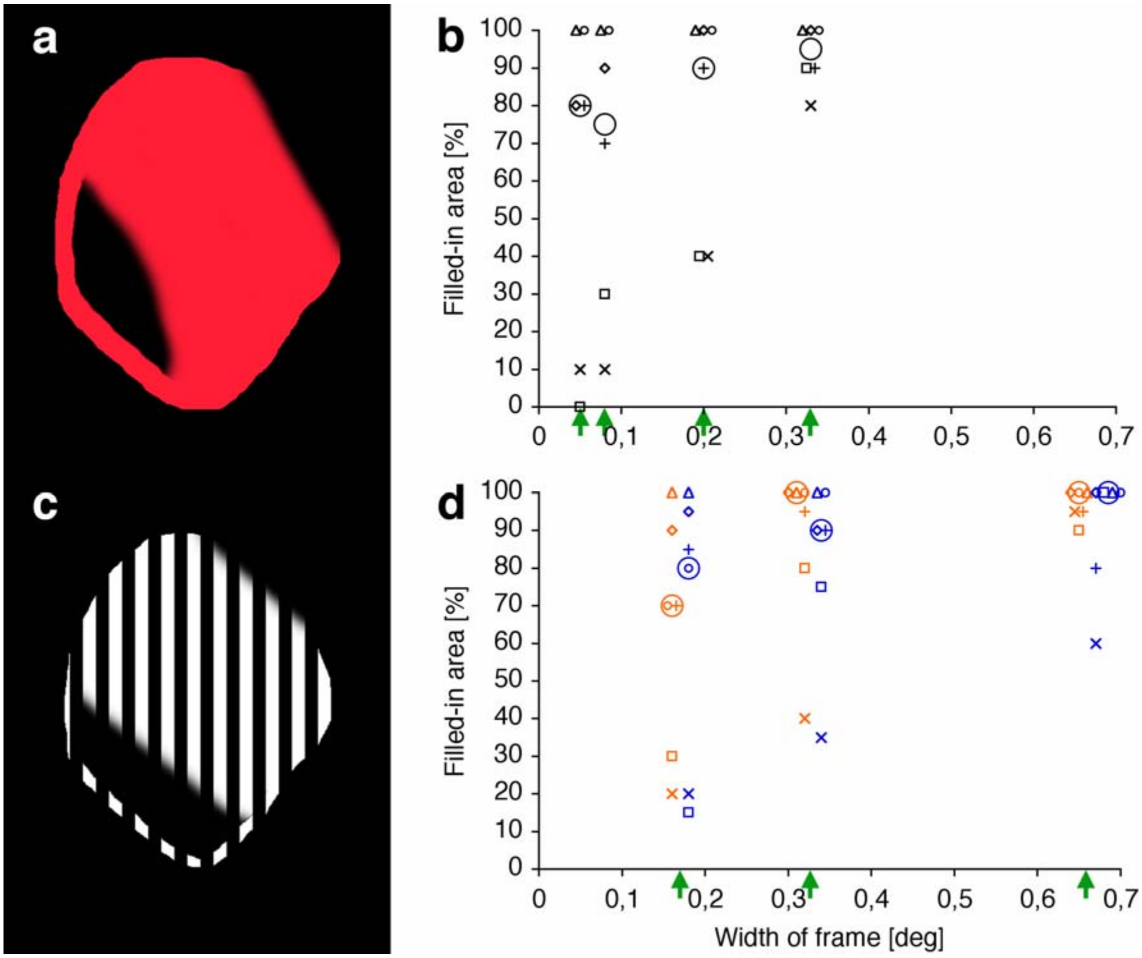

Figure 2: Qualitative observations and quantitative results on perceptual filling-in of the blind spot. Panels (a) and (c) illustrate partial filling-in of the blind spot area with either color or texture from the surrounding frame. Panel (b): Area filled-in with color is plotted against width of the surrounding frame. Each symbol represents the data of one subject and gives the median of the results for the tested colors (N = 3). The large circles represent the median over all data (N = 18) for each frame size. Arrows at the abscissa indicate the tested frame size. Panel (d): Corresponding results are given for perceptual filling-in with dot textures (orange symbols) and gratings (blue symbols); each symbol gives the median of the results of either two sizes of dot patterns or four different grating textures for each subject. The large circles again represent the median over all data (N = 12 for dot patterns and N = 24 for grating patterns) for each frame size. Note that the dot and grating textures had the same frame sizes but for reasons of clarity we display them slightly shifted. Arrows at the abscissa indicate the tested frame size.

The results for filling-in of texture are similar, except that the data are shifted horizontally towards wider frames (Figure 2, panel d). Results for dot patterns (collapsed for dot sizes; 6 subjects x 2 dot patterns) are given by orange symbols and for gratings (collapsed for orientation and spatial frequency; 6 subjects x 4 grating patterns) by blue symbols. Filling-in of texture was first observed with a frame width of 0.17 deg, yielding a median of 70% and 80%, respectively, and rising to nearly 100% when the frame width was 0.33 deg and 100% when it was 0.66 deg.

Not surprisingly, perhaps, with a perceptual task of this kind, there are consistent individual differences, with two of the observers having difficulties in observing filling-in with the narrowest frames with both colored and patterned frames.

Curiously, subjects occasionally reported that if the orientation of a grating was difficult to discern when only the stimulus was visible, that orientation became immediately apparent at the moment when filling-in occurred. This implies that the filled-in information induced into the blind spot actually enhanced the percept in analogy to a disrupted line that is seen passing through the blind area (Ramachandran, 1992a). Furthermore, this observation confirms that the smallest frame width used in our experiment was just at the threshold for detection suggesting that the minimum information needed for detection is also the minimum information needed for filling-in.

Discussion

The results show that stimulation of a very narrow region immediately bordering the blind spot is sufficient for generating perceptual filling-in of color and pattern. During filling-in, the spatial and featural properties of the stimulus frame are preserved, except in the case of partial filling-in, when a dark “shadow” marks the region of the blind spot that is not immediately bordered by the frame (Figure 2a and d). This partial filling-in effect is theoretically significant inasmuch as it suggests that filling-in is indeed caused by an active physiological process that originates from local stimulation (the surrounding frame) and may be perturbed by local stimulus changes (e.g., lack of adjacency). The results strongly suggest that filling-in depends upon physiological processes generated at a narrow region at the physiological edge of the blind spot representation. Whether signals from retinal regions beyond this physiological edge are ineffective or contribute to the filling-in phenomenon by modifying the border activity, we cannot decide from these experiments.

In general, the results are consistent with the recent model of Komatsu (2006), assuming a lateral spread of signals from oriented contrast sensitive cells along the edge of the cortical representation of the blind-spot region. Evidence for such a process under conditions producing filling-in of artificial scotomas, has been demonstrated in areas V2 and V3 of the monkey visual cortex (DeWeerd et al., 1995). However, in contrast to the gradual climbing activity in that experiment, perceptual filling-in of the blind spot is instantaneous, possibly because the filling-in process is not opposed by border signals from the area to be filled-in as is the case for an artificial scotoma.

An additional contribution to filling-in of the blind-spot may come from binocularly activated color and pattern-specific neurons whose receptive fields cover the area of the monocular blind spot, but extend beyond its borders; such neurons have been described in cortical areas V1 of the monkey (Fiorani, Rosa, Gattass & Rocha-Miranda, 1992; Komatsu, Kinoshita & Murakami, 2002; Matsumoto & Komatsu, 2005). This mechanism might explain filling-in of color and grating patterns, but has difficulties with the filling-in of dot patterns, since no feature detectors have been reported for dotted textures.

The idea has been tested that filling-in of the blind spot, rather than being caused by an active physiological process, is the result of passive physiological re-mapping whereby the “hole” corresponding to the blind spot is “sewn up” so that adjacent points in the cortex receive inputs from opposite sides of the blind spot (Tripathy, Levi & Ogmen, 1996; Awater, Kerlin, Evan & Tong, 2005). This hypothesis is not supported by either the psychophysical or brain imaging (fMRI) experiments. Awater et al. (2005), probing the cortical regions of the blind-spot surround and the corresponding monocular region of the contralateral eye, found no evidence for a spatial distortion of the physiological activity map of the ipsilateral eye, as would be expected on account of a changed topology in the cortex. Our finding that during perceptual filling-in the area defined by the stimulus frames was invaded by color and texture with no obvious perceptual spatial distortion also speaks against the passive remapping hypothesis.

Hsieh and Tse (2006) have recently conducted an experiment on color mixing during perceptual fading produced by steady fixation, with background and target stimuli of different color, and found that color perception during fading might be a mixture of target and background, but that “forbidden” colors (e.g. a reddish-green) were never observed. In supplementary observations we tested filling-in of color with half the frame in green and the other half in red. In agreement with the observations by Hsieh and Tse (2006) a forbidden color was not observed in this condition, rather filling-in appeared as a bi-partite red-green field with fuzzy borders. Thus, there is no anomalous color mixing in the blind spot area.

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Chapter 4 –

Filling-in with texture: uniform vs. random orientation[4]

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[4] This work is re-submitted and under review in a slightly different form: Hindi Attar, C., Hamburger, K., Götzl, H., & Spillmann, L. (under review). Uniform vs. Random Orientation in Fading and Filling-in.

V1 responses to an optimally oriented test line in the receptive field center may be modulated by placing lines of same or different orientations in the surround. While iso-orientation produces strong inhibition, cross-orientation enhances the response (Knierim & Van Essen, 1992). We looked for a perceptual correlate of neuronal texture modulation using perceived salience as well as fading and filling-in as response criteria. Two patterns by Vicario (1998) served as targets. One consisted of randomly oriented bars in the center and uniformly oriented bars in the surround, while the other had bars of uniform orientation in the center and bars of random orientation in the surround. Results: In spite of identical texture contrast at the boundary, the first pattern was judged more salient than the second and its center took more time to fade. When the surround was decreased in width, fading time followed no systematic trend and filling-in was increasingly replaced by filling-out. A higher salience and longer fading time for stimuli with a uniformly as opposed to randomly oriented surround was also obtained when the bars in the center were replaced by dotted arrays. However, no asymmetry was found for the converse patterns when dots were in the surround and bars in the center. Findings are interpreted in terms of strong surround suppression exerted by randomly oriented bars as compared to uniformly oriented bars.

Introduction

With strict fixation visual targets quickly fade from view by assuming the brightness and color of the surround (Troxler, 1804; Krauskopf, 1963). This assimilative spreading is called filling-in (Gerrits & Vendrik, 1970; see Komatsu, 2006 for review). It also holds for stimuli composed of different textures (e.g. Ramachandran & Gregory, 1991).

Caputo (1998) studied filling-in in texture patterns of differentially oriented line elements, using a rectangular frame presented to the other eye as a mask. He found that for a uniform pattern, the region inside the mask appeared darker with only few line elements with degenerated shape left, suggesting that the mask impeded texture filling-in. When the lines enclosed by the frame were rotated from iso-orientation to cross-orientation, they were fully preserved and the darkening was reduced, indicating that pop-out was not affected by the mask. Caputo (1998) concluded that filling-in is subserved by two processes: an early stage for the spreading of mean luminance and a later stage for the spreading of texture from the surround into the target area.

Motoyoshi (1999) similarly found that an annulus, presented shortly after a textural stimulus, suppressed the enclosed texture except for odd elements and bars oriented orthogonally to the surround. This finding was taken as evidence that pop-out occurs prior to filling-in. It further prompts the assumption that fast spreading of textural activity during filling-in is based on long-range horizontal interactions in the visual cortex known to link cells with similar orientation preferences (Wolfson & Landy, 1999).

Although the neural basis of texture segmentation is still under debate, contextual information modulating the neural response is assumed to play an important role for the detection of texture borders and pop-out (Desimone, Moran, Schein & Mishkin, 1993; Kastner, DeWeerd & Ungerleider, 2000; Nothdurft, Gallant & Van Essen, 2000). Single-cell studies in primary and extrastriate visual cortex (V1, V4) show modulating influences from beyond the classical receptive field. For example, iso-oriented lines outside the classical receptive field exert strong inhibition onto an optimally oriented line within the receptive field center, whereas cross-oriented or randomly oriented lines enhance the neural response (Knierim & Van Essen, 1992; Sillito, Grieve & Jones, 1995; Kastner, Nothdurft & Pigarev, 1999; Nothdurft, Gallant & Van Essen, 1999). This enhancement is assumed to promote perceptual segmentation of a textural image (Gilbert & Wiesel, 1990; Knierim & Van Essen, 1992). Yet it is not clear, if surround effects are always suppressive compared to the center stimulus alone, or if they can also yield facilitatory effects as proposed by several authors (Ito & Gilbert, 1999; Kapadia, Ito, Gilbert & Westheimer, 1995).

Stürzel and Spillmann (2001) investigated texture filling-in as a function of the perceptual salience of the stimuli. They used figures defined by orientation contrast, shape contrast, and order contrast. Salience, as measured by magnitude estimation and reaction time, was varied for each figure by altering the strength of the textural contrast between figure and ground. The authors found that perceptual salience increased with increasing texture contrast and both co-varied with the time required for fading and filling-in. They concluded that the salience of figure-ground segregation is an essential determinant of fading.

A look at the two texture patterns presented in Figure 1 (reproduced from Vicario, 1998) confirms this conclusion. The pattern on the left consists of vertical bars in the center and bars of random orientation in the surround. The pattern on the right is the converse of the pattern on the left. Although the textural contrast between center and surround is the same, only in reversed order, both stimuli clearly differ in salience, with the center on the right standing out more strongly than the one on the left. Because of this asymmetry, stimuli would be expected to yield different times for fading and filling-in. Indeed, Götzl (2004, unpubl.) found in 32 subjects (16 male/16 female) that filling-in of the random center by the uniform surround took about twice as long (a total of 10.23 s) as filling-in of the uniform center by the random surround (5.18 s).

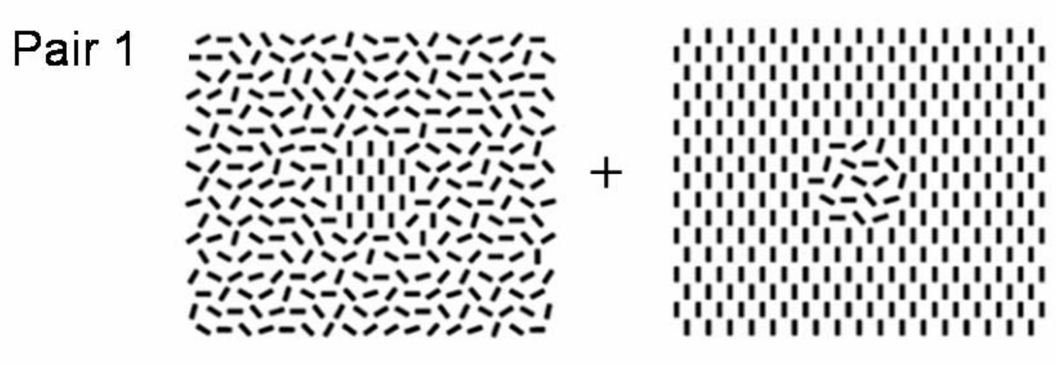

Figure 1: Stimulus pair 1. Two texture patterns by Vicario (1998). The pattern on the left has randomly oriented bars in the surround and uniformly oriented bars in the center, on the right the textures are reversed. Note that the two patterns differ in perceptual salience and fading time as can be verified by fixating on the central cross.

Similar asymmetries have been found in visual search tasks and attributed to distractor heterogeneity (Wolfe, 2001). A study on orientation differences shows that it is easier to find a tilted item among vertical items than a vertical item among items, that are all tilted in different directions (Foster & Ward, 1991). Search efficiency obviously depends on what is target and what surround (Treisman & Gormican, 1988). With regard to the Vicario patterns, uniformly oriented bars in the surround are less distractive than randomly oriented bars. Perceptual salience should therefore be higher for the former and lower for the latter.

It is not easy to reconcile this assumption with the neurophysiological findings obtained with an optimally oriented element within the classical receptive field center and variously oriented bars in the surround. Assume that both centers were reduced to one line element only. To account for the asymmetrical results caused by perceptual asymmetry associated with uniform and random orientation in the surround, one would need one and the same bar for a probe. We therefore suggest that in a pattern having randomly oriented bars in the center and uniformly oriented bars in the surround (Fig. 1, right), surround suppression is weak and excitation from the center strong. Conversely, in a pattern having uniformly oriented bars in the center and randomly oriented bars in the surround (Fig. 1, left), surround suppression is likely to be high because of the larger number of activated channels and excitation from the center low. Our results are consistent with these assumptions, showing higher salience and longer fading time for the random center and lower salience and shorter fading time for the uniform center.

A total of three experiments were performed to test the influence of uniformly versus randomly oriented bars on salience and filling-in. In Experiment 1, we extended Götzl’s (unpubl.) study of the two Vicario patterns by surrounding the center with a ring enclosure as well as by reducing the width of the surround. We hypothesized that an explicit border between center and surround as well as a reduction of surround width would prolong fading time. In Experiment 2, we tested 10 stimulus pairs derived from Figure 1. In these stimulus patterns uniformly oriented or randomly oriented bars in the surround were presented in conjunction with dotted textures in the center. This was done to study the influence of differences in surround orientation on salience and fading-time with the same stimulus in the center. Higher perceptual salience and longer fading times were expected for patterns with uniform bars in the surround because of the weaker surround suppression. In Experiment 3, the same stimulus pairs were used, but with center and surround texture reversed, i.e., no bars in the surround. Random dots are supposed to produce only weak suppression effects (Li, Thier & Wehrhahn, 2000). If surround suppression was crucial in determining salience and filling-in, no systematic difference in salience and fading time would be expected when uniformly or randomly oriented bars are in the center and dots in the surround.

Methods

Subjects

Six subjects (3 males, 3 females, aged 20 – 43 yrs) estimated perceptual salience while another group of 10 subjects (5 males, 5 females, aged 22 – 29 yrs) determined fading time (except for Experiment 1, part 1). All but three observers (including two of the authors) were naïve to the purpose of the experiments, although highly trained in fixation. Their visual acuity was normal or corrected-to-normal.

Stimuli

The two Vicario patterns (Fig. 1) and variants thereof (Figs. 6 and 10) served as stimuli. All experimental patterns were generated in Corel Draw 12 and consisted of bars versus dots in center and surround, except for stimulus pair 1 which had bars in the surround, but no texture in the center. Rectangular stimuli subtending an area of 9 x 11 deg of visual angle were presented on a 22 x 29 deg monitor screen. The diameter of the central disk was 3 deg in each case. The bars subtended 0.08 deg x 0.4 deg, while the diameter of the dots was 0.2 deg.

The luminance of the bars and dots was 16.5 cd/m2 and the luminance of the background 94 cd/m2, resulting in a Michelson contrast of 70%. Perceptual segmentation into center and surround was based merely on a texture-defined (i.e., implicit) boundary in the absence of any physical delineation (explicit border). Minor differences in element density as well as small imperfections at the interface between the two textures were deemed negligible.

General Procedure

Stimuli were presented on a 21“ Phillips 201B computer monitor (resolution 1024 x 768 pixels) with a refresh rate of 100 Hz. Two OSRAM L36W/25 universal-white fluorescent tubes delivered 95 LUX at eye level. Subjects stabilized their head on a chin-forehead rest and fixated a cross from a distance of 72 cm with both eyes. The center of the stimuli was at 9 deg eccentricity on the right side of the cross. Only one pattern was shown at a time.

Perceptual salience was defined as the strength by which the central area of a stimulus pattern stands out from the background (try Fig. 1 for an example). The degree of this perceived figure-ground segregation was measured using magnitude estimation. Subjects assigned a value between 1 and 9 to each stimulus pattern in accordance with the perceived strength of the texture contrast. Two texture stimuli served as references. The lower anchor (rating = 1) consisted of vertical bars in center and surround, i.e. a surface with no textural boundary, while the upper anchor (rating = 9) was composed of vertical bars in the center and horizontal bars in the surround, i.e. maximal texture contrast. Both anchors were periodically interspersed between the experimental stimuli as references for estimating perceptual salience. Stimuli were presented twice in a randomized order with only one pattern presented at a time. Exposure duration was unlimited.

The time for fading and filling-in was clocked electronically, starting at stimulus onset. Subjects pushed a button when the two textures in center and surround looked the same and could no longer be distinguished from each other. Subjects were instructed to describe the texture in the overall stimulus after fading had occurred (e.g., a surface with bars oriented uniformly or randomly throughout).

Experiment 1: Vicario patterns

Implicit vs. explicit border

From the unpublished study by Goetzl and own informal observations we know that the pattern on the left of Fig. 1 fades and fills-in more easily than the one on the right. Here, we tested the idea that the border separating center and surround first needs to be perceptually leveled (i.e. fading) before filling-in can occur (De Weerd et al., 1995). This is in agreement with the theory of edge adaptation (DeWeerd, Gattass, Desimone & Ungerleider, 2002) according to which filling-in occurs in two steps: adaptation to the edge of the target (“cancellation”) and subsequent neural spreading from the surround onto the target area (“substitution”). As there is only an implicit border separating center and surround in texture contrast stimuli, we predicted that fading and filling-in would take longer when a continuous line (explicit border) were used to delineate the center.

Procedure

To test this prediction, we presented the two patterns shown in Fig. 1 without and with an explicit border. In the latter condition the center was surrounded by a black ring of 0.08 deg in width. Time for fading and filling-in with and without the ring was measured twice for 4 subjects (including two of the authors).

Results

Under these conditions fading time for the delineated center increased by approximately 2 s from 12 s to 14 s for the pattern with the random surround (Fig. 1, left) and from 16 s to 18 s for the converse stimulus (Fig. 1, right).

Reduction of surround size

If a physical ring separating the center from the surround prolongs fading and filling-in, reducing the width of the surround may have the same effect. The first blocks the filling-in of surround features into the center by acting as a barrier to propagation, while the second reduces surround suppression onto the center. It therefore should prolong fading time, more so for a random surround than for a uniform surround.

Procedure

To test this hypothesis, we progressively reduced the width of the annular surround in the two Vicario patterns (Fig. 1), while the size of the disk-shaped center was kept constant. The reduction of surround width was done in three steps with patterns subtending 11 deg, 6 deg, 5 deg, or 4 deg, respectively (Fig. 2). These sizes corresponded to four ratios between the number of bars in center and surround: 1/15 (Vicario pattern, pair 1), 1/5, 1/3 and 1/1 (pairs 2 - 4). The number of bars in the center was always 19. Stimuli were presented as before.

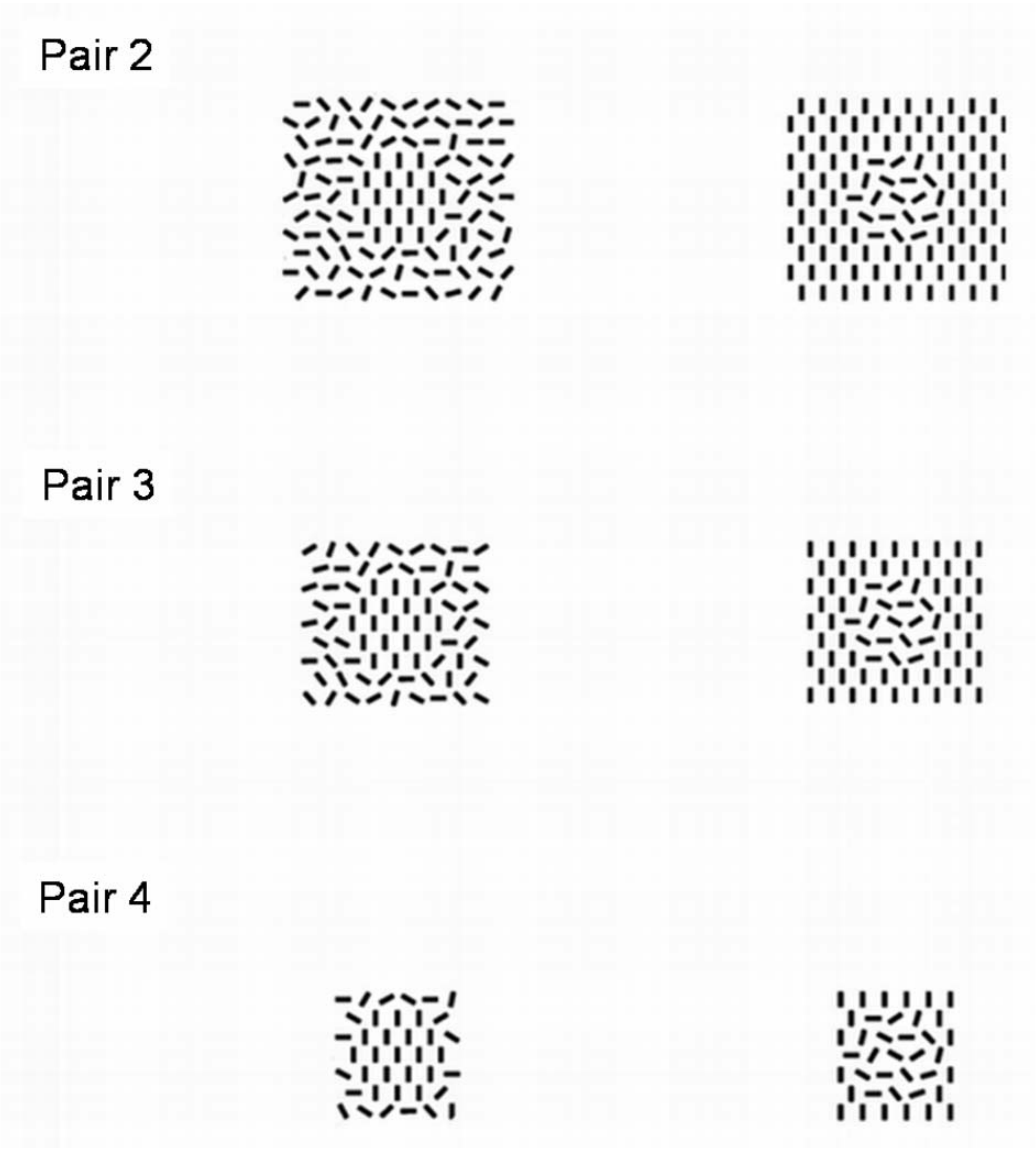

Figure 2: Stimulus pairs 2-4. The centers are kept constant, while the width of the surrounds is progressively reduced.

Results

Figure 3 plots the times obtained for fading and filling-in. Based on subjects' descriptions, two response modes for texture fading were distinguished, filling-in and filling-out. We use the term filling-out to denote the percept of texture spreading from the center onto the surround. In this condition subjects perceived the entire stimulus area as having the same texture as the center.

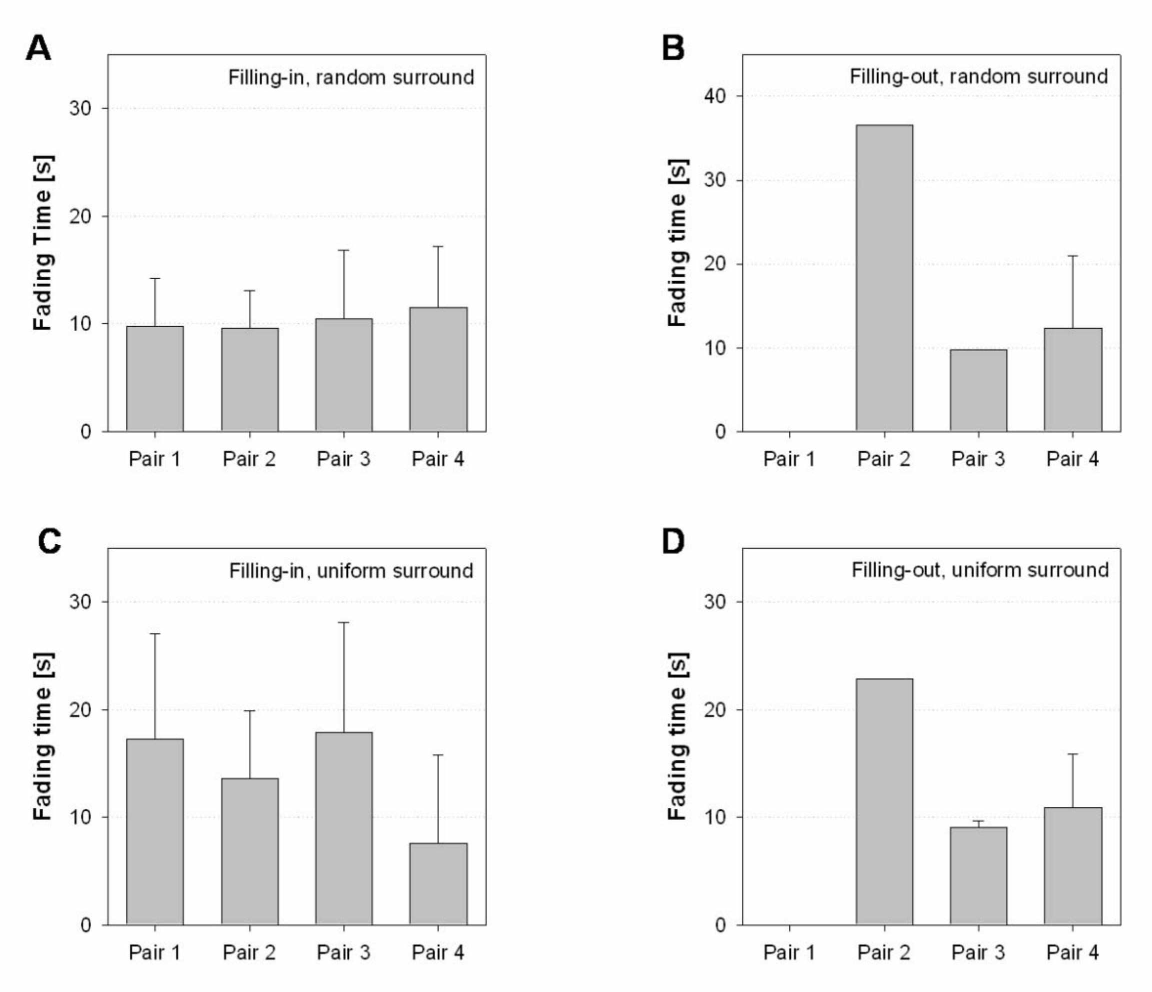

Figure 3: Mean fading time for filling-in (panels A and C) and filling-out (panels B and D) plotted for stimulus pairs 1-4. The two panels on the top refer to uniform centers and random surrounds, the two panels at the bottom to random centers and uniform surrounds.Vertical bars give the standard deviation.

For patterns with uniformly oriented bars in the center and randomly oriented bars in the surround (panel A), time for fading and filling-in increased little, if at all, from pair 1 to pair 4. In comparison, time for filling-out (B) changed substantially, being longest for pair 2 (>30 s), but much shorter for stimulus pairs 3 and 4. The time for filling-in of patterns with randomly oriented centers and uniformly oriented surrounds (C) shows no systematic trend for filling-in, but an abrupt decrease for filling-out (D).

Figure 4 plots the frequency for filling-in and filling-out as a function of surround width (in deg) for patterns with uniformly oriented centers and randomly oriented surrounds. While the curve for filling-in decreases with decreasing surround width from 100% to 80%, the curve for filling-out increases from 0% to 20%.

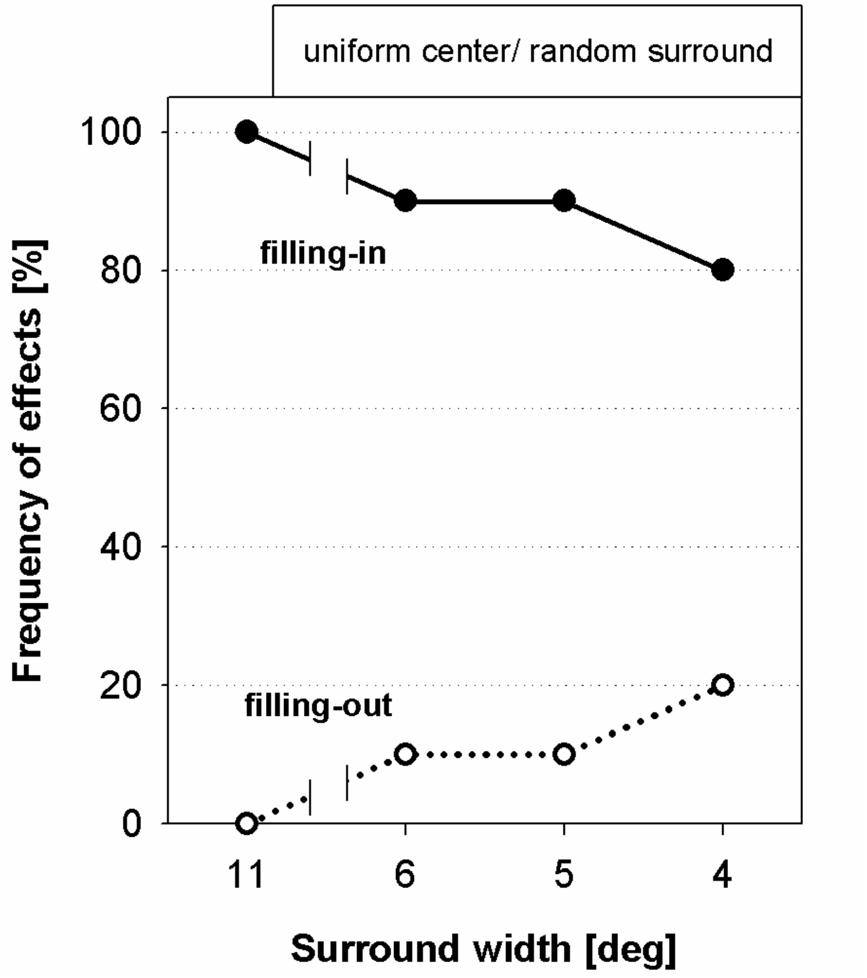

Figure 4: Frequency of filling-in (continuous curve) and filling-out (dashed curve) plotted for the Vicario patterns shown in Figure 1 as a function of surround width (Fig. 2). Results refer to stimuli having uniformly oriented bars in the center and randomly oriented bars in the surround. Center/surround ratios of 1:15, 1:5, 1:3 and 1:1 bars corresponded to pattern sizes of 11, 6, 5, and 4 deg, respectively. Each datum point represents the percentage of the responses by 10 subjects that reported one or the other effect.

Figure 5 plots frequency of occurrence for the converse stimuli, randomly oriented centers and uniformly oriented surrounds. Here, the curve for filling-in falls off more rapidly with a steep decrease from 80% to 20% for the smallest surround width (pair 4). On the other hand the curve for filling-out rapidly increases from 20% to 80%. A non-parametric Chi-square test barely failed to become significant but showed a clear trend (Chi-square = 3,6; df = 1; p = 0.058).

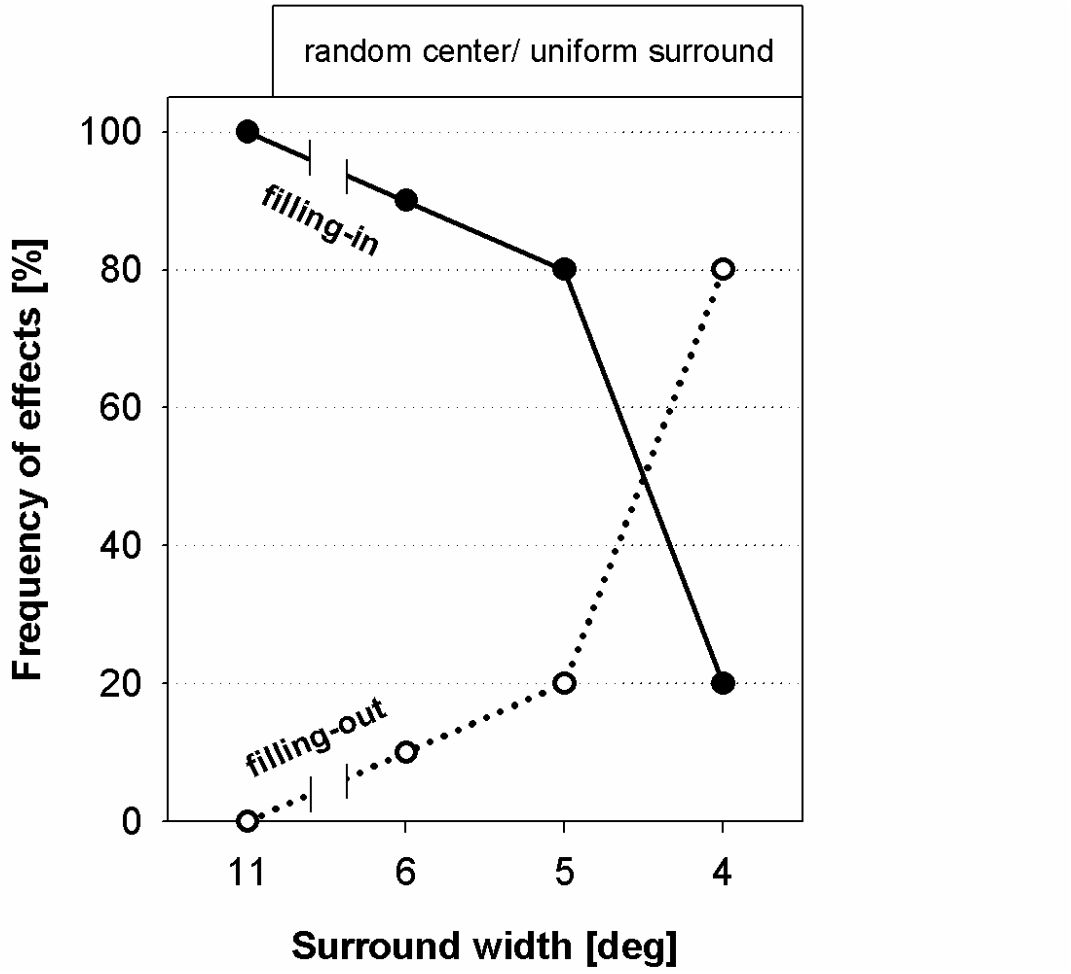

Figure 5: Same as legend to Figure 4. Results refer to stimuli having randomly oriented bars in the center and uniformly oriented bars in the surround.

Experiment 2: Dotted centers with randomly vs. uniformly oriented surrounds

The above results show that a stimulus with randomly oriented bars in the center and uniformly oriented bars in the surround appears more salient and takes more time for fading than a stimulus with the two textures reversed. This is consistent with our hypothesis that the uniform texture in the surround exerts less suppression onto the center, thus rendering it more salient. In this experiment we tested whether bars of random or uniform orientation would yield a similar asymmetry if tested with dotted textures in the center. This was done to study the influence of surround orientation on salience and fading and filling-in when the texture in the center was kept constant.

Procedure

To this extent we compared perceptual salience and fading time for various dotted textures in the center with randomly versus uniformly oriented bars in the surround (Fig. 6). The dotted arrays in the center were modeled after the arrays used by Kubovy, Holcombe and Wagemans (1998) and were common to both members of a pair. Dots were arranged randomly (pair 6), horizontally and obliquely (pair 7), or horizontally and vertically (pair 8). Stimulus pair 5 had a white center and served as a control (i.e., luminance contrast only). In addition, we again tested the two Vicario patterns (pair 1). Stimuli were presented as before.

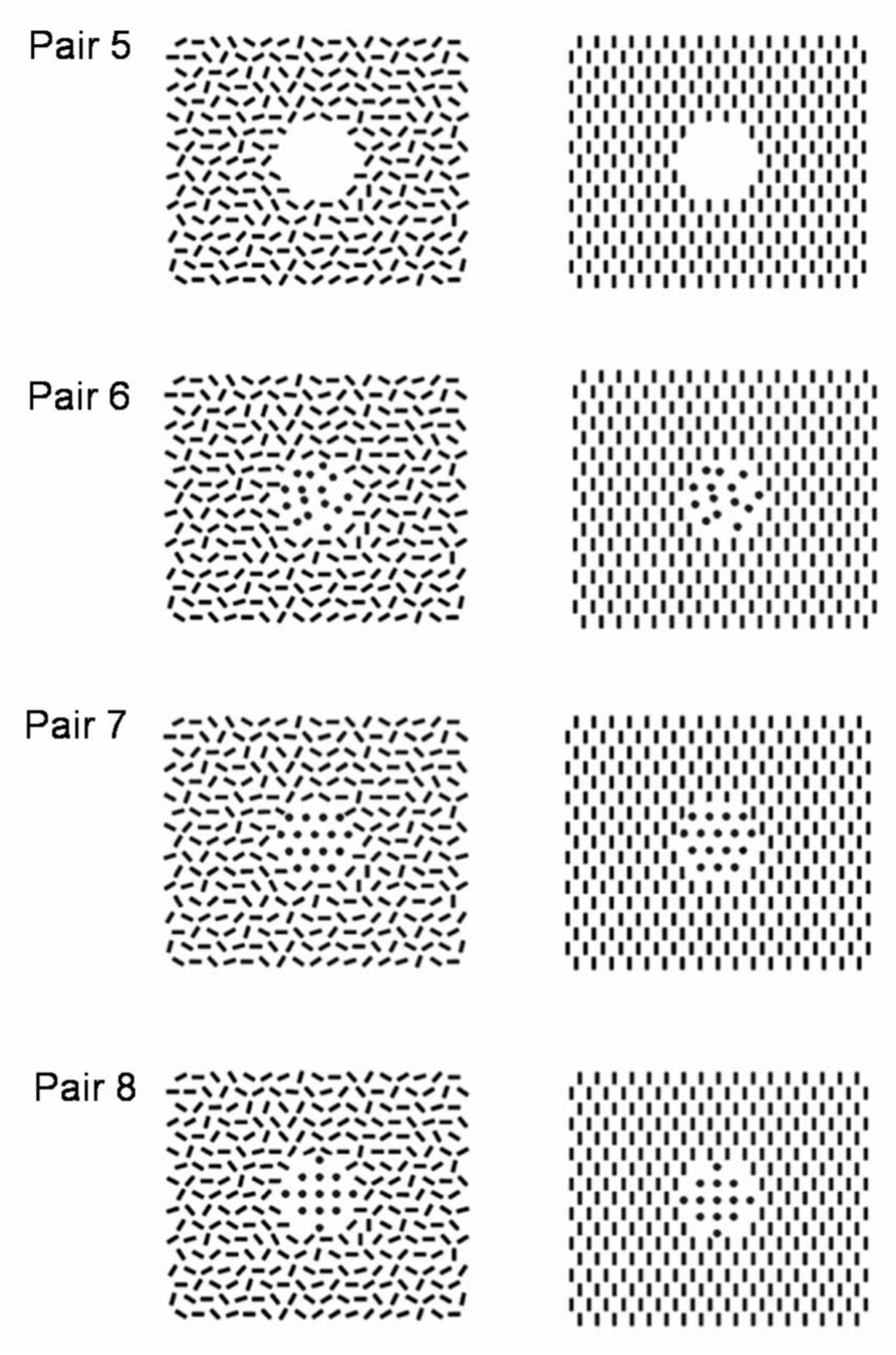

Figure 6: Stimulus pairs 5-8. The dotted centers on the left and right are identical, but the bars in the surrounds are either randomly oriented (left) or uniformly oriented (right). Compare the patterns for perceptual salience and ease of fading and filling-in.

Results

Ratings for perceptual salience are plotted in Figure 7. Patterns with a randomly oriented surround (black columns) generally had a lower perceptual salience than patterns with a uniformly oriented surround (gray columns), irrespective of the dotted array in the center. A repeated-measures analysis of variance (ANOVA) showed this difference to be highly significant (F = 18.04; df = 1; p = 0.008).

However, there was one exception. Stimulus pair 5, being devoid of a texture contrast, showed no difference between ratings for randomly versus uniformly oriented bars in the surround (ceiling effect). The high luminance contrast present in this pattern led to a strong perceptual segmentation of center and surround and produced the highest salience of all.

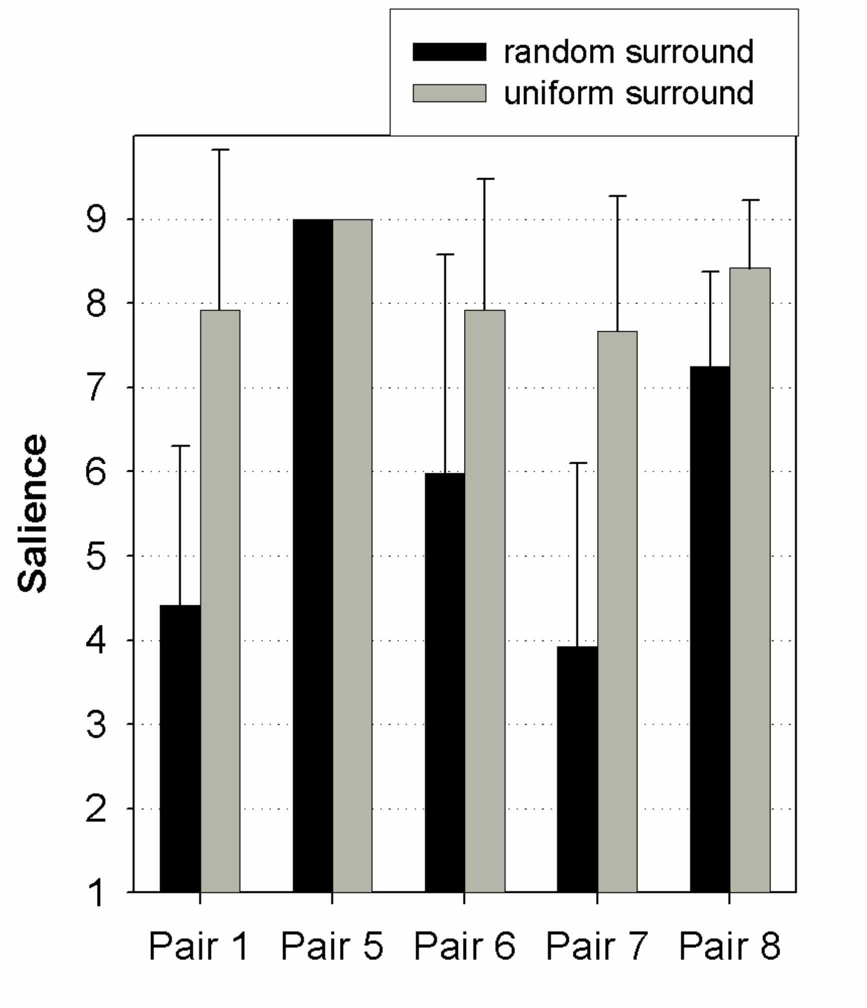

Figure 7: Mean perceptual salience plotted for the stimulus pairs shown in Figure 6. Black columns represent randomly oriented texture in the surround, while gray columns represent uniformly oriented texture. Vertical bars give the standard deviation. Each column represents the averaged data of two measures in each of 6 subjects.

Fading time for these stimuli is plotted in Figure 8. Stimulus patterns with randomly oriented bars in the surround faded significantly faster than patterns with uniformly oriented bars (gray columns) (repeated measures ANOVA: F = 22.01; df = 1; p = 0.002).

For easy visualization of the results go back to Figure 6. Except for stimulus pair 5, salience was lower and fading time shorter for stimuli on the left-hand side and higher and longer for stimuli on the right-hand side. These findings are consistent with a stronger suppression by the randomly oriented surround when the texture in the center of the stimulus pattern was the same.

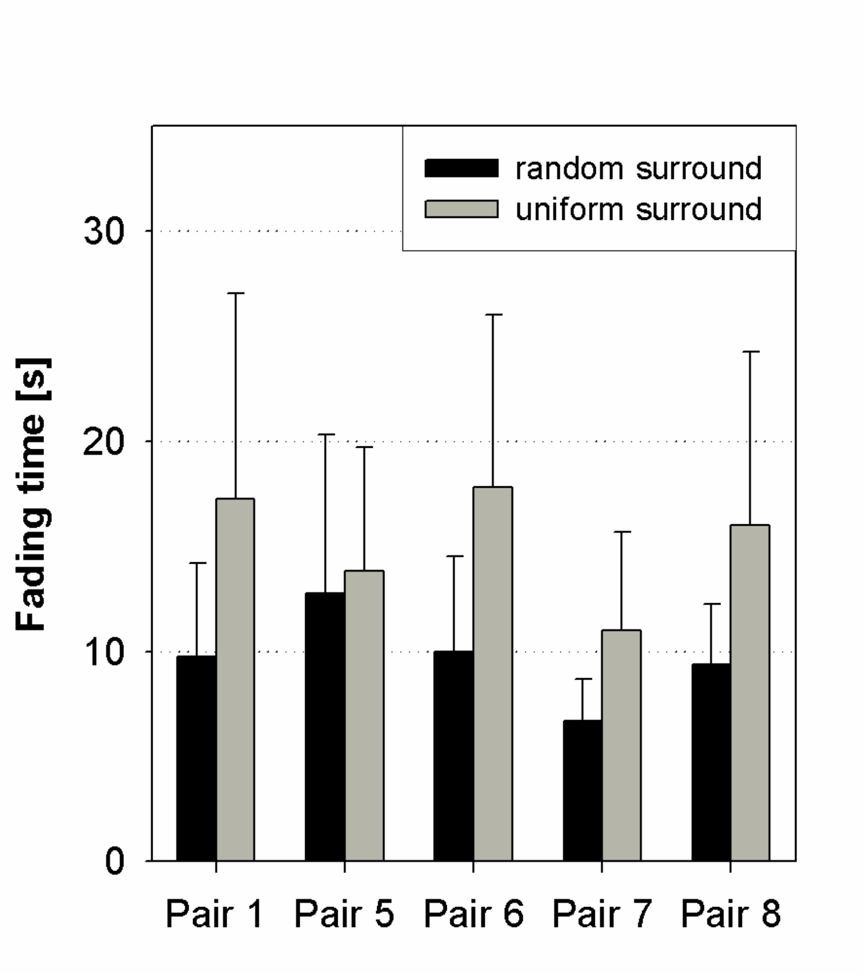

Figure 8: Mean fading time plotted for the stimulus pairs shown in Figure 6. 10 subjects.

The difference in perceptual salience between the two members of each pattern was largest for stimulus pairs 7 and 1 (Fig. 7) and in fading time for stimulus pairs 6, 1 and 8 (Fig. 8). For the Vicario patterns (pair 1) we successfully replicated the finding by Götzl (unpubl.), with an even greater difference in fading time (a total of 7.54 s in our study vs. 5.05 s in Götzl's study). Note also that for stimulus pair 5, salience was considerably higher than for the other stimuli, whereas fading time for this stimulus pair was not much different from that for the others.

Figure 9 plots fading time as a function of perceptual salience for the 5 patterns tested. Fading time increases monotonically with increasing salience for stimuli with randomly oriented surrounds (r = 0.838; p = 0.038), but shows no correlation for stimuli with uniformly oriented surrounds (r = -0.336; p = 0.290), as all stimulus patterns for this condition had approximately the same salience (one-tailed Pearson`s correlation).

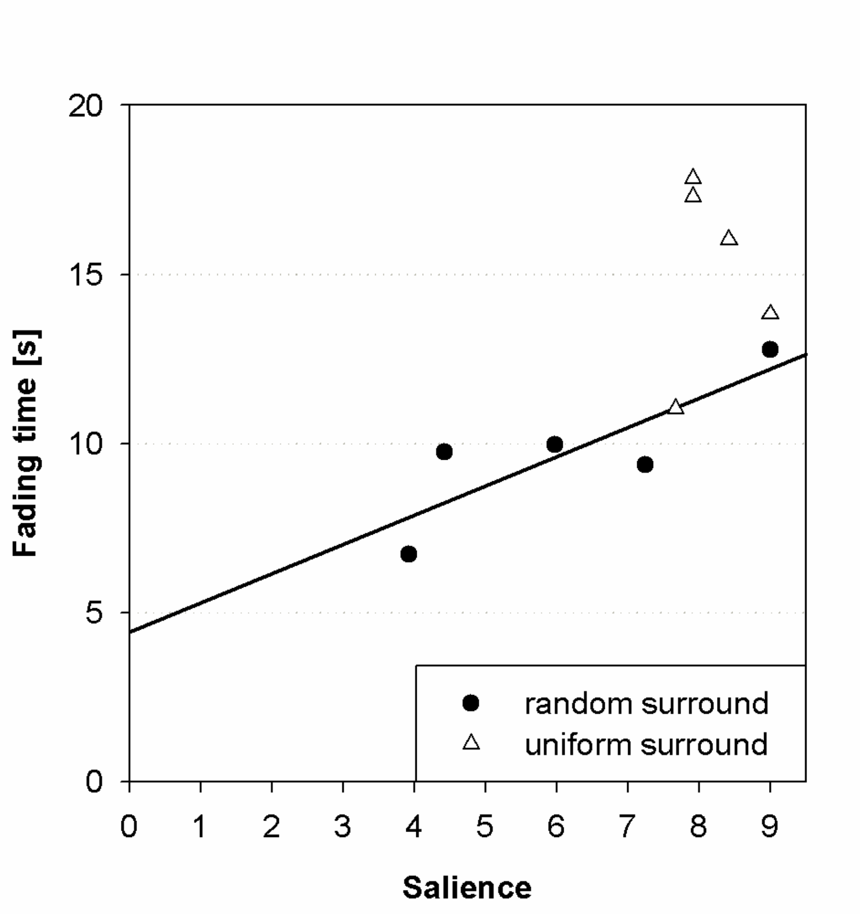

Figure 9: Fading time replotted as a function of perceptual salience for the stimulus pairs shown in Figure 6. Filled dots represent stimulus patterns with randomly oriented bars in the surround and empty triangles stimulus patterns with uniformly oriented bars in the surround. The black line is the linear regression.

Experiment 3: Dotted surrounds with randomly vs. uniformly oriented centers

The previous experiment showed that a stimulus pattern having dots in the center and uniformly oriented bars in the surround, appeared more salient and took more time to fade than a stimulus with the same dotted center, but by randomly oriented bars in the surround. Here, we asked whether an analogous difference would be obtained when center and surround texture were reversed.

Procedure

Perceptual salience and fading time were measured as before for stimulus patterns with dots in the surround and randomly or uniformly oriented bars in the center (Fig. 10). The dotted arrays in the center were again common to both members of a given pattern (pairs 9-11).

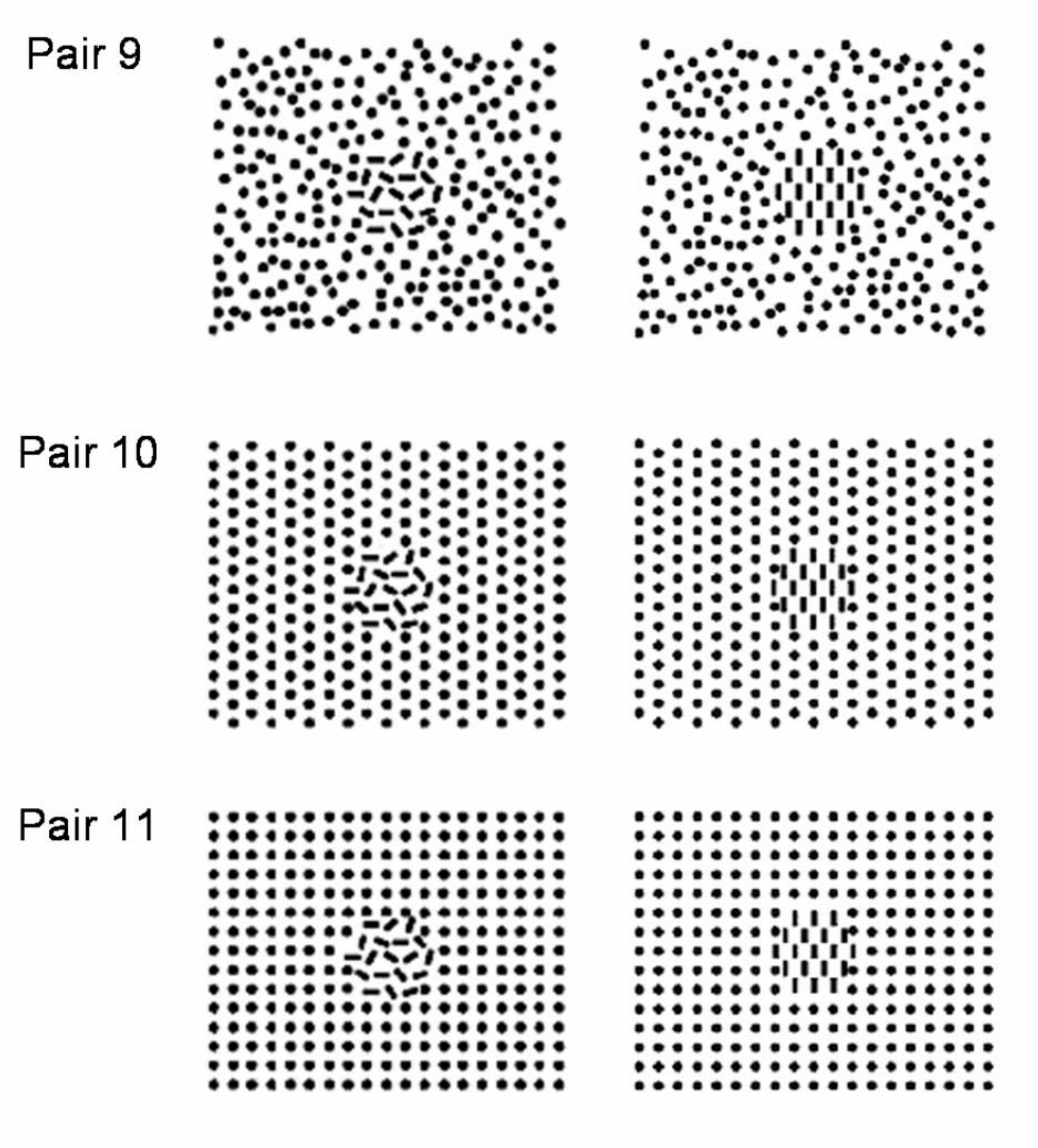

Figure 10: Stimulus pairs 9-11. The surrounds on the left and right are identical, but the bars in the center are either randomly (left) or uniformly oriented (right).

Results

Perceptual salience for all three stimulus pairs is plotted in Figure 11. There was no systematic difference in salience between patterns with randomly or uniformly oriented bars in the center and the same dotted textures in the surround. Salience was the same for the two members of stimulus pair 9. For pair 10, the uniformly oriented center was slightly more salient, whereas for pair 11 the opposite was the case. A repeated measures ANOVA showed no significant effect for the two main factors (F = 0.255; df = 1; p = 0.635), but a significant interaction (center * surround: F = 7.673; df = 2; p = 0.010).

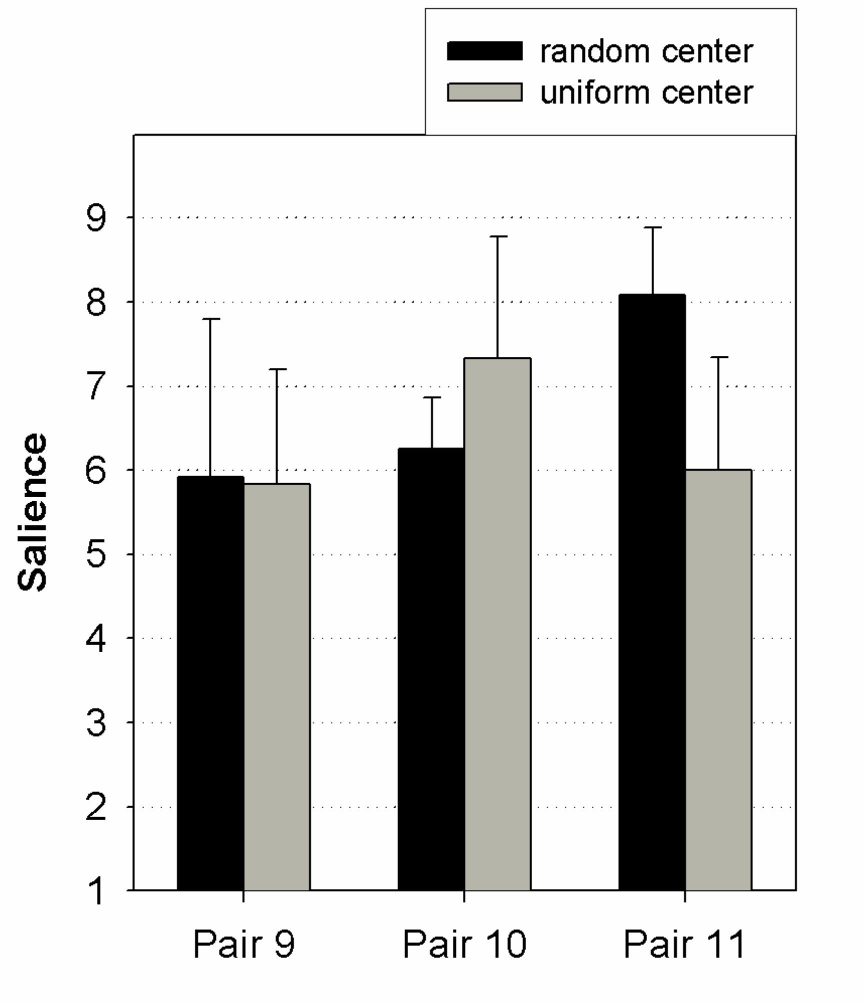

Figure 11: Mean perceptual salience plotted for stimulus pairs 9-11. Black columns represent a randomly oriented texture in the center, while gray columns represent a uniformly oriented texture. Vertical bars give the standard deviation. Each column represents the averaged data of two measures for 6 subjects.

Fading times for these stimuli are plotted in Figure 12. For pairs 9 and 10, the uniformly oriented bars in the center (gray columns) required more time for filling-in than the randomly oriented bars (black columns), while for pair 11 the opposite was the case. Again, none of these differences was significant (repeated measures ANOVA: F = 0.263; df = 1; p = 0.621). Note that fading time differs for the two members of stimulus pair 9, although both were judged equally salient (Fig. 11).

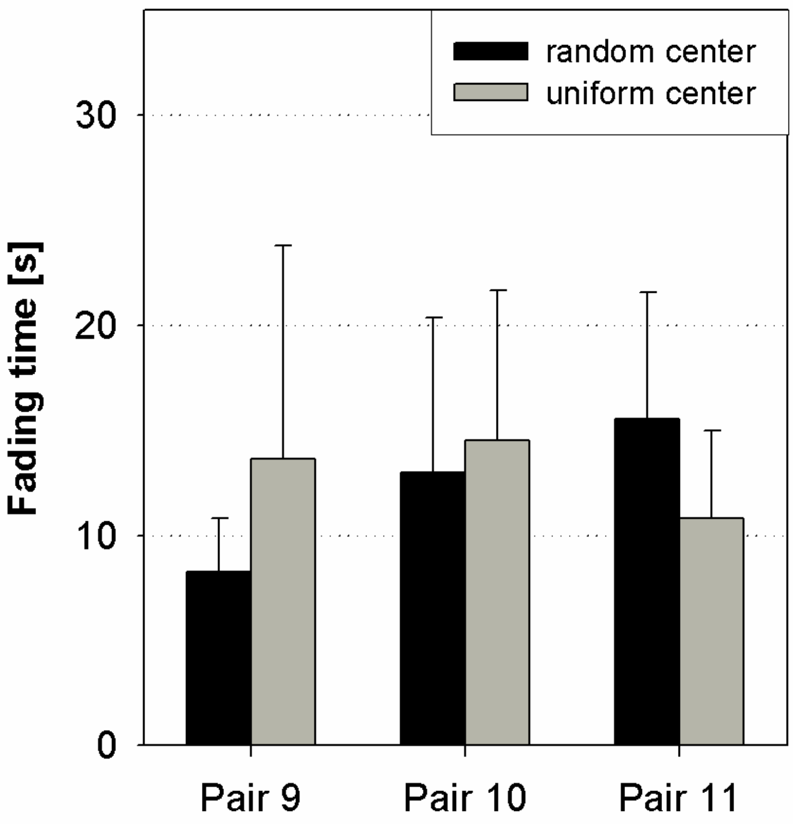

Figure 12: Same as in Figure 11, but for mean fading time. 10 subjects.

Discussion

In this study, we compared the influence of different textures in center and surround on perceptual salience and time required for fading and filling-in.

First, we studied the effect of an implicit versus an explicit border on fading and filling-in, using patterns with short bars of uniform orientation in the center and bars of random orientations in the surround or vice versa (Fig. 1). When we surrounded the center of stimulus pair 1 with a thin black border (explicit border), we found that fading time was about 2 s longer than without the border. The extra time apparently was needed for cancelling the explicit boundary (Spillmann & DeWeerd, 2003).

So far, we had tacitly assumed that a textural or implicit border is equivalent to a continuous or explicit border between center and surround. Indeed, DeWeerd (pers. comm.) suggests that the contrast between two spatially contiguous textures may constitute a perceptual barrier that is functionally similar to a physical (continuous) border delineating two surfaces of different luminance or wavelength. The results suggest that the implict border – although weaker – requires the same two mechanisms, border cancellation and feature substitution, for fading and filling-in (DeWeerd, Desimone & Ungerleider, 1998).

In addition to cancellation of boundary representations, surround width was assumed to affect the time for fading and filling-in. Li et al. (2000) demonstrated that the neural response to a test line decreased with increasing area of surround texture, suggesting more lateral inhibition. Accordingly, one might expect that the influence of the surround onto the center decreases as the surround is made progressively narrower. Indeed, DeWeerd et al. (1998) found shorter fading times with decreasing surround width when center size was kept constant.

Contrary to prediction, Figure 3 shows fading time to be largely the same for all stimuli with a randomly oriented surround and a uniformly oriented center (panel A).

This suggests that in our experiment surround size was not much of a factor for filling-in. No systematic change was obtained either with a uniformly oriented surround and a randomly oriented center (C). These results are consistent with the findings obtained in experiments on pop-out (Nothdurft, 1992), suggesting that the crucial factor was the texture contrast at the interface.

On the other hand, we found a clear decrease of time required for filling-out (B, D). Figure 4 plots the frequency of occurrence for both modes of spreading as a function of surround width. Whereas the frequency of filling-in decreased with decreasing surround width, the frequency of filling-out increased. This is particularly pronounced in Figure 5, which shows the results for a randomly oriented center and a uniformly oriented surround. Here, the greatest change occurred for the narrowest surround width (stimulus pair 4).

Filling-out has been reported before by DeWeerd et al. (1998) for texture and by Shimojo, Wu & Kanai (2002, 2003) and Hamburger, Prior, Sarris and Spillmann (2006) for color. According to DeWeerd et al. (1998), filling-in is a bi-directional process of feature spreading whereby the relative sizes of a textured surround and an enclosed gray target determine which region becomes filled-in by the other. Here we demonstrate that the direction depends on surround width as well as center/surround texture. Conceivably, with a narrower surround the suppressive effect on the central target becomes too weak and texture spreading reverses in direction from inward to outward, perhaps in the interest of a simpler figure-ground segmentation. A similar argument has been made by Shimojo et al. (2003) for color spreading-out.

In Experiment 2, we studied the influence of different textures in center and surround on perceptual salience and time for fading and filling-in. For the Vicario patterns (Fig. 1) the local texture contrast at the boundary was the same in both cases. Accordingly, one might assume that the perceived salience of figure-ground segregation and the time required for fading and filling-in would also be the same. However, this was not so. Perceived salience was significantly higher and fading time longer when the randomly oriented texture was in the center and the uniformly oriented texture in the surround than the other way around. This difference confirms the earlier observations by Götzl (unpubl.) and cannot be attributed to a difference in mean luminance. It must be a genuine effect of texture contrast.

In a next step, we compared randomness versus uniformity of texture elements in the surround with a common array of dots in the center. As for the Vicario patterns (Fig. 1), perceptual salience for all stimulus pairs was lower and fading time shorter, when the bars in the surround were randomly oriented (Fig. 6, stimulus patterns on the left). The observation that a randomly oriented surround suppresses bars and dots more strongly than a uniformly oriented surround may be attributed to the greater number of neuronal channels being activated by this stimulus. The stronger signal lowers salience making the center more susceptible to fading and filling-in.

Our assumption that different strengths of neuronal activity arising from the two kinds of surround texture account for our results is consistent with Sakaguchi (2001) who studied target/surround asymmetry for disk-ring patterns differing in grating orientation, spatial frequency, luminance, and color. Time for fading and filling-in increased with an increase in difference between the featural properties of target and surround (feature difference effect). The results of Experiment 3 further suggest that the surround dominates the center in determining perceptual salience and filling-in. No systematic difference was found for patterns with dots in the surround and randomly or uniformly oriented bars in the center, suggesting that different texture orientations in the center have little consequence for perceptual salience and fading and filling-in.

Computational studies (e.g. Grossberg & Mingolla, 1985; Raizada & Grossberg, 2000) have focused on neural models of texture boundary detection that emphasize the importance of competitive and cooperative interactions in the boundary system. According to this model, grouping may occur by recurrent interaction of V1 complex cells and V2 bipole cells. More recently, Thielscher and Neumann (2005) emphasized the role of V4 cells that respond to orientation discontinuities for inputs from area V2.

Applied to our data, we suggest that texture patterns with uniform surrounds lead to stronger V2 groupings of the line elements at the border which in turn lead to stronger V4 activation and better textural border detection. Feedback mechanisms further enhance the V2 activations at the border which strengthen the resultant boundaries and thus prolong fading time. However, to our knowledge, computational models are still short of fully explaining the phenomenon of filling-out. Instead, we propose that the difference in neural activity, as proposed here, resulting from random and uniform texture elements provides a more parsimonious way of accounting for our data.

We know that V1 neurons have receptive fields with spatially segregated and functionally distinct components (Kapadia, Westheimer & Gilbert, 2000). This suggests that contextual influences on V1 neural responses are strongly modulated by the textural properties of the stimulus elements, here the randomness or uniformity of line elements (Li & Gilbert, 2002).

Conclusion

Our results suggest that for the texture patterns used in this study the neural activities in the surround, elicited by randomly or uniformly oriented bars, determine perceptual salience and fading time. A randomly oriented texture in the center enclosed by a uniformly oriented texture in the surround stands out more strongly and persists longer than a uniformly oriented center enclosed by a randomly oriented surround when fixated. We varied these surround effects by systematically reducing surround size of the textural stimuli. Aside from filling-in, we observed a spread of texture outward from the center, when the surround became too narrow and the random texture in the center took possession of the uniform texture. We call this effect filling-out. A comparison between patterns having randomly or uniformly oriented bars in the surround and various dotted arrays in the center or vice versa further strengthens our assumption that filling-in is strongly related to the perceptual segmentation of these patterns. This process likely reflects a neural pattern, which is triggered by the kinds of orientation in nonclassical receptive fields.

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Part 2 –

Visual illusions at luminance contrast and isoluminance

Chapter 5 –

Geometric-optical illusions at isoluminance[5]

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[5] This work has been submitted in a slightly different form: Hamburger, K., Hansen, T., & Gegenfurtner, K.R. (submitted). Geometric-optical illusions at isoluminance. *Vision Research.*

It has been known for long that color and luminance are processed together by the same parvo retinal ganglion cells. It is still debated, however, whether color and visual form are processed jointly or separately in visual cortex. In particular, the idea of a largely segregated processing of color and form was supported by observations that geometrical-optical illusions vanish under isoluminance (Lehmann, 1904, Liebmann, 1927, Livingstone and Hubel, 1987, 1988), a finding that is inconsistent with other studies (Gregory, 1977, Westheimer, 1979, Li and Guo, 1995). Here we examined the strength of nine geometric-optical illusions under isoluminance (Delboeuf, Ebbinghaus, Hering, Judd, Mueller-Lyer, Poggendorff, Ponzo, Vertical, Zoellner). Subjects interactively manipulated computer-generated line drawings to counteract the illusory effect. In all cases, illusions presented under isoluminance (both for colors drawn from the cardinal L−M or S−(L+M) directions of DKL color space) were as high as the luminance versions (both for high and low contrast). In two control experiments we tested whether subjective deviations from the photometric isoluminance or chromatic aberrations may have caused the observed strong illusions under isoluminance. Again, no significant differences between the illusions under luminance or isoluminance occurred. Our findings show that geometric-optical illusions under isoluminance are as strong as when presented at luminance contrast, supporting the joint processing of oriented color and luminance contrast in early visual areas. Furthermore, the results show that our conscious percept is deceived similarly for both isoluminance and luminance conditions, suggesting that the joint processing for chromatic and luminance defined contours extends well beyond early visual areas.

Introduction

Visual illusions are neither just entertaining misperceptions nor “subjective perversions of the contents of objective perceptions” (Külpe, 1893). Rather, visual illusions demonstrate the incongruity between the real world and the world within the mind (Solso, 2003). Moreover, illusions serve as a powerful window into the neurobiology of vision, leading to new experimental techniques (Eagleman, 2001).

Geometrical-optical illusions are illusions that are constructed from lines and simple geometric forms. This class of illusions has a long tradition in vision science.

Several theories have attempted to explain the class of geometric-optical illusions or at least a few of them (e.g., Lehmann, 1904, Palmer, 1999, Gregory, 1968a, 1968b, 1997a) and attempts have been made to link the geometrical-optical illusions to the physiology of early visual processing in a parvocellular and a magnocellular pathway (Livingstone & Hubel, 1987; Li & Guo, 1995; Puts, Pokorny & Smith, 2004)

It has been known for long that color and luminance are processed together by the same parvo retinal ganglion cells (DeValois & DeValois, 1988). More recently it has been shown that in areas V1 and V2 cells respond to oriented chromatic contrast (e.g., Gegenfurtner and Kiper, 1992; Johnson, Hawken, and Shapley, 2001; Friedman, Zhou, and von der Heydt, 2003; for review see Gegenfurtner, 2003). On the contrary, a largely segregated processing of unoriented chromatic contrast and oriented luminance contrast has been hypothesized. This idea was bolstered by observations that some illusions, in particular geometric-optical illusions, vanish under conditions of isoluminance (Livingstone & Hubel, 1987, 1988). Similar findings have been reported in other studies. Benussi (1902) pointed out that color affects the Zöllner illusion. He showed that black lines resulted in the greatest effect, followed by green, red, yellow and violet, and gray. However, it might be possible that Benussi was dealing with different luminance contrasts rather than with the effects of hue itself (Robinson, 1998). Lehmann (1904) hypothesized that irradiation might cause geometric-optical illusions, meaning that stimulus elements with high luminance values spread their light onto the dark areas and therefore being perceived as larger. He also reported that illusions like the Poggendorff, Zöllner, and in part the Müller-Lyer illusion broke down under conditions of isoluminance. This interpretation has been questioned by Liebmann (1927), claiming that irradiation is also present in isoluminant stimuli. Wickelgren (1965) demonstrated that black fins on a white background in the Müller-Lyer illusion produce a greater illusory effect than combinations including gray fins or a gray background (low luminance contrast). It has also been considered that (in repeated trials) adaptation to brightness reduces contrast and hence reduces the extent of the illusion (Pollack, 1970).

Since the spatial characteristics of the early processing of color and luminance in the retina and LGN are distinct (DeValois & DeValois, 1988; Rodieck, 1998; Mollon, Pokorny & Knoblauch, 2003), one could expect that some illusory effects would be reduced or even absent under conditions of isoluminance if different properties were processed independently. Li and Guo (1995) investigated four geometric-optical illusions (Delboeuf, Müller-Lyer, Ponzo, and Zöllner) under conditions of luminance contrast and isoluminance with red-green color contrast. Illusory effects were equally strong in both conditions. Furthermore, they did not find illusory contours (Kaniza) under conditions of isoluminance, but rather required a luminance contrast of at least 1.8% to elicit illusory contours.

Overall, no conclusive answers have been given to the main question “Do geometric-optical illusions occur under conditions of isoluminance or not, and if so, are they equally strong under both conditions?”

Here we systematically investigated nine geometric-optical illusions (Delboeuf, Ebbinghaus, Hering, Judd, Mueller-Lyer, Poggendorff, Ponzo, Vertical, Zöllner) under high and low luminance contrast and two isoluminant chromatic contrast conditions, varying along different axes in DKL color space. Each condition was investigated in a series of four different psychophysical experiments. In the first experiment we investigated a variety of luminance contrast and photometric isoluminance conditions for 20 subjects. In the second experiment we repeated Experiment 1 using subjective isoluminance values for each subject. In Experiment 3 we tested several discrete contrast values between the points of photometric and subjective isoluminance in repeated sessions. In the final Experiment 4 stimuli were low-pass filtered (blurred) to control for chromatic aberration.

Experiment 1: Photometric isoluminance

To quantify the strength of the illusory effects we developed a visual paradigm, that allowed subjects to adjust length, size, or orientation of critical stimulus parameters.

Methods

Subjects

20 naïve student subjects (10 females, 10 males) participated in the experiment. In this and following experiments, subjects had normal or corrected-to-normal visual acuity and

normal color vision (based on subjective reports and tested with the Ishihara pseudo-isochromatic plates; Ishihara, 1982). All participants were right-handed. The age ranged between 20 and 48 years.

Stimuli

Nine different visual illusions were tested in all experiments (Figure 1): Delboeuf- (Delboeuf, 1892); Ebbinghaus- (e.g., Wundt, 1898); Hering- (Hering, 1861); Judd- (Judd, 1899); Müller-Lyer- (Müller-Lyer, 1889); Poggendorff- (Zöllner, 1860; Burmester, 1896); Ponzo- (Ponzo, 1928); Horizontal-Vertical- (Fick, 1851, 1852); and Zöllner-Illusion (Zöllner, 1860). Stimuli were created with the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) in Matlab (The MathWorks, http://www.mathworks.com/) and were presented in a classical luminance contrast condition (50%, dark gray/light gray), a low luminance contrast condition (10%, gray), and two isoluminance conditions along the cardinal axes of DKL color space (L−M and S− (L+M); Derrington, Krauskopf & Lennie, 1984). All stimuli subtended 17 deg of the visual field and had a constant line width of 4 pixels, corresponding to 0.14 deg. Sample stimuli for high and low luminance contrast and for the isoluminant color contrast conditions are depicted in Figure 2.

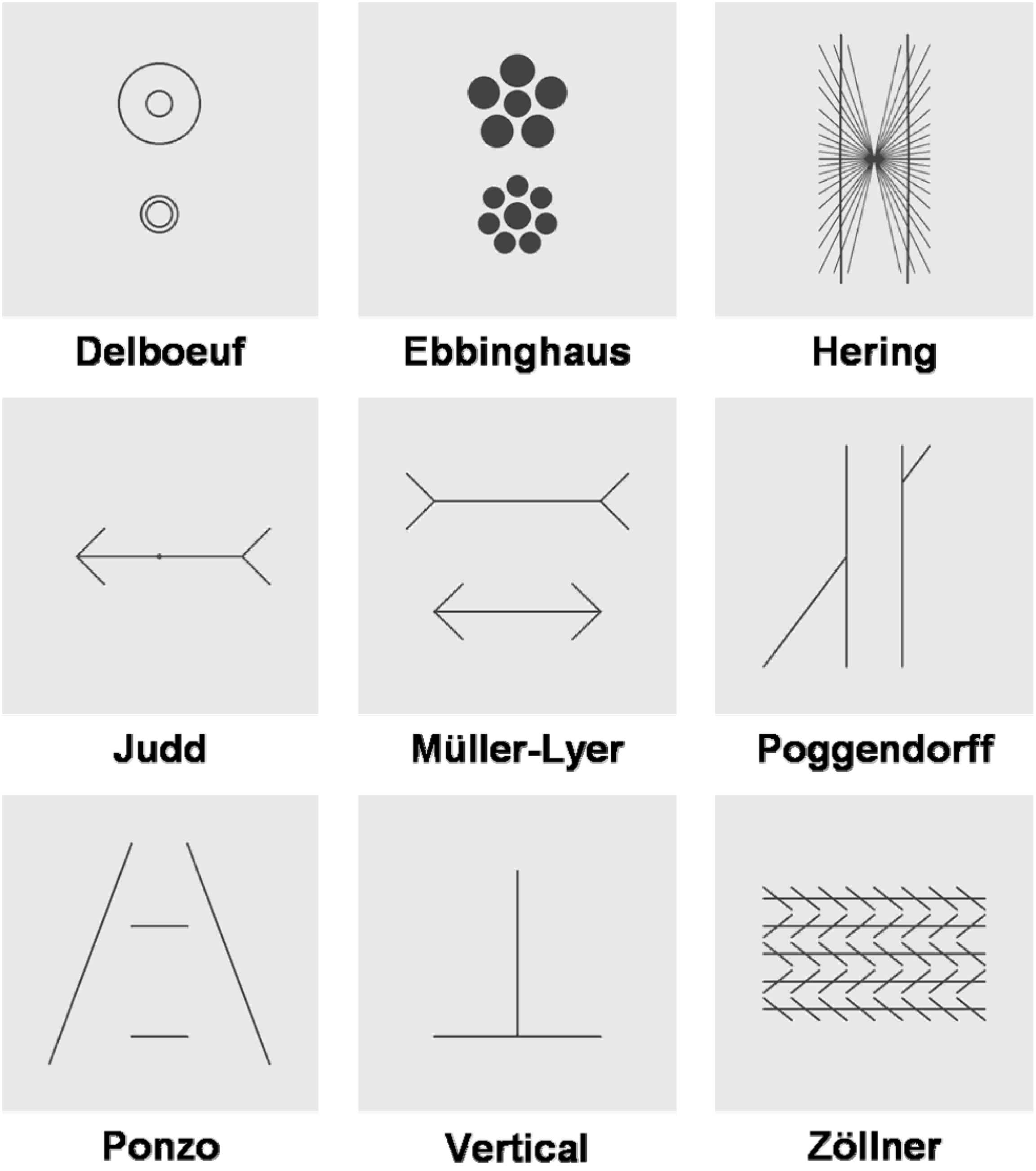


Figure 1: The classical geometric-optical illusions investigated.

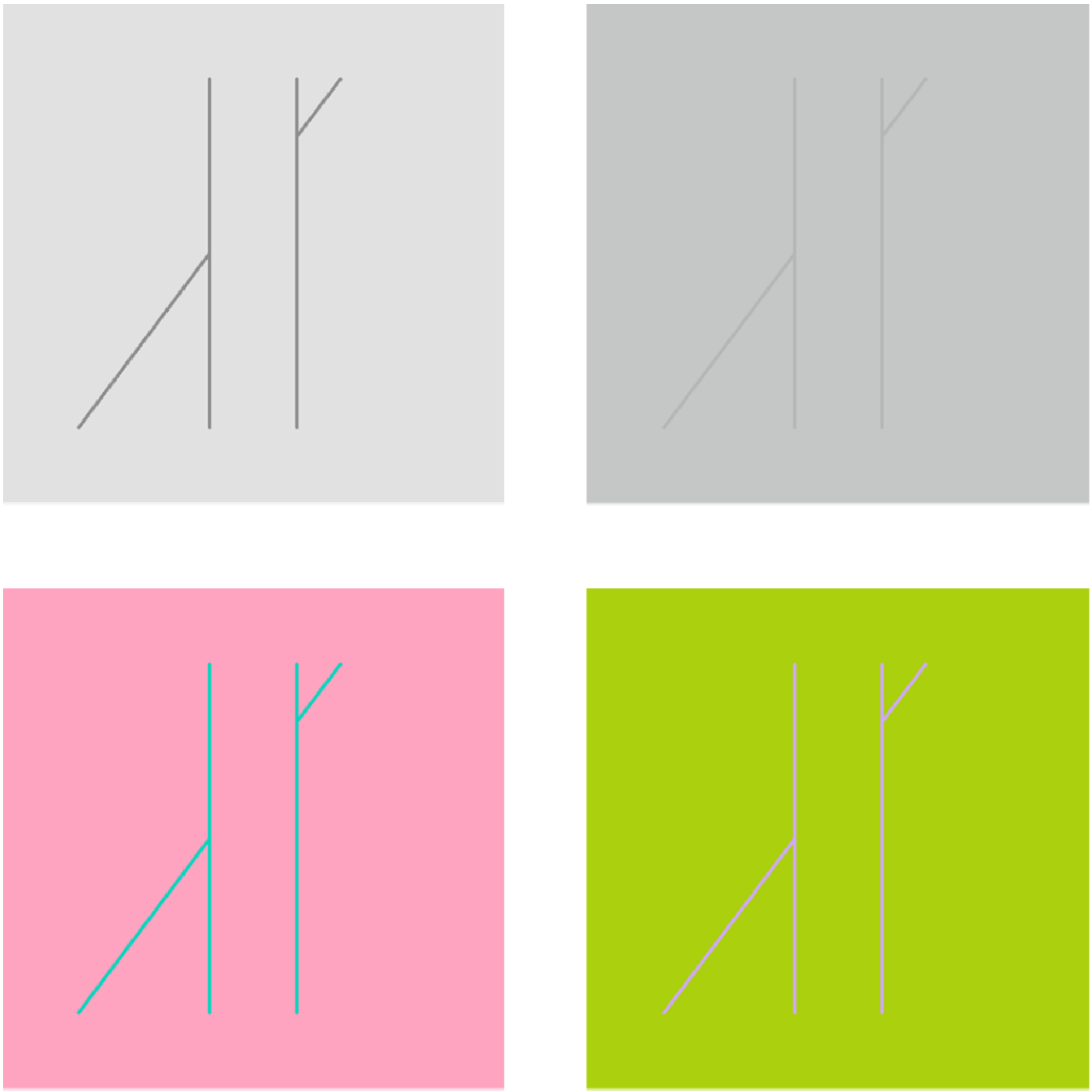


Figure 2: Four different luminance conditions exemplified with the Poggendorff illusion. 50% luminance contrast condition (dark gray/ light gray; upper left), 10 % luminance contrast (gray; upper right), isoluminance with L−M color contrast (lower left), and isoluminance with S−(L+M) color contrast (lower right).

Procedure

Subjects were instructed to adjust the length, size, or orientation in the appropriate stimuli (length: Judd, Müller-Lyer, Ponzo, Vertical; size: Delboeuf, Ebbinghaus; orientation: Hering, Poggendorff, Zöllner; similar to the classification of Oyama, 1960) by pressing the right and left arrow keys of a keyboard to achieve the state of subjective equality. Coarse adjustments were made by holding the key pressed, while fine adjustments were achieved by pressing a key just once. Observers were instructed to adjust the point of subjective equality from two directions (ascending and descending). Possible adjustments ranged from −1.4 deg (−40 steps in pixel), meaning a physical enhancement of the expected illusory effect, to +2.8 deg (+80 steps in pixel), indicating a compensation of the expected illusory effect. When subjects perceived the stimuli to have equal length, size, or orientation, they pressed the space bar to indicate their judgment and to start the next trial.

Observation was binocular and target stimuli were presented in the monitor center at subjects' line of sight. Stimuli were presented four times each in randomized order. The initial length of the adjustable value was randomly varied in each trial. Stimuli were presented on a gamma corrected 21''Iiyama Vision Master Pro 513 CRT monitor with a resolution of 1154 x 768 pixels that was driven by a NVIDIA Quadro NVS 285 graphics card at a refresh rate of 85 Hz noninterlaced. The experiment was conducted in a dark room. The observation distance was 60 cm. A chin-rest was used for head stabilization, and subjects were free to move their eyes. No time limit was given, but subjects normally completed a trial within 1 min.

Condition 1

The background luminance of the screen was 78.2 cd/m^2 in the condition of high luminance contrast (50%). The background was achromatic light gray and the stimulus elements were presented in achromatic dark gray.

Condition 2

In the low luminance contrast condition (10% luminance contrast), a light gray served as background, whereas a slightly darker gray was used for the stimuli. The luminance of the background was 56.9 cd/m^2.

Condition 3

Photometric isoluminance with pure chromatic contrast along the cardinal directions L−M of DKL color space (Derrington et al., 1984; Krauskopf, Williams & Heeley, 1982) was used. The luminance of the stimulus was 52.4 cd/m^2.

The stimuli were drawn with greenish lines (L cone contrast −6.45%, M cone contrast 11.49%) on reddish background (L cone contrast 6.45%, M cone contrast −11.49%). S cone contrast was zero.

Condition 4

Photometric isoluminance with pure chromatic contrast along the cardinal axis S−(L+M) of DKL color space was used. The luminance of the stimulus was 50.7 cd/m^2. The stimuli were drawn with purplish lines (S cone contrast 86.99%) on a yellow-greenish background (S cone contrast −86.99%). L and M cone contrast were zero.

Results

Subjects compensated for the illusory effect by adjusting the stimulus elements in the direction opposite to the illusory effect. All subjects were deceived by all stimuli under all four contrast conditions. Results are shown in Figure 3.

The Pearson's correlation coefficient was calculated for the different conditions of each stimulus over all subjects. All conditions correlated highly with each other and were highly significant with a median value of $r = .851$. The lowest correlation was obtained in the Ponzo illusion for luminance vs. L−M isoluminance ($r = .645$, $p = .002$), the highest correlation was obtained in the Delboeuf illusion for L−M isoluminance vs. S−(L+M) isoluminance ($r = .968$ and $p < .001$). The high correlation shows that subjects were very consistent over conditions: Those subjects who adjusted low or high values in one condition adjusted similar values in the other condition (Figure 4).

Illusory effects under all conditions were significantly different from zero. An ANOVA for repeated measures revealed few significant differences across conditions. The Hering illusion in the luminance condition was significantly stronger than in the low luminance and the isoluminant conditions. These differences were small compared to the overall strength of the illusion. Gender analysis did not reveal any significant differences in illusion strength between females and males across the different conditions. Gender differences were not further investigated in the other experiments.

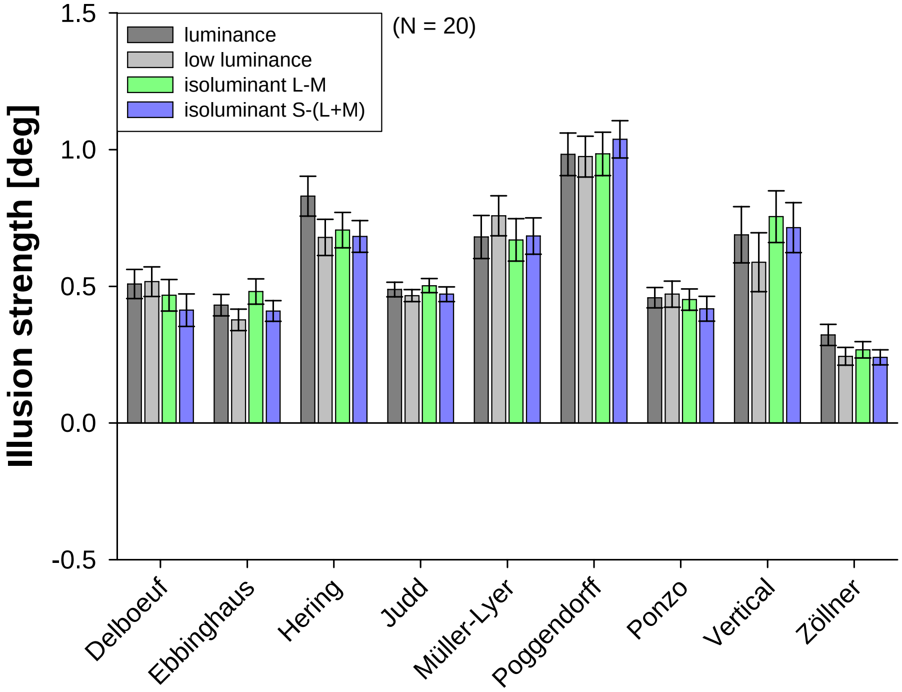


Figure 3: Results for the different geometric-optical illusions at luminance contrast and photometric isoluminance (N=20). Error bars denote the SEM. Illusory effects occur with similar strength under all conditions. Subjects were very consistent across conditions (Pearson’s correlation coefficient varied between r = .645 and r = .968 with a median of r = 0.8505).

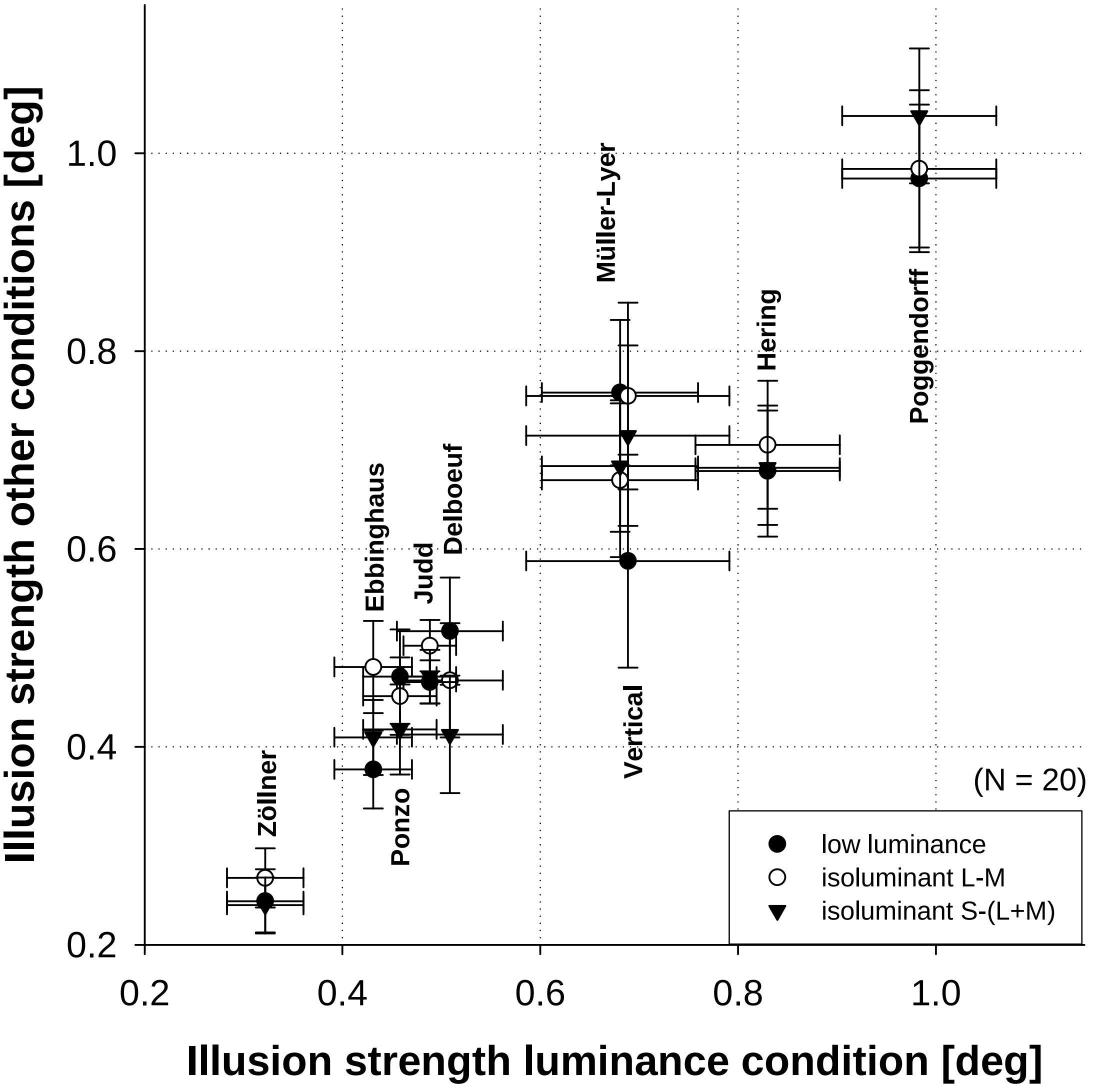


Figure 4: Correlations between the luminance condition and the other conditions tested (low luminance, isoluminance L−M, isoluminance S−(L+M)). Horizontal error bars denote the SEM in the luminance condition and vertical error bars denote the SEM in the other conditions. High correlations between the luminance and the other conditions were obtained, indicating that the illusory effects were similar across conditions. This graph also nicely demonstrates the different illusion strengths obtained for the different geometric-optical illusions. The Zöllner illusion revealed the smallest perceptual effect, whereas the Poggendorff illusion revealed the largest effect of around 1 deg.

Discussion

All subjects were deceived by all illusions under each of the four luminance and isoluminance conditions. Individual adjustments were highly consistent. Even though significant differences between illusory strengths were obtained, they did not reveal any systematic differences in eight out of nine illusions. These differences were small compared to the main and robust finding that all illusory effects occurred under all luminance and isoluminance conditions. In particular, a pure chromatic contrast elicited a deception as strong as in the luminance condition.

Experiment 2: Subjective isoluminance

Methods

Subjects

10 student subjects (7 females, 3 males) participated in the experiment. All participants were right-handed. The age ranged between 20 and 38 years. Five subjects were naïve and five already participated in Experiment 1.

Stimuli

The same stimuli as in Experiment 1 were used.

Procedure

The general procedure for the main experiment was identical to that of Experiment 1. The only difference was that the stimuli were rendered based on subjective isoluminance values. Values of subjective isoluminance were measured in a pilot experiment using a minimal distinct border paradigm (Tansley & Boynton, 1978). Subjects viewed a bipartite disk in the center of the screen. One part of the disk was filled with the line color, whereas the other part was filled with the background color. Subjects had to adjust the subjective luminance of the stimulus colors to match the luminance of the background colors. Initial luminance values were randomly varied in each trial. Each stimulus was adjusted 20 times in total, with a balanced assignment of the two colors to the two fields of the disk. The average adjustment value of these 20 trials defined the individual value of isoluminance used in the main experiment.

Results

Results for the subjective isoluminance experiment are shown in Figure 5. Again, all subjects were deceived by all illusions, and illusions occur robustly under subjective isoluminance.

We also computed the individual correlations between the values measured in the two luminance conditions in the first experiment to the values measured under the conditions of subjective isoluminance (L−M and S−(L+M)). Most conditions (25 out of 36) correlated highly with each other and were significant with a median value of $r = .836$. All but one result for the subjective isoluminance conditions correlated significantly. The lowest and only insignificant correlation for isoluminance L–M vs. isoluminance S–(L+M) was obtained in Ebbinghaus ($r = .590$, $p = .072$), whereas the highest correlation was found for the Vertical illusion stimulus ($r = .932$, $p < .001$). The median of correlations was $r = .812$.

An ANOVA for repeated measures did not reveal any significant differences of illusion strength across conditions.

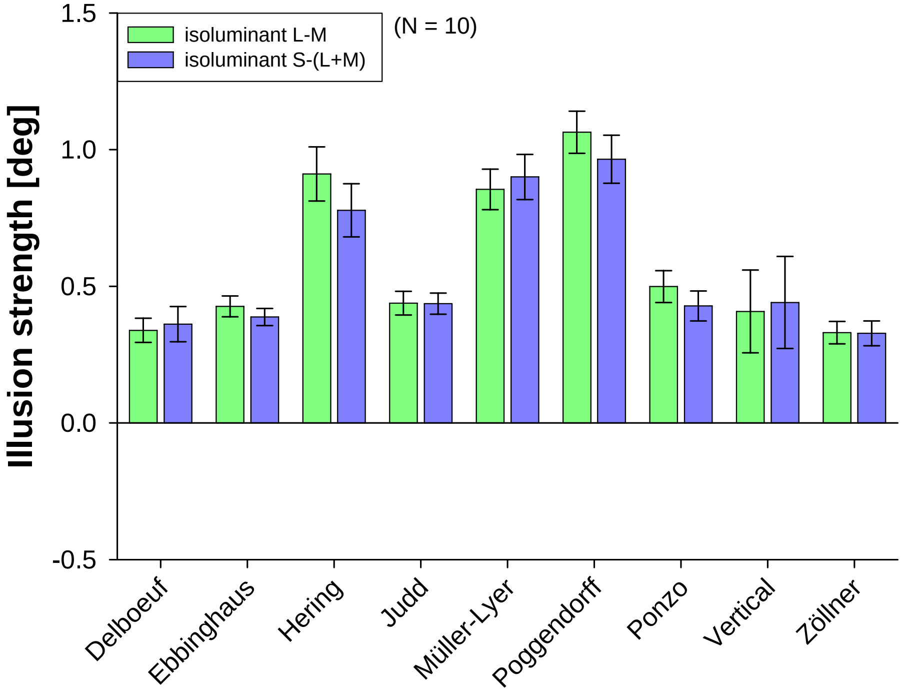


Figure 5: Results for the different geometric-optical illusions at subjective isoluminance (N=10). Error bars denote the SEM. Illusory effects occur with similar strength under all conditions.

Discussion

Again, all subjects showed illusory effects (under- or overestimation) in all illusions and under conditions of subjective isoluminance. They were almost as consistent as in Experiment 1. No significant differences between conditions occurred.

Experiment 3: Five step paradigm from photometric to subjective isoluminance

In Experiment 2 we determined the subjective point of isoluminance. To rule out that inaccurate measurement of the subjective isoluminance value may results in spurious luminance differences in our chromatic contrast, we repeated Experiment 2 using 5 different luminance values between subjective and photometric isoluminance.

Methods

Subjects

Three subjects of Experiment 2 participated (3 females) in this multi-session experiment. The age ranged between 20 and 22 years.

Stimuli

The same stimuli as in Experiment 1 were used in this experiment.

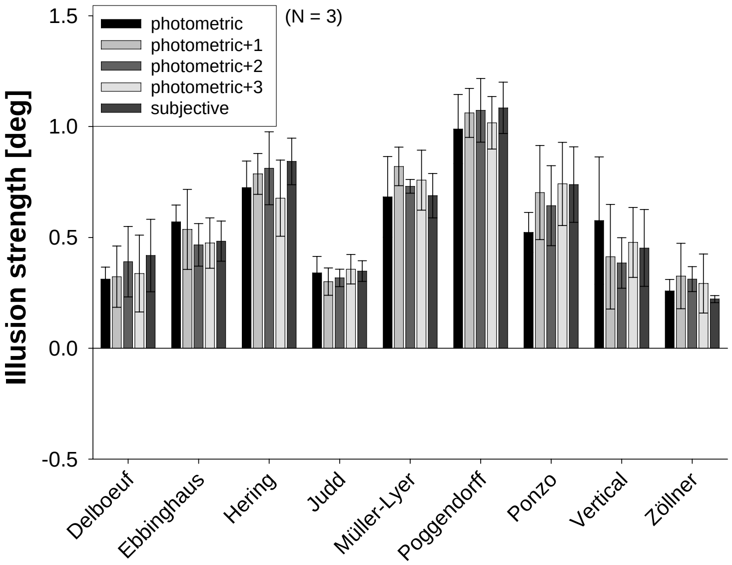
Procedure

Prior to the experiment the subjective isoluminance values were again defined with a subjective luminance adjustment task. Due to the fact that some subjects in Experiment 2 differed strongly from photometric isoluminance with their subjective adjustments (between 3 and 30%; for methodological problems in luminance adjustment see Liebmann, 1927), we decided to present the adjustment stimuli with a horizontal border instead of a vertical border. Using this measurement, subjective isoluminance values differed from photometric isoluminance only between 2 and 7%.

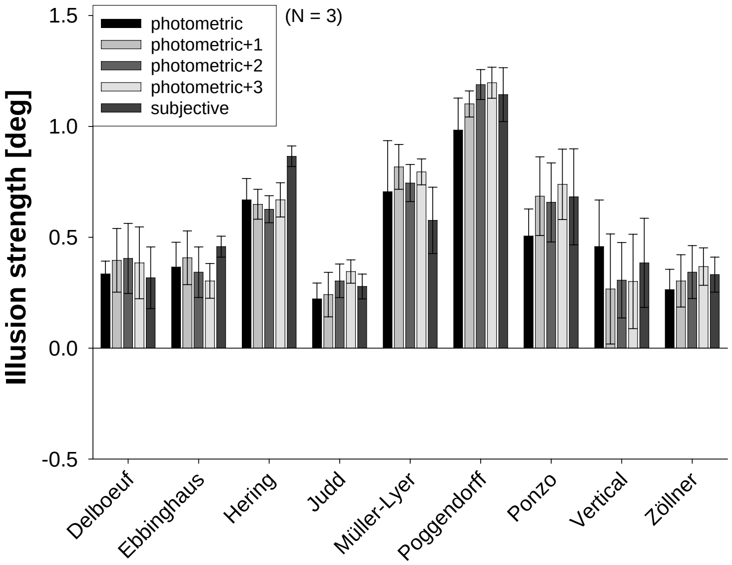
The general procedure for the main experiment was identical to that of Experiment 2. The only difference was that we used five different luminance values: photometric and subjective isoluminance and three intermediate luminances. The experiment was therefore conducted five times for each subject. Between experimental sessions there was a break of at least one day. Since we did not find any reduction of illusory effects with repeated exposition, allowing a break of one day was sufficient for obtaining reliable results.

Results

The results for Experiment 3 are shown in Figure 6. Panel A shows the data for the L−M condition and panel B shows the data for the S−(L+M) condition. Again all three subjects compensated for the illusory effects. In both isoluminant color conditions correlations were high (up to r = 1.0), without any significant differences in illusion strength for the five different luminance contrast conditions (from photometric to subjective).



A



B

Figure 6: (a) Results for the different geometric-optical illusions at 5 different luminance values varying from photometric to subjective isoluminance (N=3). Error bars denote the SEM. Illusory effects occur with similar strength under all conditions. (A) Results for the L−M color contrast condition. (B) Results for the different geometric-optical illusions in the S−(L+M) color contrast condition.

Discussion

This experiment shows that geometric-optical illusions are robust and strong under conditions of photometric isoluminance, subjective isoluminance, or discrete values between these two conditions. The illusory effects are stable and subjects are consistent. Overall, the illusory effects are robust against luminance variations.

Experiment 4: Low-pass filtered (blurred) stimulus edges

To control for chromatic aberrations that might occur in the line drawings at isoluminance, containing high-frequency color contrast edges (e.g., Liebmann, 1927), we finally run an experiment using low-pass filtered images (blurred edges).

Methods

Subjects

Nine subjects (6 females, 3 males) of Experiment 2 participated in this experiment. The age ranged between 20 and 38 years. Subjects from the former experiments were taken to allow for a comparison between high contrast and blurred edges).

Stimuli

The same stimuli as in Experiment 1 were used in this experiment. Stimuli were blurred with a discrete approximation of a Gaussian filter (binominal filter with an order of 20). The order of the binomial filter was chosen to reduce high spatial frequency components above 4cyc/deg. The chosen filter reduces the amplitude at 4cyc/deg to 2.5% of the mean value (0 frequency).

Procedure

The general procedure for this experiment was identical to that of Experiment 1. Stimuli were presented at photometric isoluminance, because the previous two experiments did not reveal any differences due to measuring with subjective isoluminance.

Results

Results for Experiment 4 are shown in Figure 7. Conditions again highly correlated with each other and were significant. The lowest significant correlation was obtained in the Hering illusion for isoluminance L−M vs. isoluminance S−(L+M) r = .674 and p = .046; whereas the highest correlation was obtained in the Ponzo illusion for isoluminance L−M vs. isoluminance S−(L+M) r = .993 and p < .001. All other significant correlations were in between these two. Three conditions showed moderate but insignificant correlations (r > .580, p < .010; Ebbinghaus luminance vs. isoluminance L−M, isoluminance L−M vs. isoluminance S−(L+M); Hering low luminance vs. isoluminance L−M). Some conditions showed low correlations and were far from any significance (r < .580, p > .10; Ebbinghaus luminance vs. low luminance, luminance vs. isoluminance S−(L+M), low luminance vs. isoluminance L−M; Hering luminance vs. low luminance, low luminance vs. isoluminance S−(L+M); and all combinations but that for luminance vs. low luminance in the Zöllner illusion.

An ANOVA for repeated measures revealed only few significant differences. Again, these differences were of minor interest, since the illusion strengths were in all cases significantly different from zero.

An ANOVA comparing the mean illusory effects in Experiment 1 (Figure 3) with those in Experiment 4 (Figure 7) did not reveal any major differences, just small effects for the Hering and Zöllner illusion.

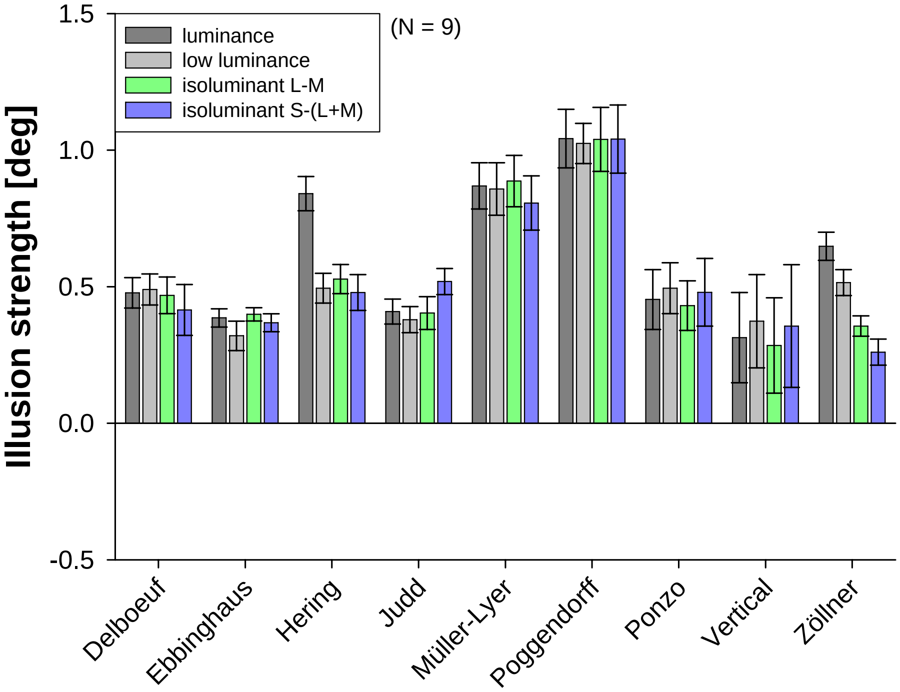


Figure 7: Results for the low-pass filtered geometric-optical illusions at luminance contrast and photometric isoluminance (N=9). Error bars denote the SEM. Illusory effects occur with similar strength under all conditions.

Discussion

All nine subjects were deceived by the blurred, low-pass filtered versions of all nine illusions. Again, subjects were very consistent within and across conditions. Repeatedly it has been argued that line illusions are diminished or even eliminated when the lines are blurred (e.g., Morgan, 1999). This was not the case in the present experiment for any of stimulus patterns or subjects. Instead, blurring did not reduce the illusions. The filtering was strong enough to prevent chromatic aberration. Results were similar to those obtained in the previous experiments. Thus, we conclude that chromatic aberration does not affect these illusions and their corresponding illusory strength under conditions of isoluminance. Furthermore, high contrast borders are not necessary for geometric-optical illusions to occur. Even with shaded areas abutting the lines (e.g., in the Müller-Lyer illusions and the Judd illusion), the length misperception is not reduced (Zanker & Abdullah, 2004). A comparison of Experiment 1 and Experiment 4 revealed some significant reduction or enhancement of illusion strength (for Hering and Zöllner), but they were unsystematically in nature. Therefore, we conclude that there are no differences between conditions of photometric isoluminance and blurred stimuli at photometric isoluminance. This might suggest that the visual system is invariant, when processing such stimulus material under different conditions.

General Discussion and Conclusion

It has been claimed that geometric-optical illusions are mediated by the magnocellular system and break down if only the parvocellular system is stimulated (Livingstone & Hubel, 1987, 1988; Hubel & Livingstone, 1987). This would make sense if there was a totally independent processing of different features (e.g. color, luminance, form) by the anatomical different pathways and a strict separation between the magnocellular pathway/dorsal stream and the parvocellular pathway/ventral stream. However, numerous studies have demonstrated much more pronounced interactions between these different pathways (Felleman & Van Essen, 1991, Sincich & Horton, 2005, Lamme & Roelfsema, 2000). Johnson et al. (2001) reported that many neurons in V1 of the macaque monkey respond robustly to both equiluminant color and luminance modulation (color-luminance cells). Few neurons prefer only luminance (luminance cells) or color (color cells). The fact that many cells in primary visual cortex are color and luminance sensitive also challenges a clear distinction of independent processing of visual features. By now it is also known that many features, such as color and form, are not processed independently but rather by the same neurons in V1 and V2 (Friedman, et al., 2003). Furthermore, it has recently been shown that for most functions the color vision system is just as efficient as the luminance system (Krauskopf, 1999). Gegenfurtner (2003) points out why previous studies (e.g., Livingstone & Hubel, 1987) obtained different results. Isoluminant stimuli are rare in our natural environment. The magno system sems to be the evolutionary older and more primitive processing system (Hubel, Wiesel & LeVay, 1977; Kaas, Huerta, Weber & Harting, 1978; Guillery, 1979; Lennie, 1980), whereas the parvo system is evolutionary younger and more elaborate. The question to be asked at this stage is then, what does the younger parvo system add to the older magno system? A widely accepted answer to this question is that detecting ripe red fruits against green foliage is improved with the color-opponent channel (Mollon & Jordan, 1988). But color vision also seems to have more general roles, such as improving the speed at which objects can be recognized or improving visual memory for scenes (Gegenfurtner & Rieger, 2000; Wichmann, Sharpe & Gegenfurtner, 2002).

Li and Guo (1995) investigated four geometric-optical illusions (Zöllner, Müller-Lyer, Ponzo, and Delboeuf), illusory contours (Kaniza) and depth in random-dot stereograms (Julesz) under conditions of isoluminance along the L−M axis. For the geometric-optical illusions under conditions of isoluminance with chromaticity contrast and heteroluminance without color contrast, they found equal illusion strengths under both conditions in all four geometric patterns. They concluded that their results suggest geometric-optical illusions of parallelness (orientation), length and size being mediated by the parvocellular system. In their line of argumentation stereoscopic depth is mediated both by the magnocellular and the parvocellular system, and illusory contours are mediated solely by the magnocellular system (since they did not find illusory contours in isoluminant stimuli). This also has to be investigated more systematically with more illusions and more luminance and isoluminance condition in future studies.

Some authors, including Livingstone and Hubel (1987), have suggested that geometric-optical illusions have strong connections to depth perception (e.g. Gregory, 1968b, 1997b). This has also been reported recently by Spehar and Gillam (2002) for the Poggendorff illusion stimuli in which the illusory strength is reduced to modal completion resulting from lower luminance contrasts. Turnbull, Driver and McCarthy (2004) have investigated depth perception in a patient with visual agnosia (damage in the occipito-temporal cortex; ventral stream). His ability of object recognition and depth perception was greatly impaired, but, surprisingly he was not deceived by classical geometric-optical illusions, such as the Müller-Lyer and Ponzo illusion. Our results could support the results of the patient study, since our subjects were still deceived at conditions of color contrast without luminance contrast. That the parvocellular system mediates the Zöllner illusion has also been reported recently (Puts et al., 2004). To make this issue even more complex, it has been reported that a patient with left hemispatial neglect due to a large lesion of posterior association cortex largely sparing the dorsolateral prefrontal cortex is still deceived by the Judd illusion and shows length misperception, even though she does not perceive stimulus features on the left side consciously (Ro & Rafal, 1996). The authors claim that even neglected features are processed, meaning pre-attentive processing of location and shape information. This speaks for early or even sub-conscious processing of geometric-optical illusions reducing the probability of top-down influences.

Subjects in our four experiments were very consistent within and across conditions. The fact that there were very high correlations between the conditions substantiates the hyphothesis that the illusory phenomena tested here are mediated by the same neural mechanisms and not – as has been suggested before – by separate processing mechanisms. This indicates that our visual system is likely to be invariant, when processing such stimuli. Thus, it is not critical, whether these illusions are investigated under conditions of high luminance contrast, low luminance contrast, photometric or subjective isoluminance (or somewhere between these two values), or at photometric isoluminance in low-pass filtered stimuli.

It has frequently been reported that some geometric-optical illusions such as the Zöllner illusion (Judd and Courten, 1905) or the Müller-Lyer illusion (Judd, 1902; Köhler and Fishback, 1950a and 1950b, Schiano and Jordan, 1990) become greatly reduced or even vanish with repeated exposure. Our data challenge these findings, since all subjects participating in more than just one of the experiments did not show any attenuation of illusory effects. Such a reduction could be due to improper instruction and top-down processes (e.g. knowledge). In a model by Gregory (1997a, 1997b), he refers to 'top-down' processes including conceptual knowledge and perceptual knowledge, and ‘sideways’ representing rules being crucial for perceptual illusions. In addition, it has been pointed out that the lateral geniculate nucleus (LGN) receives more feedback connections from the cortex than bottom-up connections from the eyes (Rockland & Pandya, 1979; van Essen, 1985; Felleman & van Essen, 1991; Sillito, 1995). Therefore, knowledge should not be totally neglected when making inferences from perceptual illusions to the visual system, even though we already mentioned early sub-conscious processing of illusions in a patient which could reduce top-down influences. We have to be aware that top-down influences could not only be crucial in eliciting the illusory effects but can also be used (consciously or unconsciously) to abolish the illusory effect. For example, if an observer knows that he is deceived in a special manner then he could compensate for this in the opposite direction. Therefore, proper instruction is critical and could explain why some researchers find a reduction with repeated exposition while others do not.

Other illusions, e.g. color illusions like the “Watercolor effect” (Pinna, Brelstaff & Spillmann, 2001) and motion illusions like the “Enigma illusion” (Leviant, 1996, Hamburger, in press) have been shown to occur under approximated isoluminance or isoluminance as well (Devinck, Delahunt, Hardy, Spillmann & Werner, 2005; Kumar & Glaser, 2006). In future experiments we want to investigate other types of visual illusions such as color illusions, e.g. the Watercolor effect; lightness illusions, e.g. the Hermann grid illusion (Comerford, Bodkin & Thorn, 2004; Comerford, Thorn & Bodkin, 2005; Comerford, Thorn & Garland, 2006; Hamburger & Shapiro, submitted); and motion illusions like the Enigma illusion.

The present study shows that geometric-optical illusions under isoluminance are as strong as when presented at luminance contrast, supporting the joint processing of oriented color and luminance contrast in early visual areas. Furthermore, the results show that our conscious percept is deceived similarly for both isoluminance and luminance conditions, suggesting that the joint processing for chromatic and luminance defined contours extends well beyond early visual areas.

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Chapter 6 –

Weaves and the Hermann grid[6]

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[6] This work is currently under review in a slightly different form: Hamburger, K., & Shapiro, A.G. (under review). Weaves and the Hermann Grid. *Perception*.

In a classic Hermann grid display, faint and ephemeral smudges are produced at the intersections of a white grid superimposed on a black background (or vice versa). Here, we introduce 'weaves', a pattern that consists of intertwined light and dark bars. We examine smudges that arise at intersections for which the vertical and horizontal bars have different luminance levels (luminance-defined weaves) and smudges that arise at intersections for which the bars have the same luminance levels (equiluminant weaves). Hermann grids are a special case of equiluminant weaves. For both luminance-defined and equiluminant weaves, the smudges occur only when the background is brighter or darker than the bars. We demonstrate that 1) The smudges occur at every other intersection for luminance-defined weaves and at every intersection for equiluminant weaves; 2) for luminance-defined weaves, the smudges are present in the high-spatial frequency components of the pattern but not in low spatial frequency components; 3) unlike the smudges for Hermann grids and equiluminant weaves, the smudges for luminance-defined weaves are not disrupted by jaggy bars, wavy bars, thick bars, or orientation changes; and 4) unlike the smudges for Hermann grids and equiluminant weaves, the smudges for luminance-defined weaves occur foveally and can be created with contrast variation (contrast-contrast weaves). One possible framework for considering these effects is that, as suggested in the theory of Schiller and Carvey (2005), the smudges arise out of the co-activation of ON and OFF simple cells with colour-selective simple cells—except that the colour selective cells represent both hue and achromatic sensations. We also suggest another possibility in which the smudges arise from a bi-product of lightness interpolation mechanisms that builds a 1st-order representation from 2nd-order information.

Introduction

A white grid superimposed on a black background (or vice versa) produces faint and ephemeral smudges at each of the grid's intersections. The phenomena are referred to as Hermann's grid after the physiologist Ludimar Hermann, who made note of them in 1870 (Hermann, 1870), although an observation of the phenomena had been made by the Rev. W. Selwyn and reported by David Brewster twenty-six years earlier (Wade, 2005; Brewster, 1844). Spillmann & Levine (1971) created a variation of the Hermann grid, in which dark bars are presented in front or behind white bars. The Spillmann and Levine display consisted of paper cut-outs of bars of varying luminance placed over a light and dark background. We have redrawn a version of the Spillmann and Levine display in Figure 1; notice that on a white background the smudges appear at intersections where light goes over dark (i.e., at intersections in the lower right triangle of panel A), and on a dark background, the smudges appear only at intersections where dark goes over light (i.e., at intersections in the upper left triangle of panel B).

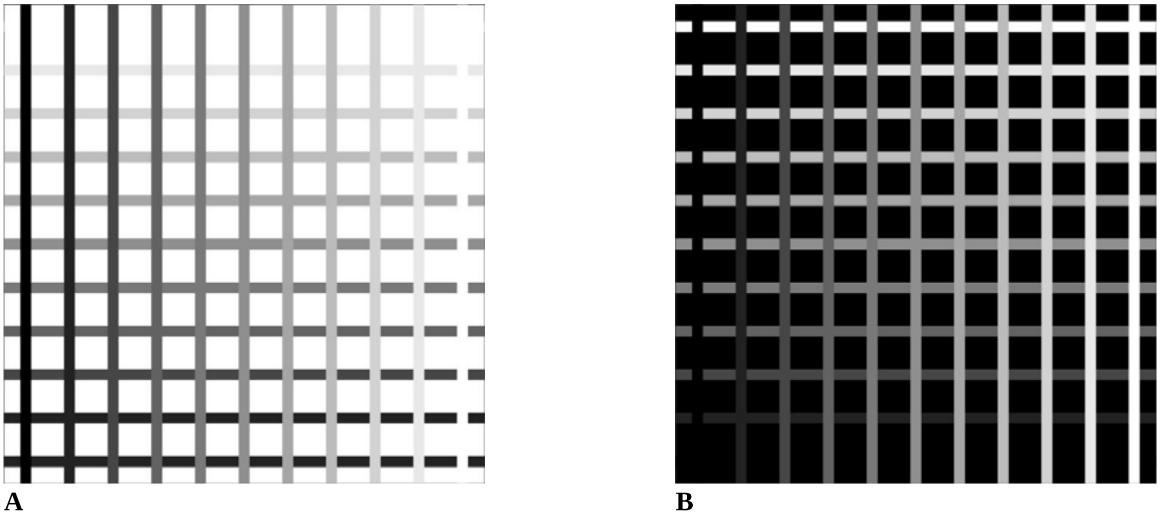


Figure 1: A version of the Spillmann and Levine (1971) display showing vertical bars of varying luminance levels placed on top of the horizontal bars of varying luminance levels. (A) the bars are placed on a white background; (B) the bars are placed on a dark background. On a white background, the perceptual smudges appear at intersections where light goes over dark (i.e., at intersections in the lower right triangle), and on dark background, the smudges appear only at intersections where dark goes over light (i.e., at intersections in the upper left triangle).

The Hermann and Spillmann displays have been important for visual science because they indicate interactions that arise across spatial regions. The classic explanation of the smudges is based on the response of ganglion cells with centre-surround receptive fields (Baumgartner, 1960); however, there have been a number of challenges to this model based on the ease of disrupting the appearance of the smudges by changing the orientation of the grid (Geier, Sera & Bernath, 2004), modifying the structure of the bars (Spillmann, 1994), or breaking up the linearity of the grid (see Schiller & Carvey, 2005 for review). A recent theory, proposed by Schiller and Carvey (2005), suggests that the smudges arise from responses of directionally tuned ON-selective- and OFF-selective-oriented simple cells (S1 cells); this model can account for a wide range of Hermann grid variations including a variety of Spillmann-and-Levine-like patterns.

We became interested in these phenomena as a method for studying the interaction between colour and luminance (see Shapiro, D’Antona, Charles, Belano, Smith & Shear-Heyman, 2004a; Shapiro, D’Antona, Smith, Belano & Charles, 2004b). As part of this investigation, we developed a Hermann grid-like illusion in which light and dark bars intertwine so that the light bars cross in front of the dark bars at some intersections and behind the dark bars at others; we refer to these patterns as ‘weaves’. As in the Spillmann and Levine display, the smudges occur when the bars that have a luminance level closer to that of the background cross in front of the other bars. For instance, on a white background, light smudges occur only at intersections for which the light bars cross *in front of* the dark bars (Figure 2A top); on a black background, dark smudges occur only at intersections for which the light bars cross *behind* the dark bars (Figure 2A bottom). Figure 2B shows the weaves pattern against a gradient background: the smudges do not occur when the background luminance is somewhere between the luminance values of the grid lines. We have also included a supplementary movie that shows how the smudges dynamically shift from one intersection to another as the background luminance modulates from light to dark (supplement 1).

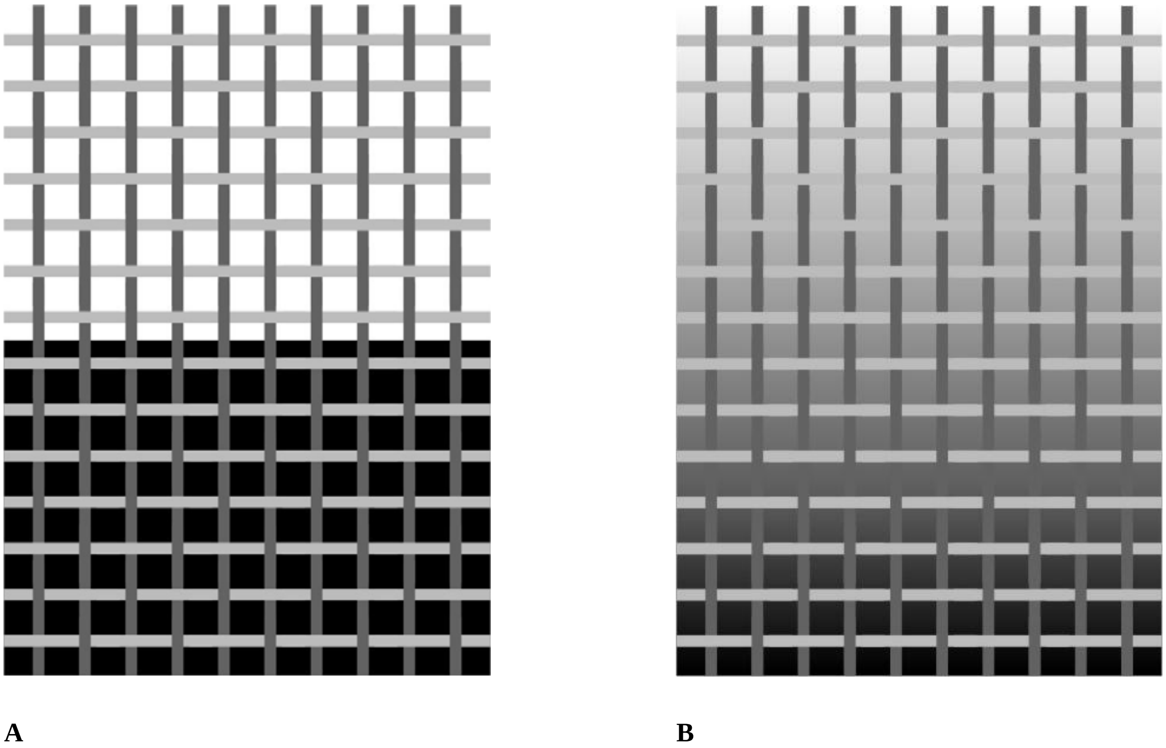


Figure 2: Demonstration of luminance-defined weaves in which light and dark bars are intertwined. (A) The weaves are placed on a white and black background. A change in perceived lightness on the intersections (‘smudges’) occurs, where one bar crosses in front of the other. On a white background smudges occur on white-on-top intersections on a black background smudges occur on black-on-top backgrounds. (B) The weaves are placed on a luminance gradient. Smudges are not perceived if the background luminance is between the luminance levels of the white and black bars.

In this paper, we demonstrate some curious phenomena that indicate that the smudges that arise from weaves (and hence, from the Spillmann-and-Levine type of grids) may be fundamentally different from the smudges that arise from the Hermann grid. We examine the smudges that arise at intersections for which the vertical and horizontal bars have different luminance levels (luminance-defined weaves) and smudges that arise at intersections for which the bars have the same luminance levels (equiluminant weaves). Hermann grids are a special case of equiluminant weaves since the horizontal and vertical bars that make up the grid are always of the same colour (i.e., all white or all black). Both luminance-defined and equiluminant weaves produce smudges only when the background is brighter or darker than the bars. Luminance-defined weaves differ from Hermann grids in the following ways: 1) luminance-defined weaves produce smudges at every other intersection, and equiluminant weaves create smudges at all intersections; 2) the information required to create the weaves' smudges is present in the high-spatial-frequency components of the pattern but not in low-spatial-frequency components; 3) jags in the bars do not disrupt smudges in weaves; 4) the smudges for the weaves occur foveally and for thick bars; 5) smudges for weaves are not as disrupted by orientation changes; 6) weave smudges can be created with contrast variation (contrast-contrast weaves); and 7) weave smudges do not vanish if the bars are wavy and non-orthogonal.

We discuss two intriguing and not necessarily contradictory theories concerning the smudges that arise in the equiluminant weaves. The first is that Schiller and Carvey are basically correct in proposing that coloured smudges arise out of the co-activation of ON and OFF simple cells with colour-selective simple cells—*except that the colour-selective cells encode both hue and achromatic sensations*. The other theory is that weaves (grids) are a product of a more general lightness interpolation mechanism, such as that suggested by Ioannides, Johnston and Griffin (2006), in which a lightness map is built up from a contrast response. In this view, the smudges are only illusory if we have a limited view of the physical stimulus; any neural system that encodes the high-spatial frequency information (such as a contrast system) should also encode the smudges.

Weaves

An examination of chromatic weaves

We originally designed weaves as a method for trying to dissect the physiological interaction of colour and luminance information; we placed weave patterns against a variety of chromatic and luminance backgrounds. The main phenomena are summarized in Figure 3. In the top panels (Figure 3A and B), the horizontal and vertical bars are equiluminant (or as close to equiluminant as variations in printing and display technologies will allow). In the bottom panels (Figure 3C and D) the horizontal bars are brighter than the vertical bars.

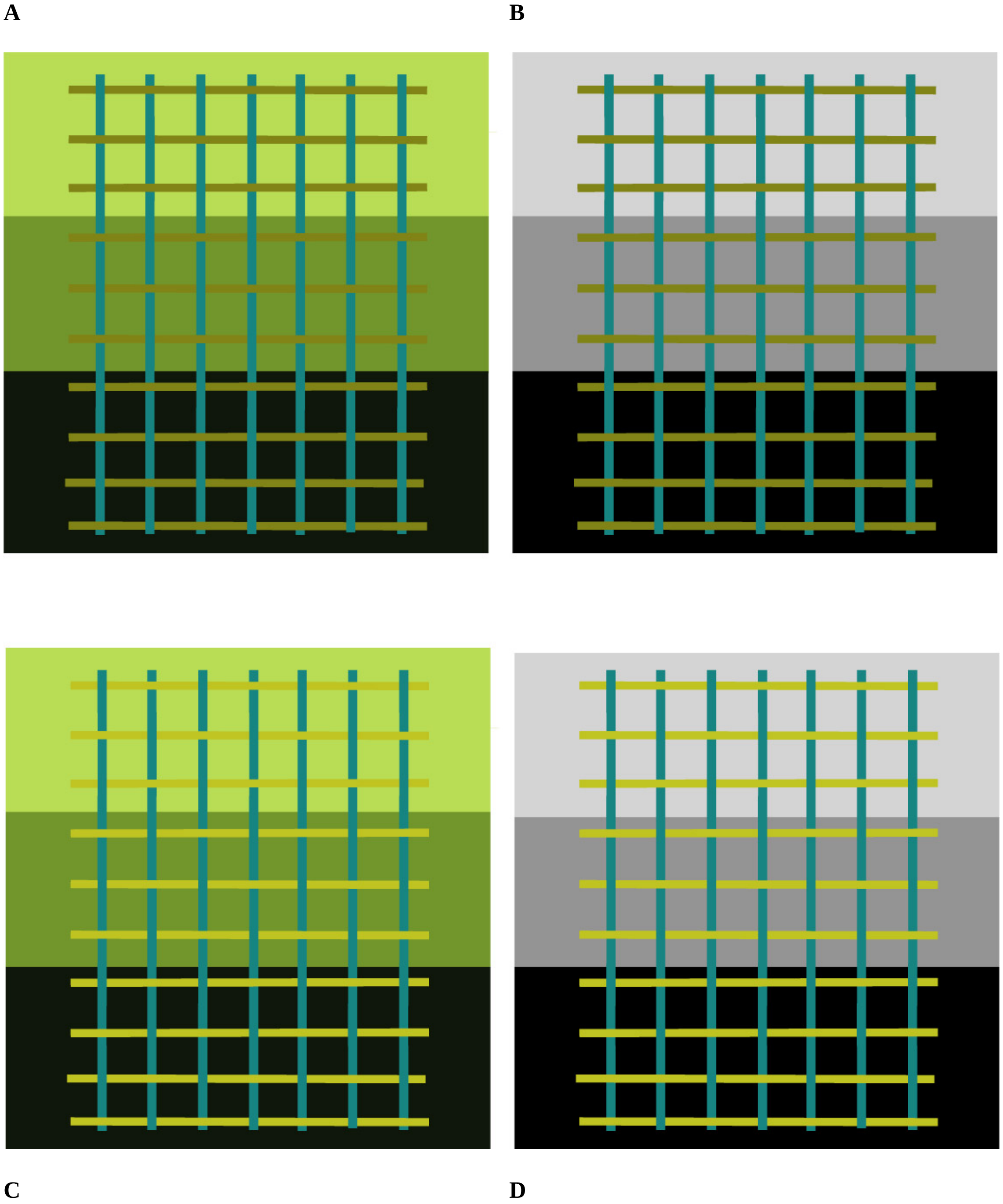


Figure 3: Coloured weaves. (A) and (B) show equiluminant weaves in which the horizontal and vertical bars have nearly the same luminance levels. The weaves are placed on coloured backgrounds of varying luminance or on achromatic backgrounds of varying luminance levels. In the equiluminant weaves the smudges occur at every intersection for both light and dark backgrounds, but there are no smudges for the mid-level backgrounds. (C) and (D) show luminance-defined weaves in which the vertical bars are darker than the horizontal bars. The weaves are placed on the same coloured and achromatic backgrounds as A and B. The smudges follow the same rules as described for the achromatic weaves (see Figure 2).

There are three important phenomena associated with coloured weaves. First, coloured smudges occur only when the bars are placed against a light or dark background, but not when the bars are placed against a mid-level background. Second, when the horizontal and vertical bars are equiluminant, the coloured smudges occur at every intersection (just like Hermann grids), but when they differ in luminance, the smudges occur at every other intersection (just like the weaves). Third, the luminance contrast alone is sufficient to produce the smudges on equiluminant chromatic bars (i.e., the chromatic content of the background does not seem to be important).

We have included an interactive demonstration that allows the user to adjust the colour of the horizontal bars, the vertical bars and the background. In supplement 2, the user can specify the colour values in an RGB space. Simple exploration shows that the appearance of double smudges occurs only when the bars are of close to equal luminance and are placed against a background that is brighter or darker than the bars. Similar types of exploration can be made in other colour spaces, such as the DKL colour space (Derrington, Krauskopf & Lennie, 1984).

We have shown that smudges are visible when the equiluminant bars are placed against luminance backgrounds. It has been documented previously that Hermann grids are minimally visible when the bars and backgrounds are all of the same luminance (Oehler & Spillmann, 1981; Schiller & Carvey, 2005). Comerford and colleagues (Comerford, Bodkon & Thorn, 2004; Comerford, Thorn & Bodkin, 2005; Comerford, Thorn & Garland 2006) reported chromatic Hermann grids in some circumstances; it seems likely to us that the conditions that produced these effects occurred when the background had different luminance levels from the bars.

As seen in the interactive demonstration, the chromatic weaves can be used as a measure of equiluminance. The observer’s task is to state where the smudges appear at every intersection or at every other intersection; when the smudges are at every intersection, the vertical and horizontal bars are equiluminant. A more complete empirical examination of chromatic weaves is to be developed in another paper. The intent of this paper is to examine some of the perceptual phenomena associated with weaves and compare them with the Hermann grid phenomena.

The smudges in weaves are contained in the high-spatial-frequency information but not in the low-spatial-frequency information

In this section we examine the effects of spatially filtering the weaves and Hermann grid patterns. In Figure 4, the luminance-based weave (panel A) summarises the main points made in the introduction: against a light background the smudges occur when the light bars are in front of the dark bars; against a gray background no smudges are present; and against a dark background the smudges are present when the light bars go behind the dark bars. Panel B shows a Hermann grid, white bars against a dark background, and panel C shows a Hermann grid, dark bars against a white background. These are typical Hermann grid patterns; the smudges are illusory and appear at every intersection.

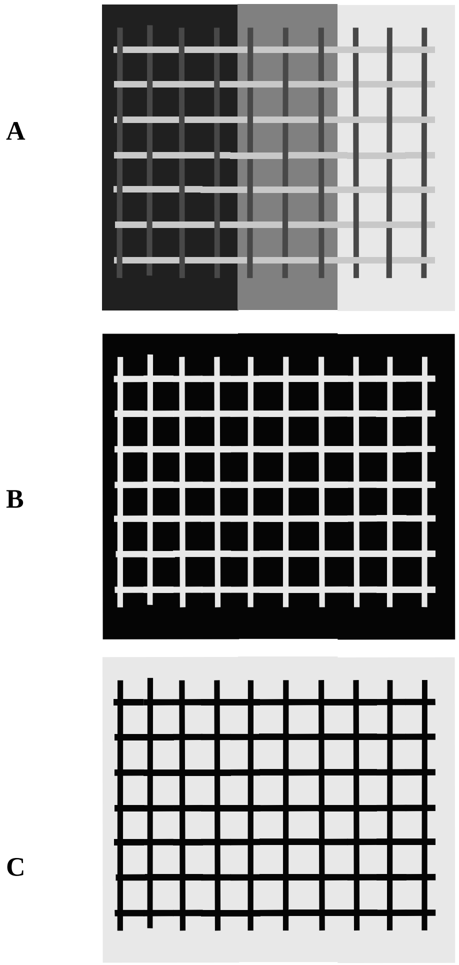


Figure 4: Achromatic weave with three different background luminance levels (A). Classical Hermann grids (B and C).

The high-pass filtered versions are shown in Figure 5. The filtered images were created with the Adobe Photoshop high-pass filter (set to 4.1). For both weaves and grids, the filtered version contains physical changes that correspond to the occurrence of the perceptual smudges in the unfiltered image. For the weaves there are actual luminance increases against the white background when the white bar is in front of the dark bar, and actual luminance decreases against a dark background when the white bar goes behind the dark bar. For the Hermann grid, there are actual luminance decreases at all intersections. The smudges are only illusory if we ignore their presence in the high-spatial frequency information (i.e., if we think of the image as composed of point sources). Any model capable of extracting high-spatial frequency information, such as Baumgartner's center-surround model or the Schiller and Carey model based on V1 simple cells, should also predict changes at the appropriate intersections. The low-pass images were created with the Adobe Photoshop Gaussian Blur filter (set to a radius of 5.0 pixels) and are shown in Figure 6. The weaves Figure (A) does not contain physical changes that can be correlated with the appearance of the smudges. In fact, the luminance values at the intersection go in the opposite direction of the perception; i.e., against a white background, the luminance value of the white-overlap intersections decreases relative to the white bars, and against a dark background, the luminance value of the dark-overlap intersections increases relative to the dark bars (these changes were assessed by checking the values of the pixels–for white backgrounds, the values of the white bars dropped from 220 on the "streets" to 176 at the intersections, and for dark backgrounds, the values of the dark bars increased from 62 on the streets to 94 at the intersection).

Unlike smudges in the Hermann grid, the smudges for the luminance defined-weaves do not appear to be present in the low-spatial frequency information. In the low-pass Hermann grids, the physical values at the intersections go in the same direction as the perception; i.e., against the dark background, the luminance of the white bars increases at the intersections (pixel values go from about 134 along the streets to 200 at the intersections), and against a light background, the luminance of the dark bars decreases at the intersection (64 on the streets to 28 at the intersections). The low-pass Hermann grids (panels B and C) create scintillating patterns (Schrauf, Lingelbach &

Wist, 1997) that are not found in the weaves. This pattern is similar to the observations by Bergen (1985), who showed that blurring a Hermann grid creates intersections that appear to be brighter (more lustrous) than the horizontal and vertical bars.

The Hermann grid and the luminance-defined weaves appear to be similar at high-spatial frequencies (both contain smudges) but not at low-spatial frequencies (the Hermann grid contains smudges, but weaves do not). In the sections below we will show that the weaves are more resilient than the grids. The question becomes whether the greater resilience is due to the absence of low-spatial frequency information in the weaves.

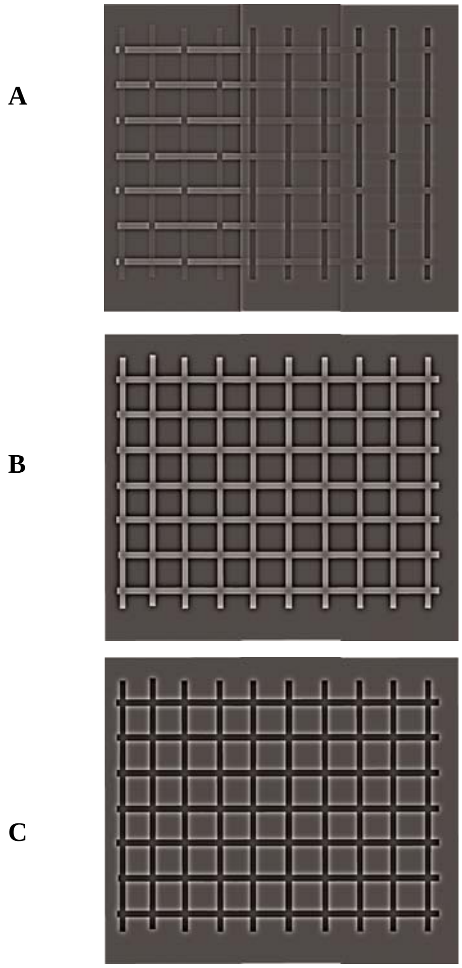


Figure 5: High-pass filtered versions of the images presented in Figure 4 (see text for details).

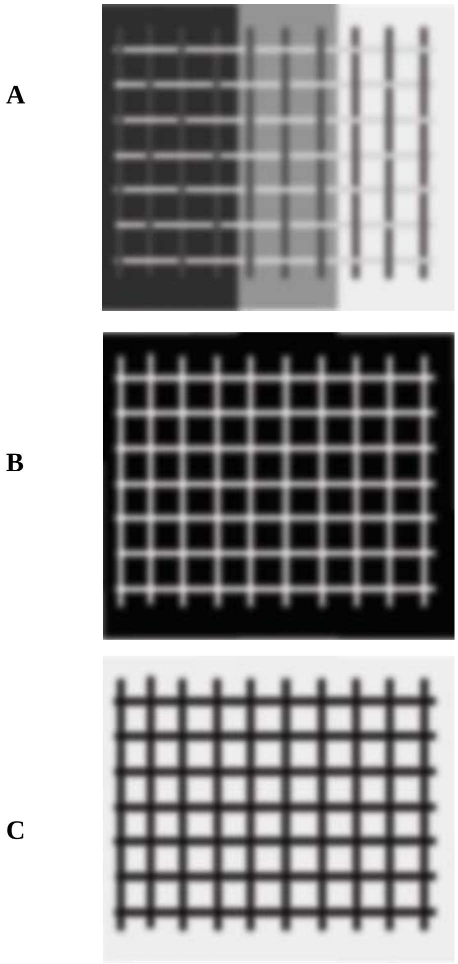


Figure 6: Low-pass filtered versions of the images presented in Figure 4 (see text for details).

Unlike smudges in the Hermann grid, the smudges in the weaves can be seen with foveal fixation and with large bars

One of the main sources of evidence for the Baumgartner (1960) receptive field account of the Hermann grid was that the smudges occur primarily in the visual periphery and depend upon the thicknesses of the vertical and horizontal bars. It has been argued that the Hermann smudges do not occur if intersections and “streets” outgrow the foveal receptive field sizes. In the periphery, perceptive field sizes become larger and therefore can match the size of a receptive field to elicit the effect (Jung & Spillmann, 1970; Spillmann, 1994; Lingelbach & Ehrenstein, 2002, http://www.leinroden.de/304herfold.htm/).

Figure 7 directly compares the effect of bar size in weaves with bar size in the Hermann grid. With thin bars (panel A), smudges in the weaves can be seen when viewed foveally, whereas the smudges for the Hermann grid cannot (panel B; this point was noted by Spillmann & Levine, 1971; Spillmann, 1994; and Schiller & Carvey, 2005 for the contrast Hermann grid; see Figure 1). This effect is even more apparent with wide bars (panels C and D). Smudges are present in the weaves even when viewed foveally (although slightly diminished), but the smudges for the Hermann grid are absent even in the periphery. The information for smudges in the weaves with wide bars is still present following a high-pass filtering of the image as in the previous section. This observation is inconsistent with the classical model, but not inconsistent with a model based on multi-scale V1 simple cells such as that proposed by Schiller and Carvey.

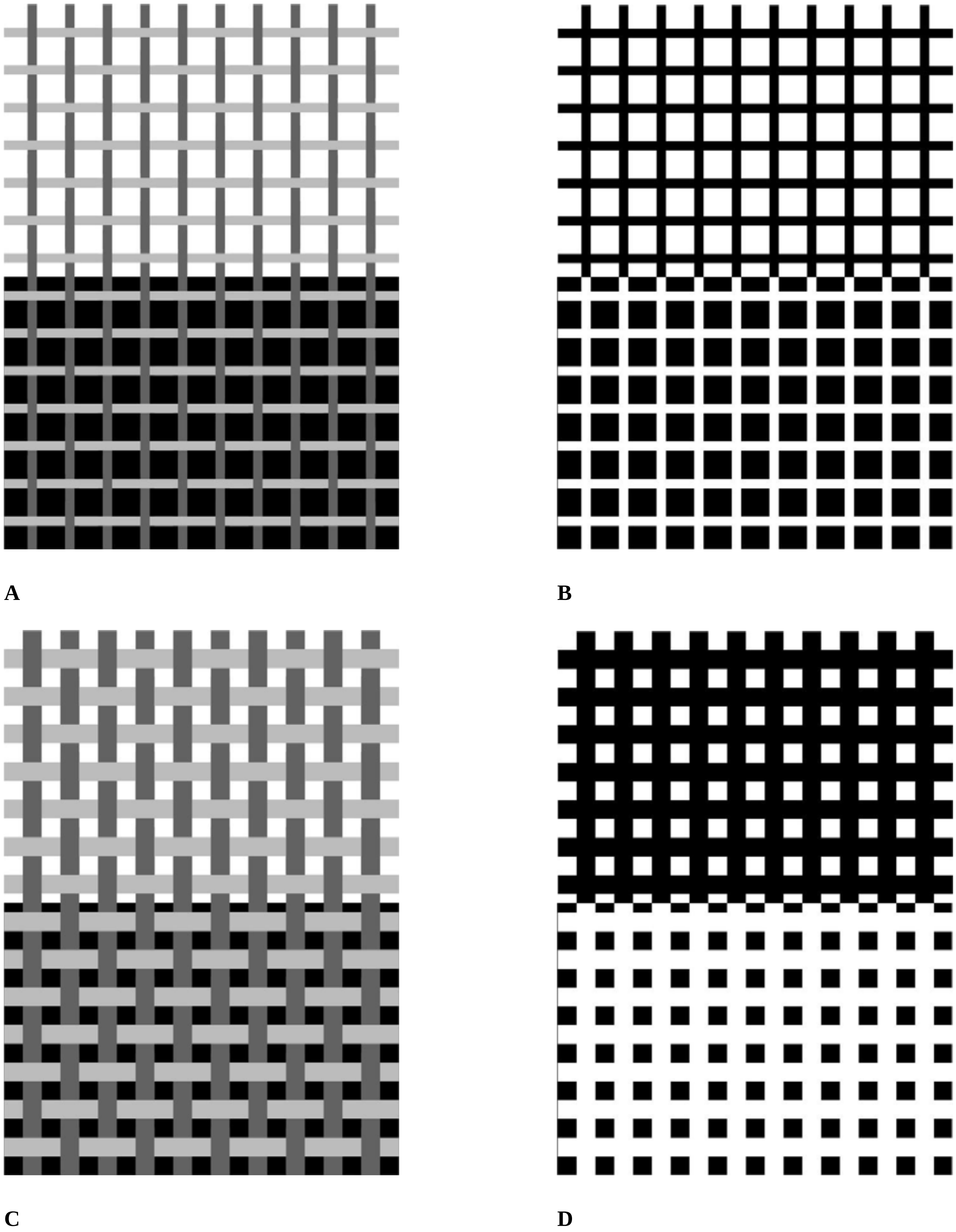


Figure 7: (A) Weaves. (B) Classical Hermann grid. (C) Perceptual smudges are still present with wide bars in the weaves. (D) But they are absent in the Hermann grid. The smudges at the intersections (lighter or darker) are stronger with narrow bars (larger background/surround). The perceptual smudges in the weaves remain with foveal fixation.

Weave-smudges are less sensitive than the Hermann-smudges to line contour changes and shape changes

One recent demonstration against the classical receptive field model is that Hermann smudges can be eliminated by changes in the contour of the lines (either increases in jaggedness, or bumps) leading to the intersections (Geier et al., 2004; Schiller & Carvey, 2005). In a similar type of demonstration, we show that jagged edges only minimally affect the smudges in the weaves (Figure 8A), whereas the same jagged edges eliminate the smudges from the Hermann grid (Figure 8B). The information for smudges in both of these Figures (weaves and Hermann grid) is carried in the high spatial frequency information (Figure 8C and D). It is a puzzle as to why the bumps and jags cause this information to be over-ridden in the Hermann grid but not in the weaves. The scintillating grid effect (which results from low-pass filtering of the Hermann grid) is also sensitive to edge variations (Lingelbach & Ehrenstein, 2004).

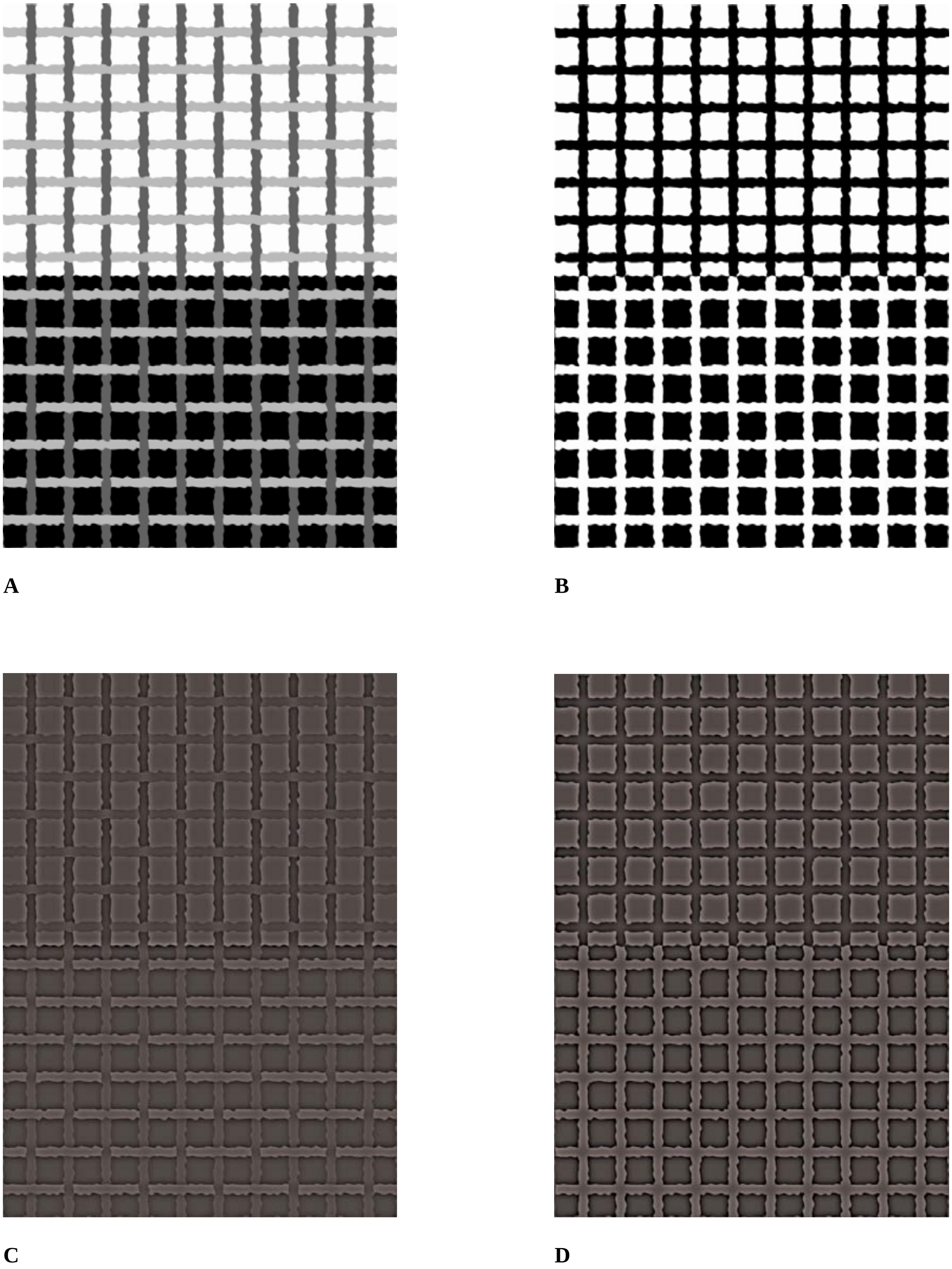
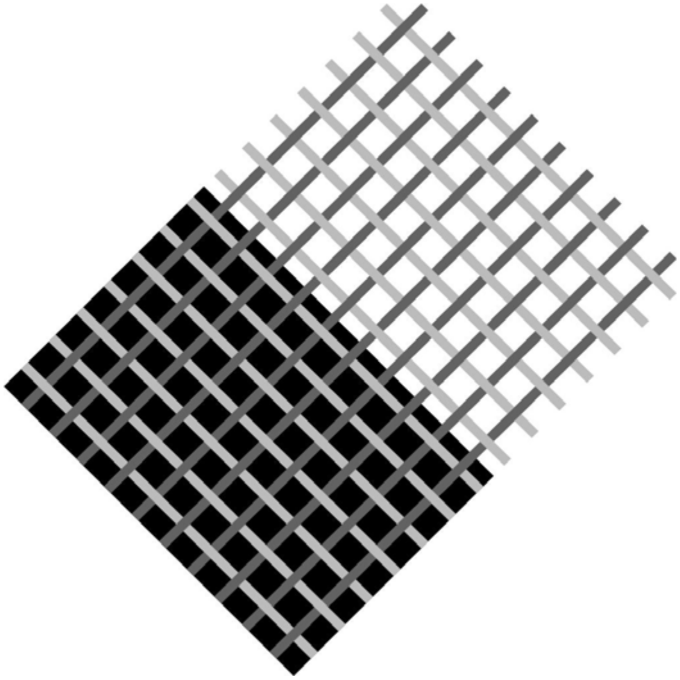


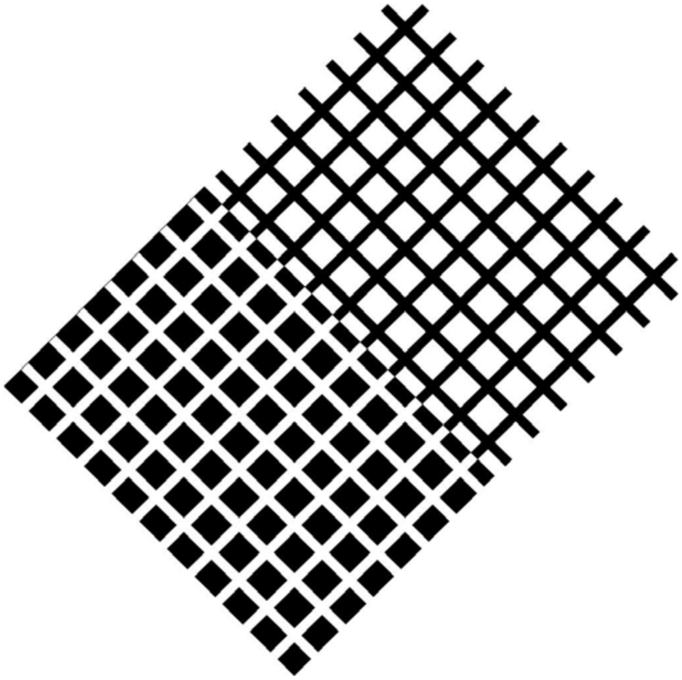
Figure 8: The effects of jagged edges on luminance-defined weaves (A) and Hermann grid (B). Jagged lines do not affect the perceptual smudges in the weaves, but disrupt smudges with the grid. (C and D) High-pass filtered versions of weaves and Hermann grid with jagged bars.

When rotated by 45 deg, the Hermann grid illusion is greatly diminished or absent, whereas the weaves are not

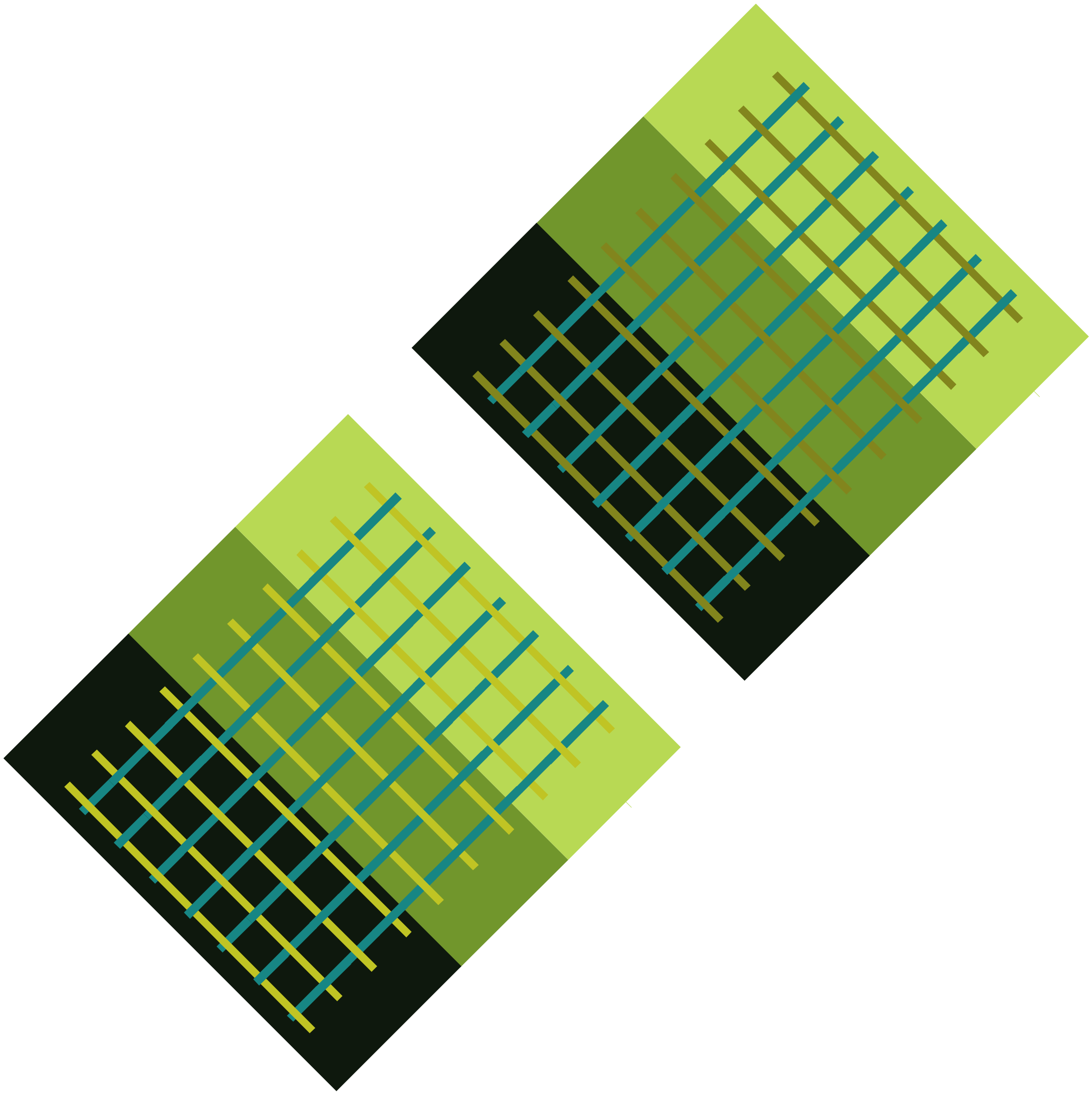
Hermann grid smudges are greatly reduced when the image is rotated by 45 deg (Spillmann, 1971, 1994; Spillmann & Levine, 1971; Levine, Spillmann & Wolfe, 1980; de Lafuente & Ruiz, 2004—see Figure 9B). De Lafuente and Ruiz (2004) measured the size of the illusory effect psychophysically and found a reduction to 1/3 of the original illusory effect when the Hermann grid was rotated by 45 deg. But, consistent with other measurements of tilt effects (Clifford, Spehar, Solomon, Martin & Zaidi, 2003), there exist great inter-observer differences (ranging from 20% to 90% reduction of the illusory effect). The abatement of smudges at oblique angles is one source of evidence for a simple cell account of the Hermann grid (Schiller & Carvey, 2005), the reduction in sensitivity being attributed to the fact that orientation-selective neurons exist in a much higher number for horizontal and vertical representation (DeValois & DeValois, 1988). The weaves, however, are still present and strong when the pattern is rotated by 45 deg (Figure 9A) or to any other angle–even if seen foveally. Figure 9C shows the same comparison for coloured weaves. Tilting equiluminant weaves (top) eliminates the smudges, whereas tilting luminance-defined weaves (bottom) hardly affects the appearance of the smudges.



A



B



C

Figure 9: The effect of rotation on the weaves and grid pattern. (A) When weaves are rotated by 45 deg the perceptual smudges on the intersections are still quite strong, even if observed foveally. (B) Perceptual smudges disappear in the Hermann grid when it is rotated by 45 deg. (C) The same pattern holds for luminance defined and equiluminant coloured weaves.

The smudges appear in contrast-contrast versions of the weaves but not in contrast versions of the Hermann grid

Several classes of illusions have been demonstrated for 2nd-order (i.e., contrast-modulated) stimuli: for instance, for Mach bands (Lu & Sperling 1996), simultaneous contrast (Chubb, Sperling & Solomon, 1989; D'Zmura & Singer 1996, Zaidi 1999), and reverse phi motion (Lu & Sperling 1999). Such stimuli are of interest because they indicate that there are contrast-sensitive systems that can also produce the phenomena. Here, we show that smudges can be generated for 2nd-order weaves; we have not been able to generate smudges for 2nd-order Hermann grids despite our best efforts.

An example of a contrast-contrast weave is shown in Figure 10. The stripes have the same averaged luminance; noise was added to the stripes using the Adobe Photoshop Gaussian noise filter. Panel A (top) shows the effect against a background with low contrast noise; the horizontal bars have medium contrast noise, and the vertical have high contrast noise. Faint smudges appear when horizontal bars go in front of the vertical bars. Panel A (bottom) shows the effect against a background with high contrast noise, the horizontal bars have low contrast, and the vertical have medium contrast. Smudges appear when the horizontal bars go behind the vertical bars. Panel B shows two contrast-contrast Hermann grids; these patterns show no smudges. Identification measurements (do you see smudges at the intersection of the Figures?) showed that five out of eight naïve observers perceived smudges in the top pattern of Figure 10A, and all eight subjects reported smudges at the appropriate intersections for the bottom panel of the Figure. None of the eight subjects reported any smudges in the two Hermann grids (B).

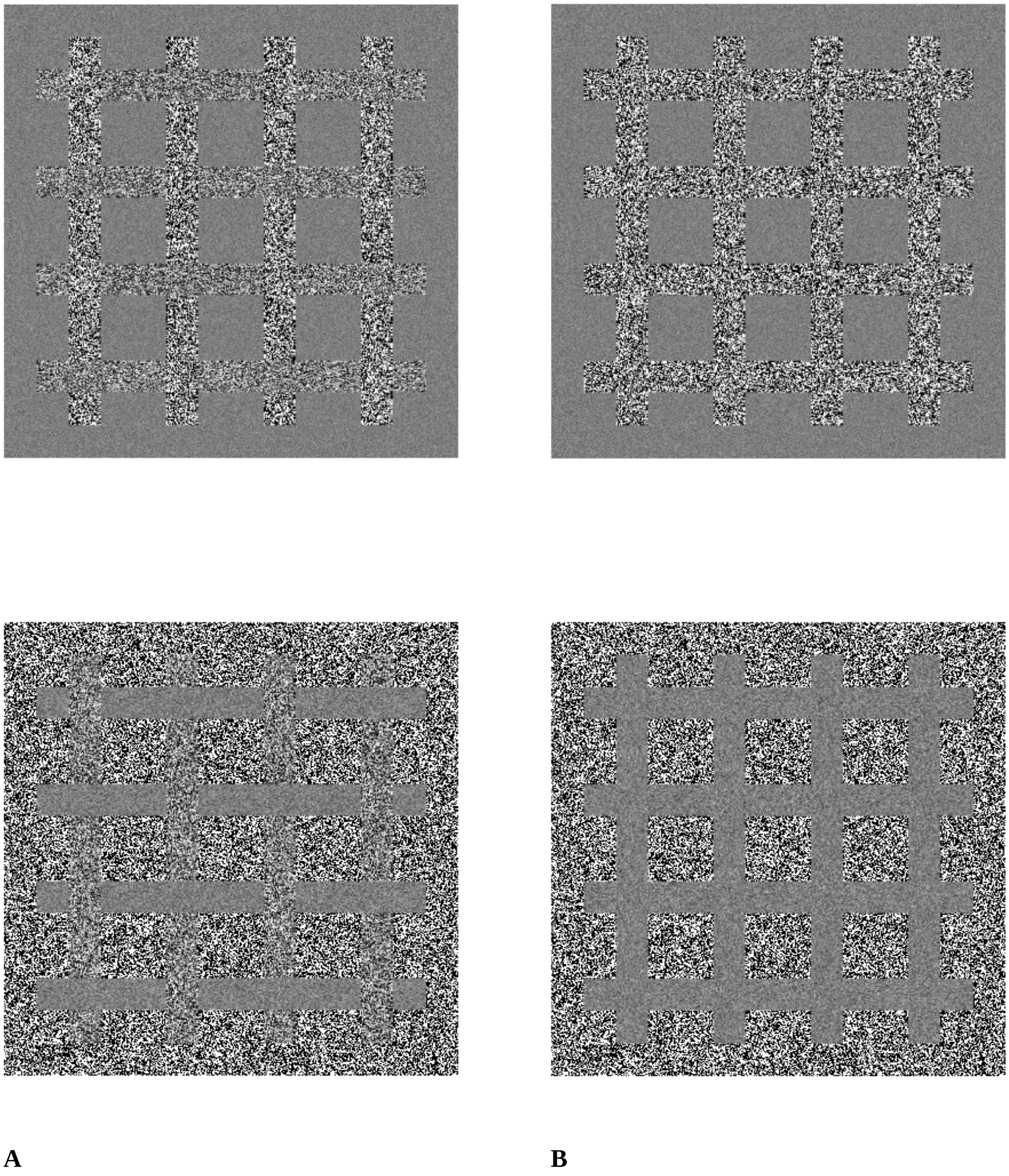


Figure 10: (A) Contrast-contrast weaves. The stripes have the same averaged luminance; noise was added to the stripes using the Adobe Photoshop Gaussian noise filter. The top panel shows the effect against a background with low contrast noise; the horizontal bars have medium contrast noise, and the vertical have high contrast noise. Faint smudges appear when horizontal bars go in front of the vertical bars. The bottom panel shows the effect against a background with high contrast noise, the horizontal bars have low contrast and the vertical bars have medium contrast. Smudges appear when the horizontal bars go behind the vertical bars. (B) Contrast-contrast Hermann grids; these patterns show no smudges.

Hermann grid smudges disappear with wavy bars, whereas weaves smudges persist

Geier et al. (2004) demonstrated that when the bars of a Hermann grid become wavy (they used sinusoidal bars), the perceptual smudges disappear (for an interactive demonstration, see Bach, 2005, http://www.michaelbach.de/ot/lum_herGridCurved/index.html). In Figure 11, we present a weaves pattern with wavy lines (panel A) and a Hermann grid with the same wavy lines (panel B). In the weaves, the perceptual smudges persist, particularly where the intersections are foveated, whereas in the Hermann grid they are greatly diminished or even absent. The difference between the wavy-weaves and the wavy grid is particularly evident when the lines are placed against a temporally modulated background (see supplements 3 and 4). The disappearance of the smudges for the wavy Hermann grid is consistent with the responses of oriented cells (Schiller & Carvey, 2005). However, it is not clear then why the smudges for the luminance-based weaves should persist under such conditions.

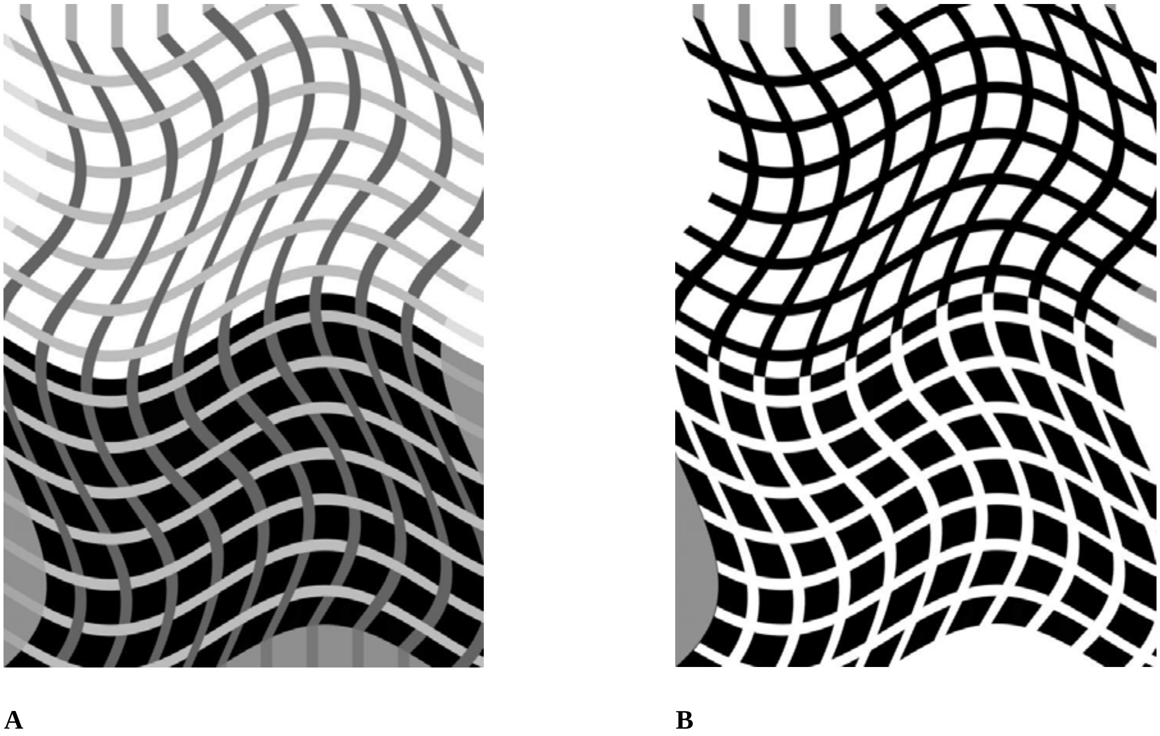


Figure 11: Patterns made with wavy bars. (A) Weaves and (B) Hermann grid. The smudges for the weaves are barely affected by the wavy pattern, but the smudges for the Hermann grid are nearly absent (see also Geier et al., 2004).

Discussion

We have introduced ‘weaves’, a visual display in which horizontal and vertical bars intertwine so that the horizontal bars cross in front of the vertical bars at some intersections and behind the vertical bars at others. In luminance-defined weaves, the horizontal and vertical bars differ in luminance; when placed against a light or dark background, the luminance-defined weaves produce smudges that occur at *every other* intersection. In the equiluminant weaves, the vertical and horizontal bars have the same luminance; when equiluminant weaves are placed against a light or dark background, the smudges occur at *all* intersections. The smudges produced by equiluminant weaves are easily disrupted by stimulus variations, but the smudges produced by luminance-defined weaves are resistant to a wide range of stimulus variations.

The equiluminant weaves clearly demonstrate an interaction between colour and luminance: equiluminant bars create chromatic smudges only in the presence of a bright or dark background. This finding is consistent with the model of Schiller and Carvey (2005), who used chromatic versions of a Spillmann-and-Levine-type display to make a similar point. Schiller and Carvey explain their results in terms of co-activation of colour-selective simple cells with ON- and OFF-oriented simple cells and note that “activating colour selective cells alone is insufficient to produce the smudges.” The interaction of colour and luminance under these conditions is consistent with other models of colour vision (Clifford et al., 2003, Gegenfurtner & Kiper, 2003).

We believe the Schiller and Carvey account of chromatic smudges to be fundamentally correct, but we make two additional observations that have implications for the interpretation of the Hermann grid. First, the classic Hermann grid is a special form of the equiluminant weaves (i.e., the equiluminant weaves and Hermann grid can be considered as part of the same phenomenal class because in both cases the horizontal and vertical bars have the same luminance level, and the intersection of the bars does not produce an internal luminance edge). Equiluminant weaves and Hermann grids have some phenomenal similarities. As can be seen in the interactive demonstration, the smudges appear at every intersection when the vertical and horizontal bars have the same luminance, and appear at every other intersection when the vertical bars are adjusted to be brighter/darker than the horizontal bars. The smudges from both Hermann grids and equiluminant weaves are fragile relative to the smudges produced by the luminance-based weaves. Second, in terms of the Schiller and Carvey model, it could be that the smudges arise when there is a co-activation of ON- and OFF-oriented simple cells with colour-selective cells—except that colour-selective cells encode both hue and achromatic sensations. This means that ON- and OFF-oriented simple cells may not be sufficient to produce a Hermann smudge by themselves, but would always require the additional response of a colour-selective cell—albeit that the cell would signal an achromatic sensation. This idea was most recently addressed by Liu and Wandell (2005), who stated that "candidate cortical regions for colour computation must respond well to signals in all colour dimensions (luminance and chromatic) to contain the full range of colour information." Indeed, fMRI studies show that the ventral occipital lobe (VO) and area V1 encode both luminance and chromatic information (Liu & Wandell, 2005; Kleinschmidt, Lee, Requardt & Frahm, 1996; Engel, Zhang & Wandell, 1997), and this has been shown for area V1 with single cell studies (Johnson, Hawken & Shapley, 2004).

We have also shown that the smudges produced by the luminance-defined weaves are resistant to a wide range of stimulus variations that disrupt smudges in the equiluminant weaves (including the Hermann grid). While we can see how a model based on simple cell responses (such as Schiller & Carvey) can account for the smudges in luminance-defined weaves, it is not immediately clear how such a model by itself would predict the disappearance of the smudges under all these conditions. For example, while an oriented filter model can account for the disappearance of smudges in the Hermann grid following changes in orientation (Figure 11B), spatial scale (Figure 7B), or jags in the bar (Figure 8B), why would the model not predict a disappearance to occur for the luminance-defined weaves (Figures 11A, 7A, and 8A)? The most telling of these examples is shown in Figure 11, which shows that the Hermann smudges disappear when the bars are wavy. The disappearance of the smudges can be accounted for by a simple cell model by showing that oriented detectors cannot integrate over the length of the curvy line. However, the smudges remain when the wavy pattern is produced as a luminance-defined weave. Is it that the simple cells are now able to integrate over the length of the line?

One possible key to resolving this issue concerns the important observation that any visual scene contains information about luminance and contrast, and that the visual system always maintains at least these sources of information always represented (see Whittle, 2003 for a history of this idea in visual science). This is particularly apparent in recent demonstrations that show that the visual system maintains separate responses for 1st- and 2nd-order information (Shapiro et al., 2004a, 2004b; Shapiro, Charles & Shear-Heyman, 2005).

With this idea in mind, we make two speculations concerning the differentiation between luminance-defined and equiluminant weaves—neither of which necessarily contradicts the Schiller and Carvey model. First, it is possible that the smudges are a bi-product of lightness interpolation mechanisms. The visual system encodes contrast (2nd-order) information, and yet we perceive contrast and luminance/chromatic (1st-order) information. This is particularly apparent in demonstrations that show that the visual system maintains separate responses for 1st- and 2nd-order information (Shapiro et al., 2004a, 2004b, 2005). Ioannides et al. (2006) have recently proposed a model in which the 1st-order information is constructed from the response of cortical cells that encode 2nd- (and higher-) order statistics. The smudges for the luminance-defined weaves are resilient because they are present in the 2nd-order response. The smudges for the Hermann grid and equiluminant weaves arise as the visual system constructs and integrates a 1st-order (lightness/chromatic) map from the 2nd-order information. These smudges can be made to disappear because the construction of the 1st-order map is particularly sensitive to stimulus variables. The smudges produced by the luminance-defined weaves and the classical Hermann grid are two different phenomena: the weave smudges arise as a product of simultaneous contrast; the Hermann grid smudges arise only when the bars are equiluminant (i.e., a response that is not processed through standard channels).

Another speculation concerns the spatial frequency information that is available in the display. We have shown that for the luminance-defined weaves the smudges are present in the high-spatial-frequency information, but not in the low-spatial-frequency information. In the Hermann grid, the smudges are present in the high-spatial-frequency information, and a scintillating pattern is present in the low-spatial-frequency information. Therefore, any neural system that encodes the high-spatial frequency information (such as a contrast system) should produce smudges in both equiluminant and luminance-defined weaves. The question becomes, why should the response to high-spatial-frequency information be overwritten for some of the equiluminant weaves (and Hermann grid) manipulations but not for the luminance-defined weaves manipulations? We do not currently have a satisfactory answer to this question. However, it does seem to us that at some stage, the visual responses to low-spatial-frequency information have to be mapped onto the visual responses to high-spatial-frequency information. The mapping process must involve high-order or learned inferences about the environment as well as adaptation to particular stimulus conditions. The demonstrations presented here show that the Hermann grid and the equiluminant weaves lack internal luminance edges at the intersections, whereas standard weaves and overlapping grids (like those of Spillmann and Levine, Figure 1) contain internal luminance edges. It would not be surprising if these internal luminance edges (which would be contained in the high-spatial frequency map) create some of the constraints concerning how the mapping takes place.

Conclusion

This paper concentrates on the phenomenal aspects of luminance-defined and equiluminant weaves and compares them to the phenomenal aspects of the Hermann grid. We have shown that the smudges produced by luminance-defined weaves are more resistant to stimulus variations than are smudges from the equiluminant weaves and the Hermann grid. The results can be interpreted within the Schiller and Carvey theory that the Hermann smudges result from the activity of S1 cells; we make the important addition that the cells that are selective for colour also encode achromatic sensations. The results may also be interpreted within the frameworks of other lightness theories (which are not necessarily inconsistent with Schiller and Carvey) that propose separate visual processes for 1st-order information (luminance/chromaticity) and 2nd-order information (contrast). We plan a larger project in which we make quantitative measurements on weaves in order to test quantitative versions of these theories.

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Chapter 7 –

Grouping by contrast—
figure-ground segregation is not fundamental[7]

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[7] This work is in preparation and will be submitted to Perception in a slightly different form: Shapiro, A.G., & Hamburger, K. (in preparation). Last but not least: Grouping by contrast–figure ground segregation is not fundamental.

A central tenet of Gestalt psychology is that the visual scene can be separated into Figure and Ground. Here we show two illusions that demonstrate that gestalt processes can group spatial contrast information that cuts across the figure and ground separation. The finding suggests that visual processes that organize the visual scene do not necessarily require structural segmentation as their primary input (such as scission into different layers).

Introduction

The term Gestalt refers to the formation of distinct perceptual units that are fundamental to our perceptual construction of the world. Central to the Gestalt approach is the concept of Figure-Ground segregation (Rubin, 1915): a “Figure” possesses a “Thing character” that is spatially cohesive and enclosed (i.e., demarcated by a contour, and filling the entire surface inside its border); a “Ground” possesses a material character that extends behind the figure. Any visual scene can be parsed into Figure and Ground based upon the well-known gestalt grouping factors (symmetry, proximity, closure, common fate, etc.; for review see Spillmann & Ehrenstein, 2004).

Spatial contrast, on the other hand, refers to a comparison of luminance values across space. Spatial contrast can be defined within a Figure, within a Ground, or across the Figure/Ground separation. Contrast that cuts across Figure/Ground separation (or, for that matter, across any scission boundary) can not be considered part of either the Figure perceptual unit or the Ground perceptual unit.

If the Figure/Ground distinction is fundamental to all visual representations, then spatial contrast that cuts across the Figure/Ground border should not follow the fundamental grouping rules. Here we present two new illusions that demonstrate that Gestalt grouping can arise from contrast information that cuts across the Figure/Ground border. Our perception, therefore, does not necessarily depend upon processes that have already organized the scene into Figure and Ground or into distinct surface layers.

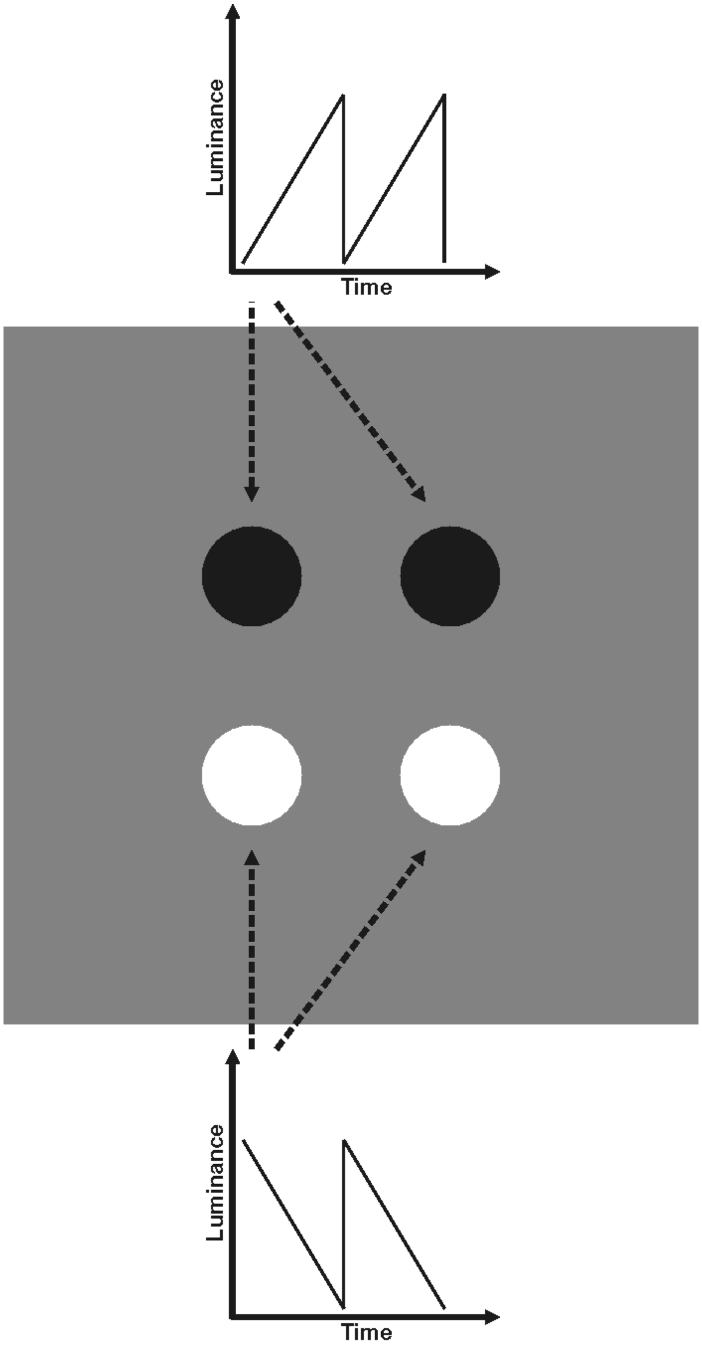
Grouping and the contrast asynchrony

The term *contrast asynchrony* refers to configurations that contain in-phase luminance modulation and out-of-phase contrast information (Shapiro, D’Antona, Charles, Belano, Smith & Shear-Heyman, 2004a; Shapiro, Charles & Shear-Heyman, 2005). For instance, when two identical disks are modulating from light-to-dark and one disk is placed against a light background and the other against a dark background, the disks appear to modulate out of phase with each other (in-line with the contrast signal), even though they are still changing from light to dark at the same time (in-line with the luminance signal). The perception of out-of-phase modulation represents the visual response to the contrast and not visual “salience” because similar effects can be perceived for several types of luminance/chromatic modulations, but not when the disks modulate along equiluminant lines if the surrounds are achromatic (Shapiro, D’Antona, Smith, Belano & Charles, 2004b).

Figure 1 depicts disks whose luminance levels modulate in time with a sawtooth wave form (see supplement 1). Two of the disks modulate from dark-to-light (top row), two of the disks modulate from light-to-dark (bottom row). The disks are shown against either a grey background (panel A) or a split light/dark background (panel B). In the grey background configuration the contrast and luminance information disks in the top row are in phase with each other, and the contrast and luminance information for the disks in the bottom row are in phase with each other. The split light/dark background configuration is a contrast asynchrony: the luminance information for the disks in each row modulates in phase, but the contrast modulation for the disks in each row is out of phase.

The disks group in rows when the background is gray, but group diagonally when the background is split light/dark background (i.e., against a split light/dark background the light-to-dark disk against the white background groups with the dark-to-light disk against a dark background). The demonstration shows that observers tend to group the disks by contrast even though the disks with identical luminance levels get light and dark at the same time.

Some observers note that they can switch between grouping diagonally and grouping by top and bottom, implying that these observers are able to switch between a framework based on contrast information and a framework based on luminance information. The interactive supplement 1b shows a similar effect for a color/luminance display, indicating that observers are responding to the contrast information and not simply to the perceptual salience of the disks.



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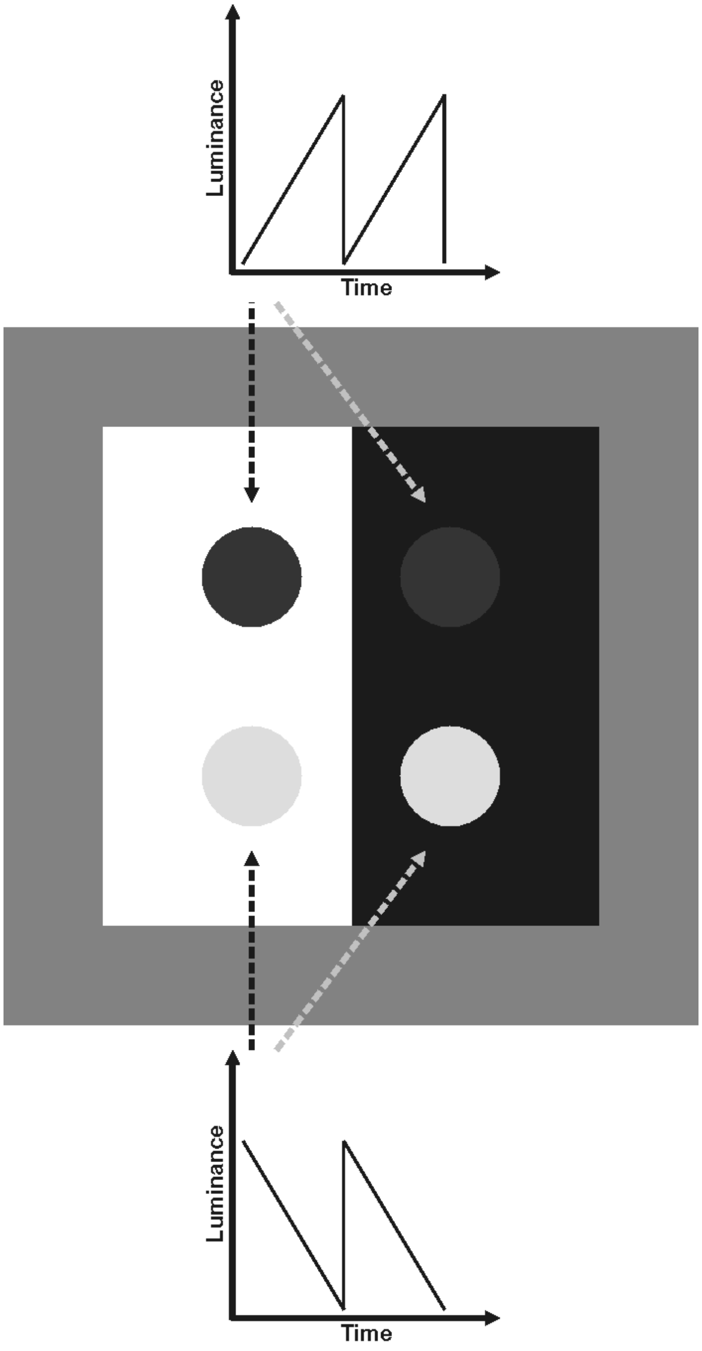


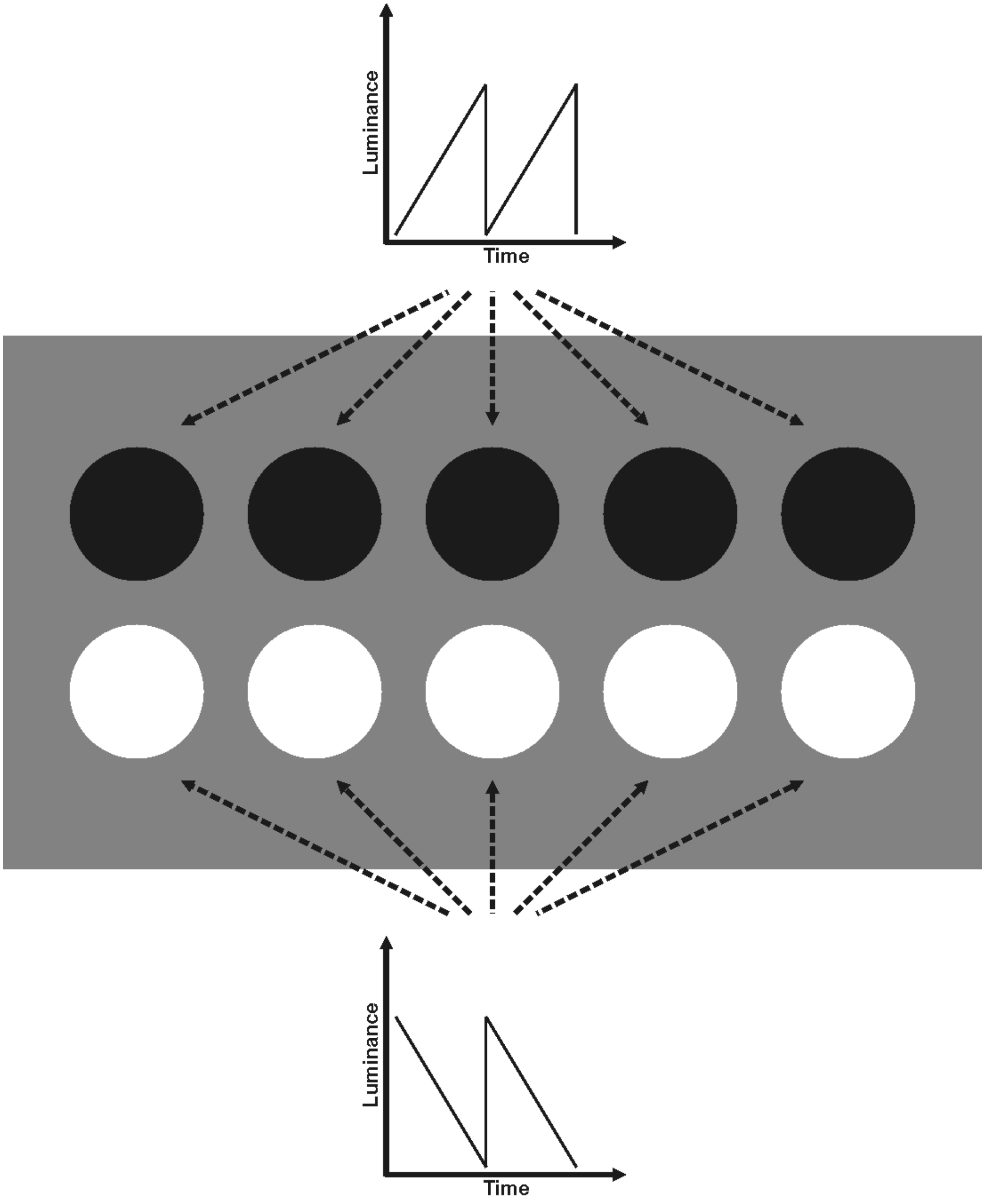
B

Figure 1: Luminance levels of four disks modulate in time with a sawtooth wave form. Two modulate from dark to light (top row), two modulate from light to dark (bottom row). When the background is grey (panel A), the dark-to-light disks group together, and the light-to-dark disks group together; when the background is split light/dark (panel B), the disks along the diagonals group together. Supplement 1b shows a similar demonstration with colour- luminance disks.

Grouping and contrast-defined motion

The effect in figure 1 can be extended to show that grouping can also occur for motion generated by contrast information (second-order motion). Figure 2 shows five disks that modulate from dark to light (top row) and five disks that modulate from light to dark (bottom row) in a sawtooth wave form. The background is gray in panel A and is two spatially-shaded gradients in panel B (light-to-dark on top and dark-to-light on bottom). Against gray, the disks in the top row group together, and the disks in the bottom row group together. The grouping pattern should be expected since the luminance information and the contrast information in each row modulate in phase with each other (similar to figure 1A).

Against the shaded gradients, the grouping follows the appearance of a sweeping motion that shifts from disk-to-disk across the display. The motion makes sense in terms of contrast information--the phase of contrast for each disk is shifted relative to the neighbouring disk(s)--but not in terms of the luminance information, which remains unchanged from the grey background (see Shapiro et al., 2005, Figure 6). The implication is that the grouped appearance depends upon information that is neither part of the Figure (i.e. the disks) nor Ground (i.e., the shaded gradients).



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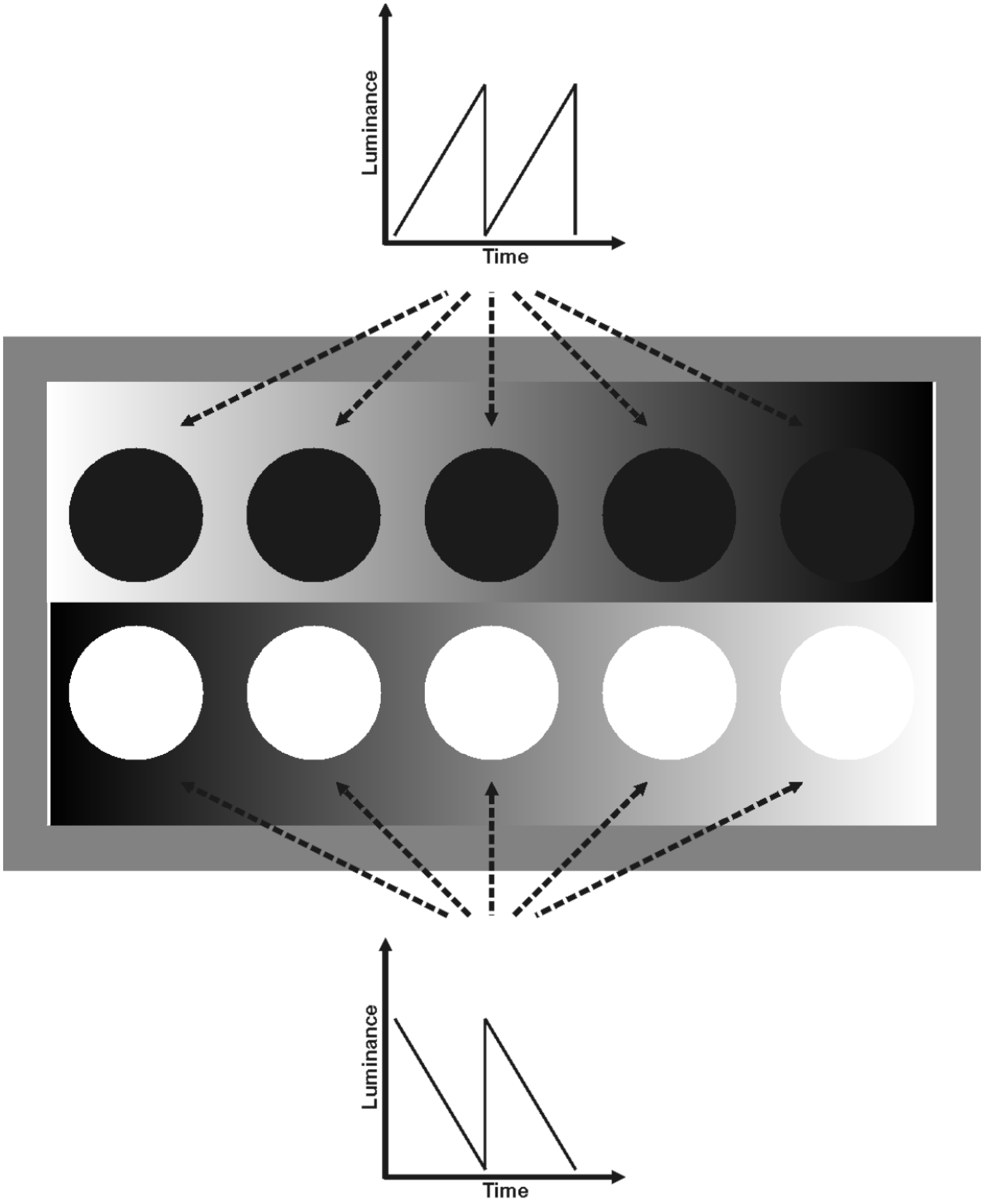

B

Figure 2: Two rows of five disks each, the top row modulates from light to dark and the bottom row from dark to light (sawtooth pattern) on a medium grey background. When the background is grey (Panel A) the disks in row group together. When the background consists of two gradient backgrounds (from light-to-dark on top; from dark-to-light at bottom; Panel B), apparent motion sweeps from right-to-left in both rows. In this condition, the elements of different luminance levels in the top and bottom row are grouped together and seem to move in unison.

Conclusion

Any visual scene can be described by a variety of stimulus characteristics (spatial frequency, luminance, contrast, temporal frequency, chromaticity, etc.). The visual system represents these properties through parallel neural channels, each of which responds to only a small range within a few of these dimensions. Presumably, the processes that organize the visual scene into gestalt groupings must do so by selecting a sub-population of the neural channels.

The examples in this paper indicate that the input into mechanisms that group the stimulus does not necessarily correspond to visual representations that have already organized the visual scene into scissioned layers. The demonstrations are therefore consistent with models that suggest that grouping results from temporal correlations of elemental modulation (see Blake & Lee, 2005, for review), and with evidence for visual systems that operate across coplanar divisions (e.g., Spehar & Zaidi, 1997).

One question that arises from these demonstration concerns how many grouping mechanisms could exist. The visual system contains dorsal and ventral streams that differentially respond to motion and to objects. Conceivably, each of these streams has their own set of processes for organising the visual scene.

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Part 3 –

New insights from static motion illusions

Chapter 8 –

Apparent rotation and jazzing in Leviant's Enigma illusion[8]

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[8] This work has been accepted in a slightly different form and is currently in press: Hamburger, K. (in press). Apparent Rotation and Jazzing in Leviant's Enigma Illusion. *Perception*.

In 1981 Leviant devised Enigma, a figure that elicits perceived rotary motion in the absence of real motion. However, despite its striking appearance there is no good explanation for this motion illusion to date. Gregory (1993) pointed out a similarity to MacKay's "complementary" afterimage in his ray pattern and suggested accommodative fluctuations and small eye movements as a potential origin for these phenomena. Furthermore, Zeki, Watson, and Frackowiak (1993) found PET-activation in response to Enigma in visual area V5 and immediately surrounding areas (called V5 complex) suggesting that the illusory motion could be mediated by the same neurons as real motion. In the experiments reported here, I show that the rotary motion is perceived on colored as well as achromatic annuli intercepting the radial lines. More importantly, the illusory streaming motion continues to be seen with a cycloplegic lens as well as through a pin-hole (i.e., ruling out transient changes of accommodation), and in the positive afterimage (i.e., in the absence of eye movements). Apparent rotation is strongest with radial inducers impinging at right angles onto the annuli, but persist, although to a lesser degree, when the inducing lines are tilted in opposite directions, non-collinear, replaced by dotted lines or lines with rounded terminators. For an explanation the Enigma illusion requires a neural mechanism that uses lines abutting an empty annulus to elicit orthogonal streaming motion in one or the other direction.

Introduction

Ever since its introduction by Leviant in 1981, the *Enigma* figure has intrigued artists and vision researchers interested in illusory motion perception (Figure 1). The original figure consists of 110 black radial lines intercepted by three bi-colored annuli. With central fixation streaming motion is seen on the annuli alternating between clockwise and counter-clockwise rotation (Leviant, 1996; Gori, Hamburger & Spillmann, 2006). Leviant (1996) showed that the illusion persists with a wide range of radial lines and annulus colors. In a follow-up study, Kumar and Glaser (2006) have recently defined the optimal stimulus parameters for the appearance of rotary motion.

A major difference that distinguishes the *Enigma* illusion from other motion illusions, such as the 'Pinna-Brelstaff-Illusion' (Pinna & Brelstaff, 2000), the 'Rotating-Snakes Illusion' (Kitaoka, 2000), and the 'Rotating-Tilted-Lines illusion' (Gori & Hamburger, 2006), is the spontaneous reversal from clockwise to counter-clockwise motion in the *Enigma* figure, although motion in both directions can sometimes be seen concurrently on different annuli. This reversal in direction occurs on average every 4.7 s (Gori et al., 2006). In contrast, the three illusory phenomena described above occur lawfully and might phenomenologically be reminiscent of a motion phenomenon (spatial displacement) previously reported by Gregory and Heard (1983). Furthermore, the Rotating-Snakes Illusion is a more aesthetic variant of the 'Peripheral Drift Illusion' (Fraser & Wilcox, 1979; Faubert & Herbert, 1999; Kitaoka & Ashida, 2003). Another difference is the restlessness ("jazzing") perceived in the *Enigma* pattern, but not with the Pinna-Brelstaff or Rotating Snakes illusions (Murakami, Kitaoka & Ashida, 2006).

Jazzing seen in *Enigma* is reminiscent of a phenomenon known from 'Op Art' such as in Riley's – 1963 – *Fall*. It has been attributed to moiré effects resulting from the superposition of the afterimage onto the stimulus pattern and its displacement by saccadic eye movements (Wade, 2003). An analogous explanation was set forth by Gregory (1993, 1994, 1995) who pointed out a similarity of Leviant's *Enigma* illusion to the "complementary" afterimage in MacKay's (1957a, b, 1958) ray and bull-eye patterns. Gregory hypothesized that changes in image size and retinal position caused by accommodative changes and rapid eye movements give rise to retinal motion signals.

This explanation, although plausible, does not fully hold up. Zeki (1994, 1995) demonstrated that streaming motion continued to be seen in the *Enigma* figure despite an atropinized lens, ruling out accommodation and suggesting fixational instability as a possible source of origin for the streaming motion and the accompanying jazzing in the *Enigma* figure (Mon-Williams & Wann, 1996; Fermüller, Pless & Aloimonos, 1997). However, we already know that jazzing is not seen without eye movements. This has been shown with a stimulus pattern (O' Neal's *Square of Three*) stabilized on the retina (Kupin, Haddad & Steinman, 1973); a flash exposed MacKay pattern (Gregory, 2002); and by recording microsaccades during viewing of Bridget Riley's *Fall* (Zanker, Doyle & Walker, 2003). Furthermore, jazzing can be seen with closed eyes after prolonged viewing of a grating stimulus such as used by MacKay. This aftereffect suggests a neural component; moiré fringes cannot explain this result.

In order to learn about the mechanisms (and boundary conditions) underlying streaming motion in the *Enigma* illusion, I performed four experiments. Specifically, I tested the *Enigma* illusion with

(i) chromatic and achromatic annuli,
(ii) a paralyzed lens and a pin-hole (to control for accommodative changes),
(iii) an afterimage (to control for eye movements),
(iv) various kinds of inducers.

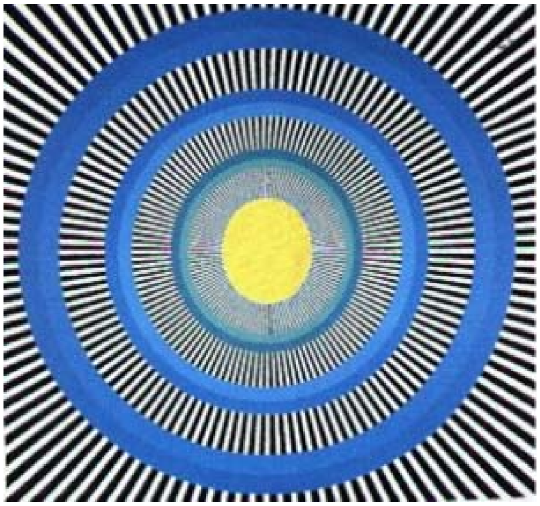


Figure 1: Original *Enigma* figure by Isia Leviant (1981, see Leviant 1996). Rotary motion in either direction may be perceived on the three colored annuli.

Experiment 1: Annulus color

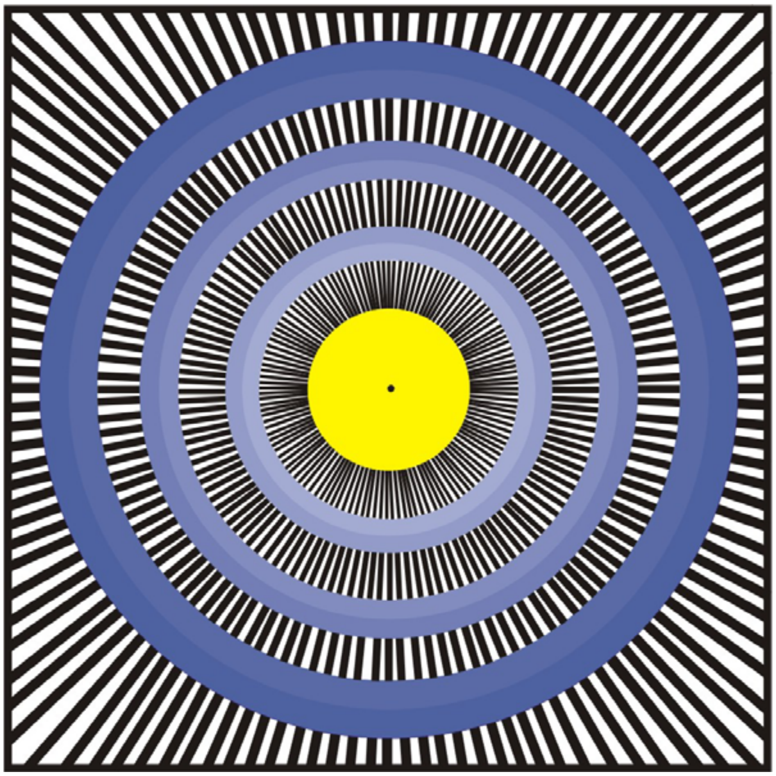
First, I asked whether some annulus colors would elicit illusory streaming motion in the *Enigma* figure more strongly than others and whether colored annuli were needed at all.

Methods

A stimulus with three bipartite annuli having different shades of blue (Figure 2a); a stimulus with three bipartite annuli having different shades of gray; one with three bipartite annuli with the same shade of red on the outside and the same shade of green on the inside; and a stimulus with a dark blue/light blue outer annulus, a violet and purple annulus in the middle, and a dark orange/light orange inner annulus (Figure 2b) were used in this experiment (4 stimuli). Blue and gray annuli typically consisted of a more saturated, darker outer perimeter and a less saturated, brighter inner perimeter. The various color stimulus (Figure 2b) consisted of six different hues and luminances. The central disk of the stimuli was always yellow. The RGB-coordinates of these colors as measured with a Spectra Scan PR650 (Photo Research) are given in Table 1 as are their luminances. No effort was made to control for hue, saturation, brightness (HSB) and spectral purity of the stimuli, since I was just interested in the question whether color as such is crucial or not.

Table 1: Colors used in all studies. RGB values are given as well as the luminance (cd/m2) and color coordinates (x and y). No effort was made to control for the chromaticity and spectral purity of the stimuli.

Color	**R**	**G**	**B**	**cd/m^2**	**x**	**y**
blue (dark)	68	68	255	1.78	.159	.105
blue	85	85	255	1.90	.159	.107
blue	119	119	255	3.03	.161	.121
blue	136	136	255	5.12	.164	.138
blue	153	153	255	8.59	.170	.157
blue (light)	170	170	255	11.7	.179	.173
gray (dark)	31	26	23	.49	.253	.244
gray	77	73	72	2.02	.239	.238
gray	114	112	111	6.71	.248	.250
gray	150	149	148	15.5	.262	.260
gray	194	193	193	37.1	.279	.276
gray (light)	222	222	221	61.0	.299	.298
yellow	255	245	0	49.3	.467	.462
red	218	37	29	14.9	.624	.351
green	0	146	63	8.34	.272	.500
purple	40	22	111	1.57	.168	.108
blue	0	147	221	13.7	.173	.174
violet	151	69	120	8.0	.387	.235
orange (dark)	218	37	29	14.9	.624	.351
orange (light)	231	120	23	20.3	.599	.369
white (background)	255	255	255	82.0	.324	.328



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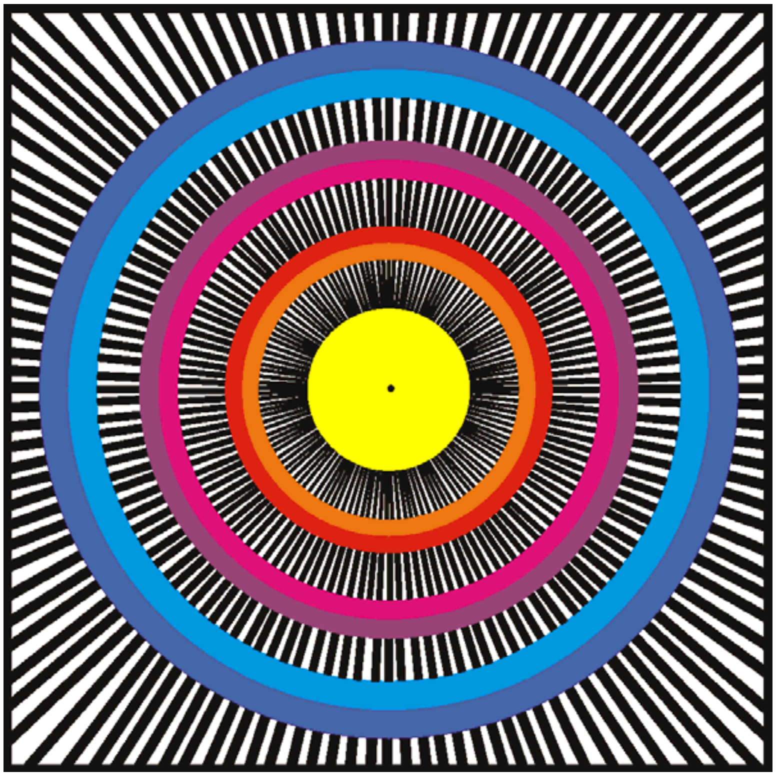

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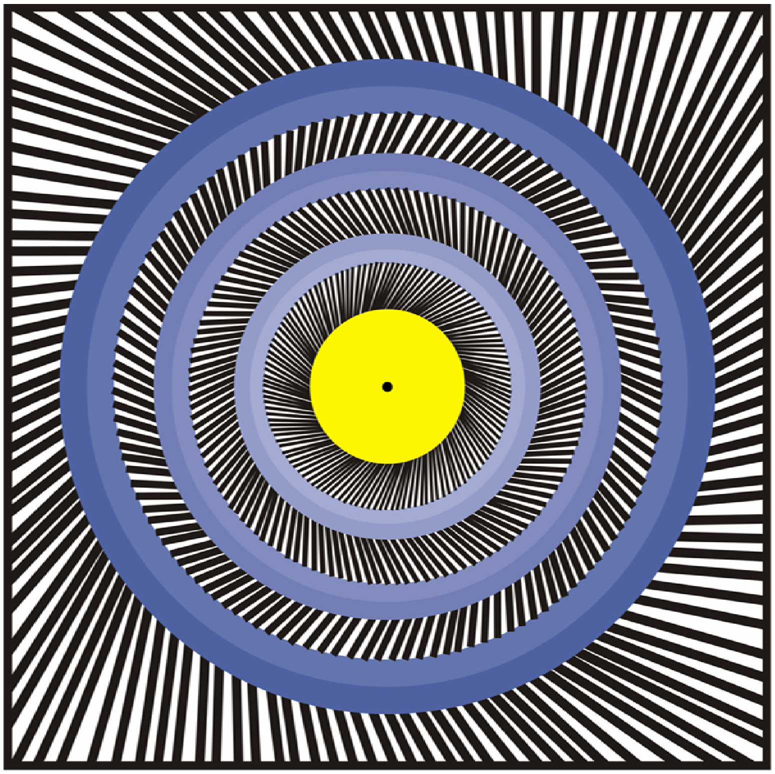

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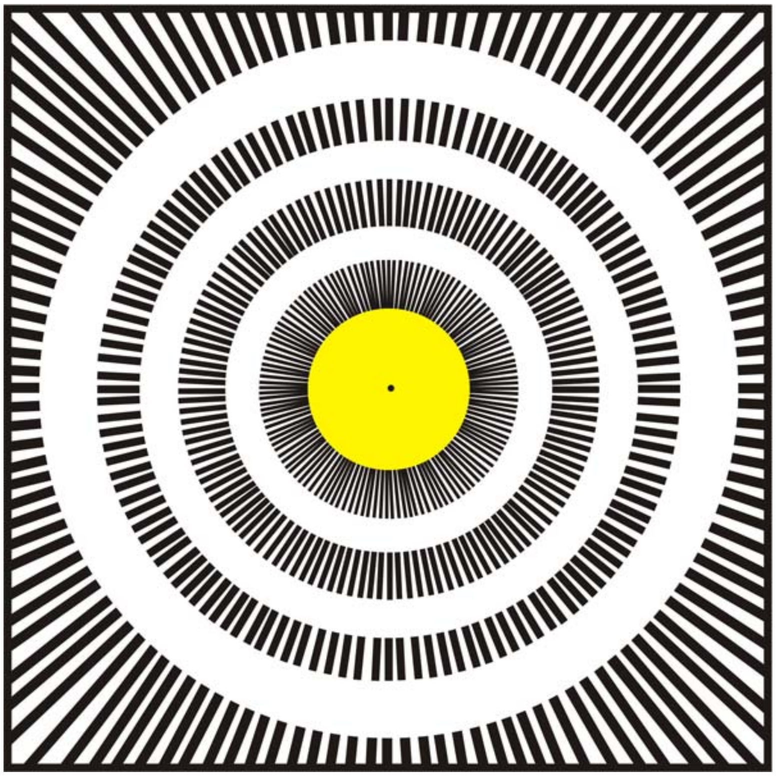

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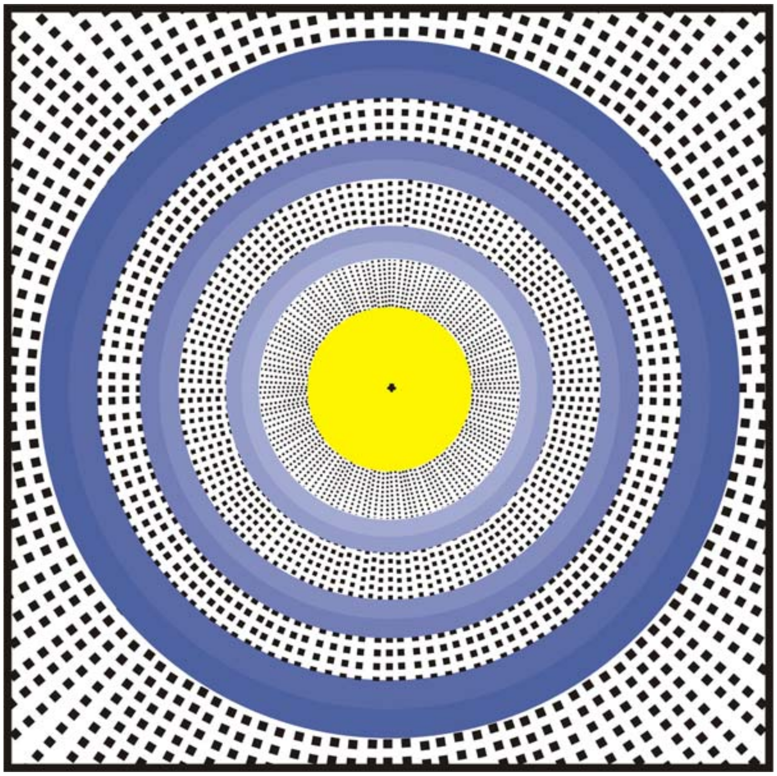

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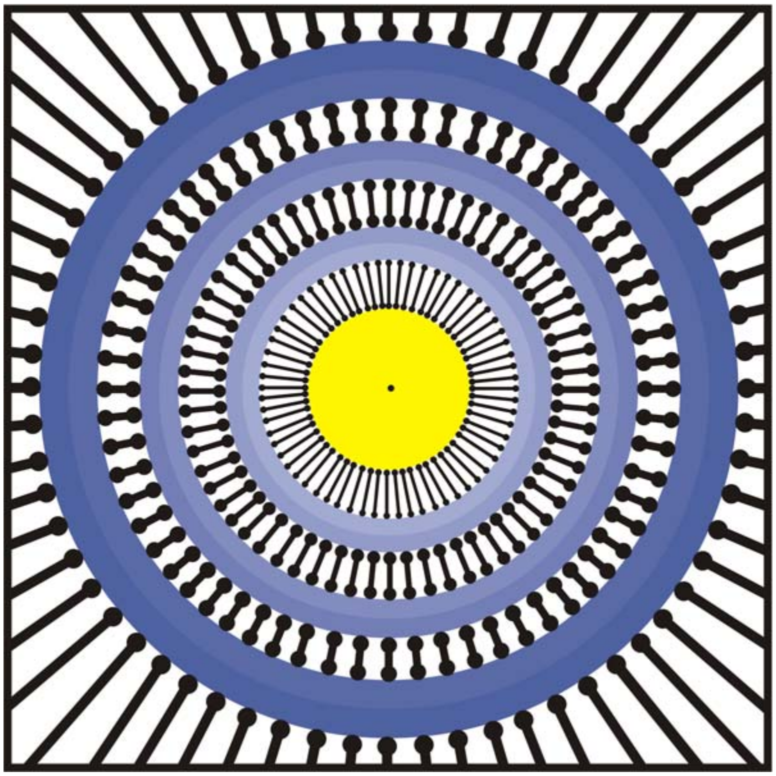

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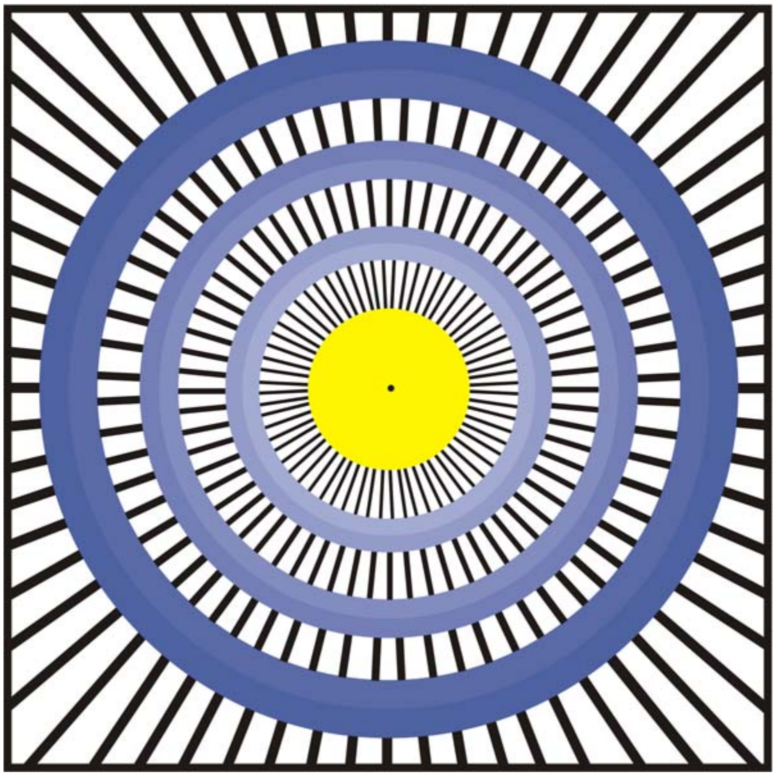

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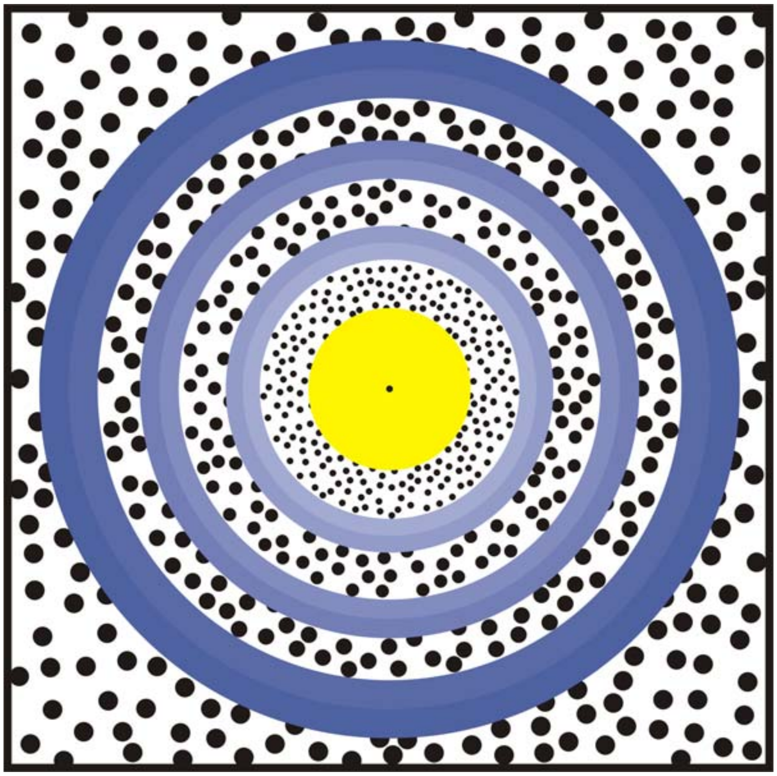

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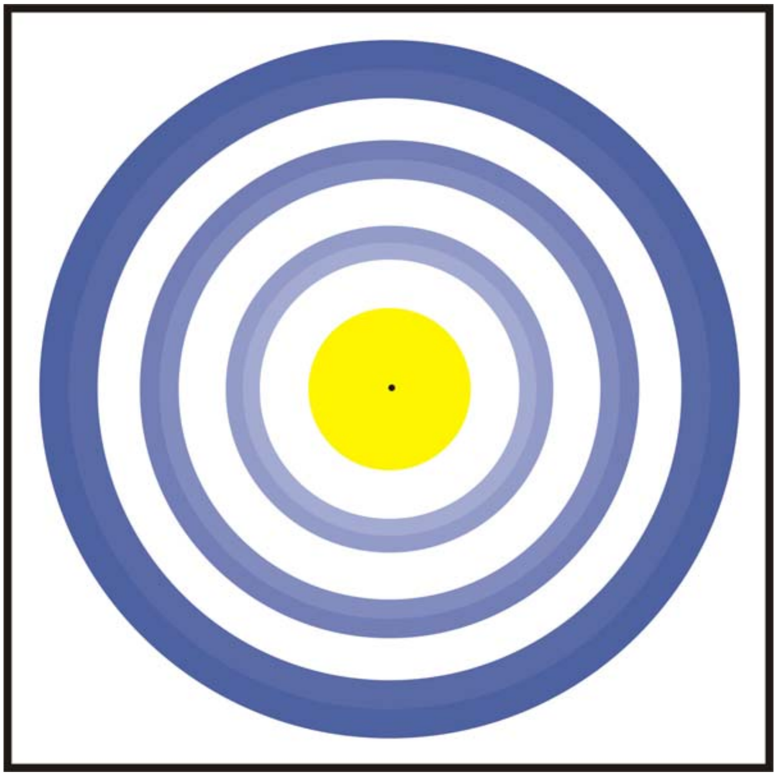

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Figure 2: (a) and (b) Computerized versions of Leviant's *Enigma* (used in Experiment 1). (c) The radial lines of the *Enigma* figure were tilted in opposite directions by 25 deg and 335 deg, respectively. This pattern can also elicit a Pinna-Brelstaff-like rotation of the black lines if one approaches the stimulus or recedes from it (Gori & Hamburger, 2006). (d) Annuli colors were removed and illusory contours defined white annuli, since the luminance was identical to the background. (e) Discontinuous lines replacing the solid lines. (f) Round blobs (terminators) were added to the tips of the radial lines. (g) Number of radial lines is halved to 114. (h) Randomly distributed dots were presented on the background replacing the radial lines. (i) No texture shown. This stimulus served as a control, showing that no streaming motion is present without surrounding texture.

These variants of the original *Enigma* figure (and all other stimuli used) were created in CorelDraw 12. Stimulus patterns consisted of 128 black radial lines with three concentric annuli superimposed onto them. The lines had a duty cycle of 1:1. Stimuli had a black fixation point in the centre and were presented on a Fujitsu-Siemens Amilo-A digital flat screen with a resolution of 1024x768 pixels in a dark room. Additionally, paper print-outs of the same figures were presented under an overcast sky at noon time to rule out possible artefacts resulting from the monitor refresh rate.

All stimuli were viewed once from a distance of 50 cm, corresponding to an angular subtense of 25.4 deg. Perceived strength of apparent rotation was measured using magnitude estimation with 0 (no motion, Figure 2i) and 4 (strong motion, Figure 1a) serving as lower and upper anchors. Magnitude estimates within this range could be used in steps of 0.5. Seventeen subjects (mean age 23.2 years; SD = 1.4) with normal or corrected-to-normal visual acuity and normal color vision participated in the experiment.

Results and Discussion

All subjects reported seeing annular streaming motion on the screen as well as on the print-outs with all colors and color combinations. It was slightly stronger on the paper print-outs. All subjects also reported clockwise- vs. counter-clockwise motion. Occasionally, opposite directions of motion were perceived on neighbouring annuli and even on both halves of the same annulus. Jazzing occurred only in the area between the radial lines.

Data for stimuli presented on the monitor and on print-outs were collapsed as there was little difference between them. Rotary motion was strongest for blue annuli (mean = 2.6; SEM = 0.19), followed by gray annuli (mean = 2.4; SEM = 0.21), annuli composed of different colors in Figure 2b (mean = 2.1; SEM = 0.20), and red-green annuli (mean = 1.3; SEM = 0.31). The order of perceived strength is plotted in Figure 3 for the different color combinations. The strength of rotary motion perceived on the three different annuli strongly depends on the viewing distance (Leviant 1996). But, it is very difficult for subjects to differentiate between the strength on these different annuli.

Therefore, I did not analyse differences in perceived strength on different annuli within a single pattern, but rather had subjects judge the overall strength in a stimulus pattern.

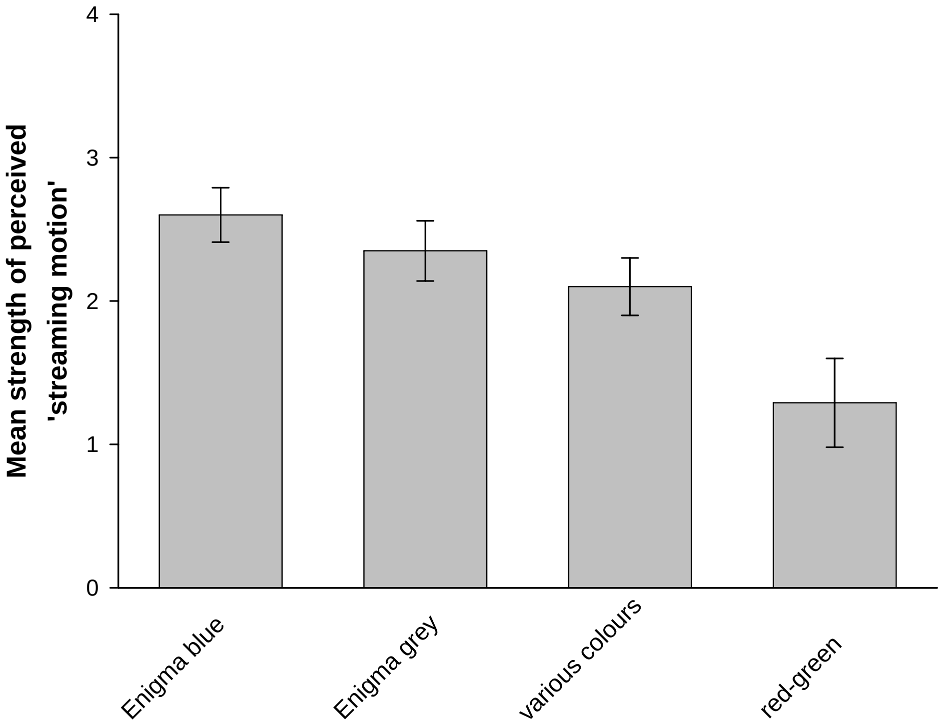

Figure 3: Mean strength of rotary motion for the stimuli tested in Experiment 1. The *Enigma* with blue colors revealed the strongest effect, followed by the achromatic gray version, and the various colored version. The weakest motion percept elicited the red-green condition.

Paired-sample t-tests using the Bonferroni correction revealed a significant difference only between mean ratings for blue vs red-green annuli (p = .006). Mean ratings for gray annuli were almost as high as those for blue annuli and even higher than for all the other annuli used, indicating that color is not a requirement for the *Enigma* illusion. Motion was generally more conspicuous on the lighter than on the darker half of a bi-colored annulus.

Results suggest that color is not critical for perceived rotation, but the luminance contrast between the annuli and the background (or rays) could be important. But meanwhile, Kumar and Glaser (2006) have shown that the streaming motion also occurs under conditions of isoluminance. They further showed that the annuli do not necessarily have to be bi-partite, a single annulus color is sufficient for the perceived rotation.

Experiment 2: Accommodative fluctuation

I next asked whether transient changes of accommodation are needed for seeing rotary motion in the *Enigma* figure, since assumptions and results on this issue are ambiguous (Gregory, 1993, 1994; Mon-Williams & Wann, 1996; Fermüller et al., 1997; Zeki 1994, 1995; Kumar & Glaser, 2006; MacKay in a personal communication with Gregory, reported in Greory, 2002).

Methods

To rule out transient accommodative changes, I first rendered the ciliary muscles of one eye cycloplegic by instilling two drops of 0.5% *Tropicamid* (Mydriaticum Stulln) into the orbital sac. This procedure is similar to using Atropine (Zeki, 1994). The author (KH) and an additional naïve subject served as observers. The pattern depicted in Figure 2a was presented on the monitor and as a paper print-out.

In addition to immobilizing the crystalline lens, I used a 2 mm pin-hole centred before the natural pupil (Gregory, 1993). This hole admits only axial and paraxial rays and thereby increases the depth-of-focus rendering accommodation unnecessary. Figure 2a was presented again on the monitor and as a paper print-out and viewed with one eye by each of five observers (mean age 24.6 years; SD = 4.39) with normal or corrected-to-normal visual acuity. One subject was familiar with the *Enigma* illusion, while the other four were naïve. Subjects could not see the outer edges of the stimulus pattern and did not have any information on depth (i.e., the distance of the stimulus to the eye).

Results and Discussion

Rotary streaming motion was unimpaired despite the cycloplegic lens in both subjects, confirming the observation by Zeki (1994) with atropine. Likewise, all five observers using a pin-hole reported rotary motion as well; however, it was weaker than without the artificial aperture. There was no difference between the illusory percept seen on the monitor and on the paper print-outs. In comparison to streaming motion, jazzing between the radial lines was absent under both conditions, confirming Gregory's observation with MacKay's ray pattern. Evidently, accommodative changes are not necessary for the *Enigma* illusion to be seen.

Experiment 3: Rapid eye movements

Here I asked whether rotary streaming motion in the *Enigma* figure could be seen without eye movements.

Methods

To rule out the effects of eye movements, I produced a long-lasting, positive afterimage of the *Enigma* figure. Subjects first familiarized themselves with the *Enigma* illusion using a paper print-out of Figure 2a. They were then dark adapted for 15 min and thereafter fixated a dim laser point in the centre of an achromatic *Enigma* print-out that itself could not be seen. A chin rest was used to stabilize the head. After 3 s of fixation the figure was flash-exposed using a Metz Mecablitz, Modell 32 Z-1. This resulted in a positive afterimage of about 10 s. Nine naïve subjects (mean age 31.6 years; SD = 13.5) with normal or corrected-to-normal visual acuity participated. The experiment was repeated with two naïve subjects with normal vision using no fixation point. Following dark adaptation these subjects looked straight ahead in the direction of the *Enigma* figure for flash exposure of the stimulus (for the illusory effect it is not crucial to look right into the stimulus centre). This latter method controls for residual light falling onto the stimulus which might result in jazzing of the original image.

Results and Discussion

Apparent rotation was present in the positive afterimage for all subjects; however, the motion was spurious and faster, not the same as seen with direct viewing of the stimulus figure. When the radial lines began to fade, the streaming motion on the annuli also became weaker and soon thereafter disappeared.

I conclude that microsaccades are not a prerequisite for the *Enigma* illusion, although they may enhance the perceived rotary streaming motion. Also, the perceived motion was not only weaker, but also faster than in the original stimulus pattern. Thus, an experiment using a stabilized image of the *Enigma* figure, similar to O'Neal's *Square of Three* (Kupin et al., 1973) would be desirable. No jazzing was observed in the afterimage, confirming Gregory's (1993) observation using MacKay's ray figure.

Experiment 4: Inducers

To account for jazzing following prolonged viewing of his bull-eye and ray figures, MacKay (1957a) hypothesized that stimulus patterns with densely spaced, oriented lines would lead to "complementary" motion by a mechanism that produces competing signals at right angles when stimulated in one orientation. For example, exposure to a star figure with densely packed radial rays would be followed by a percept of spurious circular motion. By the same token, prolonged viewing of a figure consisting of high spatial frequency concentric annuli would result in perceived radial motion.

In this last experiment I asked whether the radial lines of the *Enigma* figure impinging orthogonally onto the bipartite annuli may be responsible for the apparent rotation perceived in this illusion. To test for this hypothesis, I presented the black inducing lines of the *Enigma* figure tilted in opposite directions, thus off-setting both orthogonality and collinearity of the inducers. Five additional variations of the *Enigma* figure were also tested.

Methods

The following variants of the *Enigma* figure in addition to Figure 2a were used: (i) black lines tilted by 25 deg on one side and 335 deg on the other (Figure 2c); (ii) an empty, annular zone between the inducers (Figure 2d; only tested on a paper print-out); (iii) dotted lines instead of continuous lines (Figure 2e); (iv) round blobs added to the tips of the lines (Figure 2f); (v) fewer radial lines (64 lines instead of 128) (Figure 2g; only tested on a paper print-out); and (vi) black dots randomly distributed on the white background (Figure 2h), i.e. no radial lines at all.

Five naïve subjects (mean age 25.4 years; SD = 2.9) with normal visual acuity were tested. Stimuli were presented once as before on the flat screen of the monitor. Stimuli 2c – h were also presented on paper ten times each and in a random sequence. The strength of rotary motion was rated on a scale ranging from 0 (no motion as in Figure 2i) to 10 (streaming motion as in Figure 2a). A trial was terminated after 40 s and subjects reported what they had seen.

Results and Discussion

Results are shown by the columns in Figure 4. Compared to Figure 2a (computerized), rotary motion was greatly diminished for all four stimulus patterns in the monitor condition. Mean ratings were: 5.6 (SEM = 0.75) for tilted lines; 4.8 (SEM = 0.37) for dotted (discontinuous) lines; 6.8 (SD = 0.97) for blobs at the end of terminators; and 4.6 (SD = 1.03) for a randomly dotted background. All differences, but the one for the blobs, between the variants and the standard *Enigma* figure were significant (Wilcoxon Signed Ranks Test and Bonferroni corrected t-test for paired samples; $p < .005$, since 10 t-tests were possible). Ratings for the four stimulus variations did not differ statistically from each other.

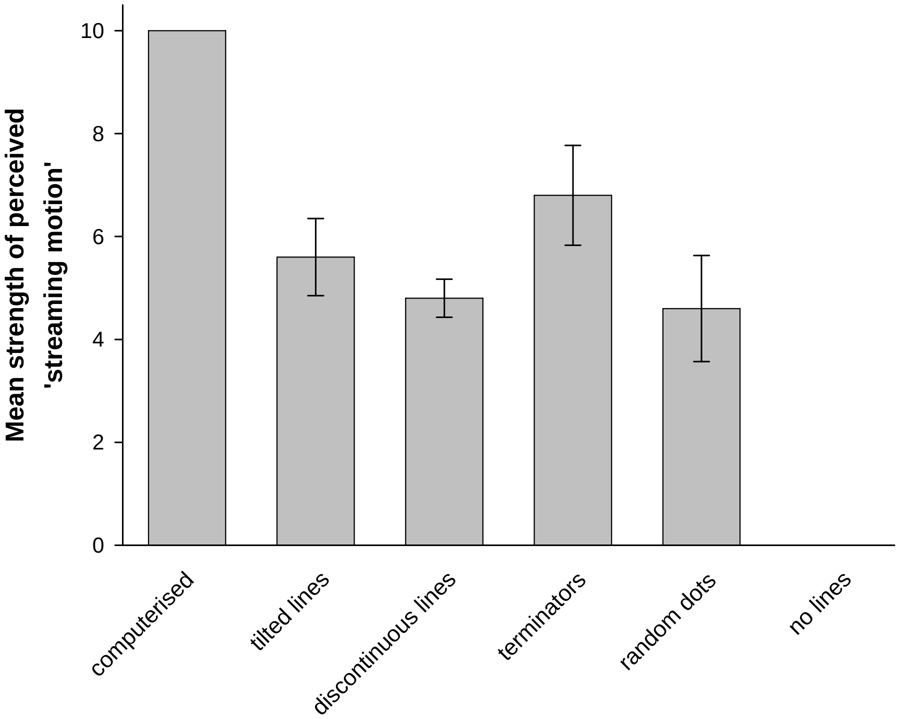

Figure 4: Mean strength of rotary motion for the stimuli tested in Experiment 4 *(Condition 1*, monitor). Figures 2a and i served as references (rating of 10 and 0 respectively).

Results for the paper print-outs are shown by the columns in Figure 5. Compared to the standard stimulus (Figure 2a; computerized), perceived rotary motion decreased from Figure 2c to 2h. Mean ratings were: 8.2 (SEM = 0.50) for tilted lines; 7.3 (SEM = 1.36) for the stimulus with empty annuli; 4.7 (SEM = 0.16) for the terminal blobs (terminators); 4.6 (SEM = 0.33) for the stimulus with fewer lines; 4.1 (SEM = 0.56) for the discontinuous, dotted lines; and 2.3 (SEM = 0.49) for a dotted background. Statistical analysis was done *using* Bonferroni corrected paired-sample t-tests; $p < .002$; since 27 t-tests were possible.

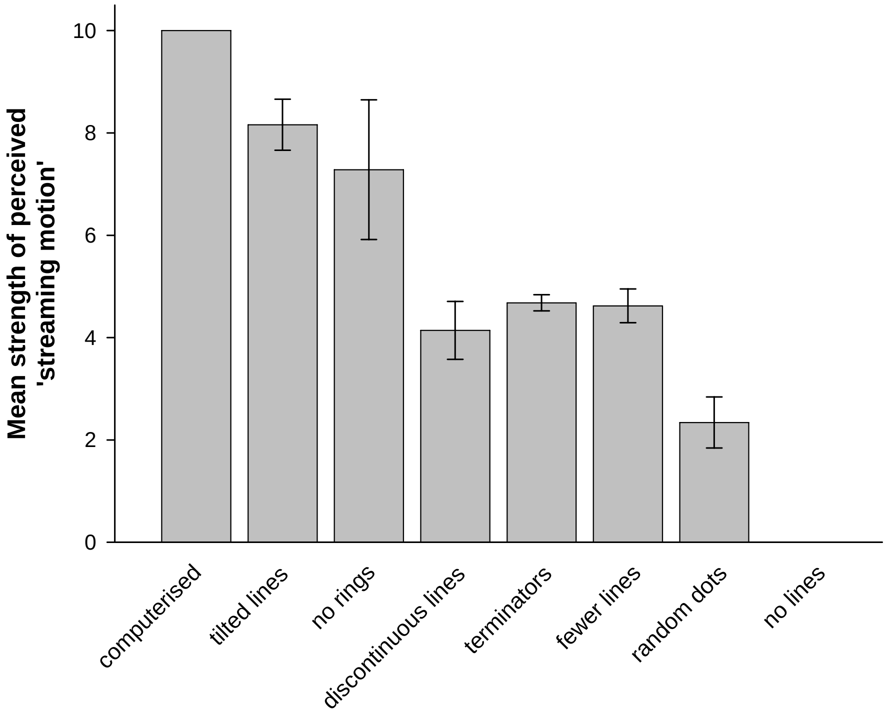

Figure 5: Mean strength of rotary motion for the stimuli tested in Experiment 4 *(Condition 2*, print-out). Figures 2a and i served as references (rating of 10 and 0 respectively).

In all pair comparisons, ratings for the second stimulus were significantly lower ($p < .0001$) than for the first original stimulus (Figure 2a; computerized). Further significant differences were found for the comparison between tilted lines vs. fewer lines, tilted lines vs. terminators, tilted lines vs. no lines, terminators vs. no lines, and fewer lines vs. no lines ($p \leq .001$).

The finding that the illusory rotation on the annuli is diminished when the inducing lines are not radially oriented, suggests that orthogonality is essential for eliciting the illusory motion. This is in agreement with results obtained by Gori et al. (2006), reporting a monotonic decrease in strength of streaming motion with a decreasing angular difference between the lines on one hand and the abutting zone on the other. I here demonstrate that oppositely tilted lines induce a moderately strong motion, thus collinearity is not needed either. The very weak motion on the randomly dotted background stimulus was reminiscent of jazzing rather than clear streaming motion on the annuli and can thus be neglected.

It is noteworthy, that physical annuli are not needed for the *Enigma* illusion, since I was able to demonstrate that annular zones that became part of the white background elicited the illusion as well (Figure 2d).

General Discussion and Conclusion

The findings reported here show that colored annuli are not required for the *Enigma* illusion, achromatic annuli do as well. If color is used, blue shades produce the most vivid streaming motion in the stimuli tested. So does a high contrast between the annuli and the background (Exp. 1). Even annuli with illusory boundaries (Figure 2d, Exp. 4) can elicit the illusory effects.

Accommodative changes may be ruled out as causative for the *Enigma* illusion as streaming motion was virtually undiminished with a cyclopegic crystalline lens. Lens paralysis with Atropine (Zeki, 1994) and Tropicamid (this study) yielded the same results (Exp.2).

Rapid eye movements (Exp. 3) are not required for eliciting the illusion as it can still be seen in the afterimage following flash exposure of the stimulus pattern. Yet, microsaccades may enhance the illusion and an experiment testing for illusory rotation with a stimulus that is stabilized on the retina (but has not yet faded) remains to be done.

The obtained results are in line with Kumar and Glaser (2006) who suggested that eye movements do not play a significant role in generating the illusory streaming motion. Jazzing was not perceived under any of the conditions in Experiments 2 and 3.

Tilting the inducing lines (Exp. 4) weakened, but did not abolish the illusory effect. Thus, it is not necessary for the inducing lines to impinge orthogonally on the concentric annuli for the *Enigma* illusion, although the illusion is seen best with radial lines (Gori et al., 2006; Kumar & Glaser, 2006). The observation that dotted lines and lines with blobs on the tips also produce streaming motion shows that the *Enigma* illusion cannot be explained within the context of occlusion of radially oriented, collinear rays. Neither can it be accounted for in terms of end-stopped cells (e.g. Pack et al., 2003), responding to terminators as it would be expected to break down when the terminators are pertubated.

For an explanation, one would need to postulate a neural mechanism that signals rotary motion when stimulated by rays, just as MacKay (1957 a, b) did, to account for the occurrence of jazzing in high-frequency, oriented stimulus patterns. Forty years later, Kumar and Glaser (2006) similarly speculate that high luminance-contrast gratings that border "empty" stimulus channels of uniform luminance produce high activity in edge-detecting neurons that in the absence of neural activity in these empty channels may induce illusory motion. Neurons conforming to this description are yet to be found. Direction-sensitive neurons in areas MST/ MSTd (e.g. Saito, Yukie, Tanaka, Hikosaka, Fukada & Iwai, 1986; Tanaka, Hikosaka, Saito, Yukie, Fukada & Iwai, 1986) could be possible candidates for the illusory effects observed. However, both Fermüller et al.

(1997) as well as Gori et al. (2006) have shown that illusory motion comparable to *Enigma* rotation occurs also in straight and undulating grating patterns.

The finding by Zeki et al. (1993) that brain activation in response to *Enigma* occurs in visual area V5 (as well as other brain areas that are not activated when stimulated by real motion) suggests that the perception of illusory motion and real motion is mediated by the same specialized region in the brain. This finding localizes the illusion, but it does not explain it. Thus, although the boundary conditions of the *Enigma* illusion are now fairly well known, the neural mechanism underlying it remains to be unveiled.

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Chapter 9 –

Reversal of apparent rotation in the Enigma figure with and without motion adaptation and the effect of T-junctions[9]

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[9] This work was published in a slightly different form: Gori, S., Hamburger, K., & Spillmann, L. (2006). Reversal of apparent rotation in the Enigma-figure with and without motion adaptation and the effect of T-junctions. *Vision Research, 46 (19),* 3267-3273.

We studied the time course of apparent rotation and directional reversal in Leviant's Enigma figure. On average, periods of clockwise rotation lasted 5.0 s as opposed to 4.4 s for counter-clockwise rotation, resulting in an average reversal frequency of 6.4 within 30 s. At the beginning of a trial, clockwise rotation was perceived almost twice as often as counter-clockwise rotation. This bias could be shifted by previous adaptation to a black-and-white rotating sector disk, suggesting a neural interaction between real motion and illusory motion. We further studied Enigma-type motion on a chromatic bar superimposed onto a black-and-white linear grating. Illusory motion was strongest when the bar was oriented at 90 deg to the grating lines and became progressively weaker with a decrease in angle. This suggests that T-junctions formed by the radial rays impinging onto the colored rings of the Enigma figure are instrumental for eliciting the rotary motion and may rule out a low-level sensory origin of the illusion.

Introduction

In 1981, Leviant devised a figure that elicits spontaneous perception of rotary motion in the absence of real motion. The figure consists of a black and white ray pattern with narrowly spaced radial lines onto which three chromatic rings are superimposed (Figure 1). The spurious rotation seen on the rings gave rise to the name *Enigma*.

The number of rays in Leviant's figure was 120 and the duty cycle between black and white lines was 1:1.5 (Leviant, 1996). For an explanation of the illusion, Gregory (1993) suggested transient changes of accommodation and rapid eye movements. As an alternative, Mon-Williams and Wann (1996) proposed that optical aberration in conjunction with small eye movements produces Phi-motion between the radial lines of the Enigma figure leading to illusory motion on the rings.

Fermüller, Pless and Aloimonos (1997) put forward a computational model based on 3D- motion. Their idea is that certain bi-dimensional patterns may be interpreted in terms of three-dimensional motion. Within this context the spatial structure of the Enigma figure is assumed to represent a copoint vector field. The radial lines of the pattern are perpendicular to the copoint vectors while the rings are tangential. In order to support their theory, the authors show that patterns similar to the Enigma figure produce illusory motion. However, this happens when the motion vectors belong to the copoint vector fields, and not to other or to multiple classes.

To test for ocular artifacts, Zeki (1994) and Hamburger and Spillmann (2005) immobilized the crystalline lens with a cycloplegic. In addition, the latter authors produced a long-lasting afterimage of the Enigma figure by illuminating the stimulus with an intense photoflash. Under both conditions subjects reported seeing illusory motion in the Enigma figure. Thus, the apparent rotation cannot be accounted for by accommodative fluctuations of the lens or image shifts on the retina, although the latter may enhance the illusion. There must be an additional factor. Another observation that speaks against an ocular artifact is the periodical change from clockwise to counter-clockwise rotation (Leviant, 1996). This reversal in direction suggests an involvement of higher-level processes.

Assuming a cortical origin Hamburger and Spillmann (2005) tested the influence of T-junctions and found that the illusory rotation became weaker, when the rays were replaced with slashes or strings of dots. A reduction in strength was also obtained when the lines were arbitrarily tilted in opposite directions relative to the rings (by 25 deg). These findings were interpreted in terms of orthogonal terminators being instrumental for the perception of rotary motion.

In the present study we were interested in both the spatial and the temporal properties of the Enigma illusion. First, we measured the duration for clockwise versus counter-clockwise rotation by recording the time between reversals of perceived rotation direction (Experiment 1). Next, we asked whether the onset and initial direction of rotation could be influenced by previous adaptation to real rotation (Experiment 2). Finally, we tested the strength of illusory motion in a simplified version of the Enigma composed of a chromatic bar superimposed onto a linear grating stimulus, when the angle between the bar and the grating lines was systematically varied (Experiment 3).

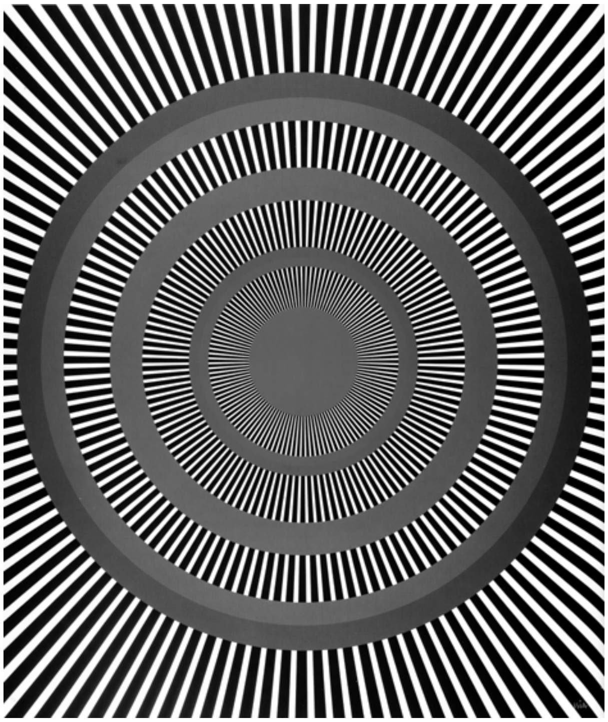

Figure 1: Enigma figure by Isia Leviant (1981). Rotary motion alternating between clockwise and counter-clockwise direction may be perceived on the three chromatic annuli.

Experiment 1: Time course of illusory rotation

Here we investigated the temporal behavior of illusory rotation in the Enigma illusion. The duration of clockwise versus counter-clockwise rotation was measured by recording the time when the apparent motion reversed its direction. We were also interested if the reversal time was comparable to that of other bistable illusions.

Methods

Subjects

Seven naïve subjects (mean age 28 yrs; SD = 7.1) participated in the study. All had normal or corrected-to-normal visual acuity and normal color vision (tested with the Ishihara pseudo-isochromatic plates).

Stimuli

Leviant's Enigma figure as reproduced by Livingstone (2002) served as a stimulus (Figure 1). The background of the figure subtended 14.8 x 14.8 deg. The outer ring had a radius of 5.65 deg; it was 1 deg wide and was composed of two different shades of purple. The middle ring had a radius of 3.85 deg; it was 0.7 deg wide and was composed of purple and red. The inner ring had a radius of 2.3 deg; it was 0.4 deg wide and was composed of two different shades of red. A small point in the center of the stimulus was used for fixation.

Procedure

Subjects were seated 1 m away from a 21 inch-monitor (Sony Multiscan 6520) having a resolution of 1344 x 1008 pixels and a refresh rate of 120 Hz. A chin rest was used to stabilize the head; fixation was binocular. Subjects first familiarized themselves with the Enigma illusion including the spontaneous reversals of motion direction. Thereafter they were exposed to the stimulus for 30 s. The task was to press the Enter-key on the keyboard of the computer as soon as the illusory motion was seen. Key #1 was pressed for counter-clockwise motion and key # 9 for clockwise rotation. The time intervals between key presses defined motion duration in one or the other direction. Measurements were repeated 5 times for each ring and subject in a random order. Thus, the total number of test periods was 105 (5 repetitions x 3 rings x 7 subjects). The time interval between successive trials was 1 min. The experiment was performed in a dark room.

Results

The responses for all 7 observers were normalized to 100%. In Figure 2, the percentage of cumulated responses for clockwise rotation is plotted as a function of time after stimulus onset. (Responses for counter-clockwise motion may be derived by subtracting the percentage for clockwise rotation from 100). Results for each ring are given by a different curve. All three curves show an oscillatory behavior with occasional phase shifts; however, these differences between the rings are not significant (Kruskal-Wallis test = 1.75, p = 0.417). Also, the dynamic oscillations are much the same within and between subjects.

On average, illusory motion was first perceived after a delay of 2.1 s (SD = 1.2 s) following stimulus exposure. Mean duration of uninterrupted clockwise rotation was 5.0 s while that for counter-clockwise rotation was 4.4 s. This translates into a mean number of directional reversals of 6.4 (SD = 2.5), with minor differences among the three rings (ANOVA repeated measure F2, 102 = 0.38). The number of reversals decreased monotonically from a mean of 2.38 in the first 10 s to 2.16 in the second and 1.86 in the last.

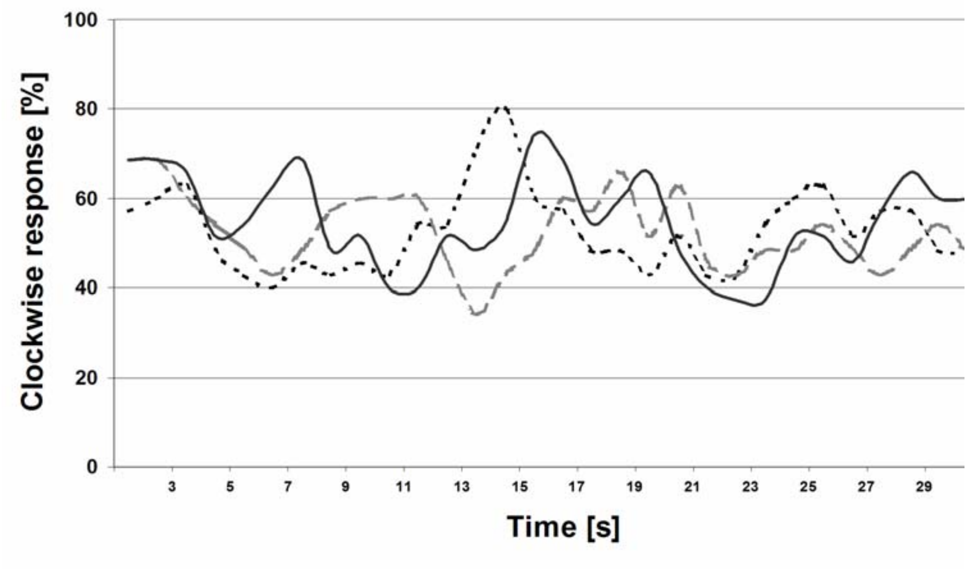

Figure 2: Time course of clockwise rotation (given in percent) in the Enigma figure for each of the three rings (solid curve = outer ring, dashed curve = middle ring and dotted curve = inner ring). Curves are based on averaged responses obtained in 105 trials with 3 rings by 7 subjects. Bin width was 1 s.

When analyzing the data, we found a strong bias at the beginning of a trial in favor of seeing clockwise motion (64.8%) vs. counter-clockwise motion (35.2%). Also, the total number of responses for all rings and subjects cumulated over 30 s was somewhat higher for clockwise rotation than for counter-clockwise rotation (53.54% vs. 46.46%).

In addition to these quantitative results, subjects reported that the direction of rotation on the three rings was not always the same. For example, while perceived rotation on one ring may have been in the clockwise direction, on the other two it was in the opposite direction, etc. Also, rotation in both directions could occasionally be seen simultaneously on the same ring, clockwise on one shade of color and counter-clockwise on the other. Finally, perceived speed was reported to be faster on the inner ring than on the middle and outer ring.

Discussion

The time lag of about 2 s preceding the onset of rotary motion suggests that whatever mechanism is responsible for the apparent rotation in the Enigma illusion requires a minimum time of stimulation to produce the effect. The average duration of 4.7 s (5.0 s for clockwise direction vs. 4.4 s for counter clockwise direction) for apparent rotation further suggests an internal "clock" that switches the percept from one to the opposite motion direction. Such a switch is unlikely due to involuntary eye movements, but may reflect saturation or adaptation not unlike the known reversals in other bi-stable figures. There are several different studies about the wagon wheel illusion that showed diverse evidence in the direction of this interpretation. For example, Duffy and Wurtz (1997) and Paolini, Distler, Bremmer, Lappe and Hoffmann (2000) presented electrophysiological evidence from single cell studies in monkey that both motion onset and abrupt changes in flow trajectory are followed by peaks in the response of MSTd neurons. In line with these results Tolias, Smirnakis, Augath, Trinath and Logothetis (2001) obtained in an fMRI study with nonhuman primates an adaptation of BOLD response in motion sensitive areas during unidirectional rotation of a visual motion stimulus, whereas sudden direction changes were followed by a peak in the BOLD response. Moreover, Sterzer, Russ, Preibisch and Kleinschmidt (2002) found in their fMRI study transient activation in the human motion complex in response to perceived sudden changes in motion direction during the observation of the wagon wheel illusion. They suggested an adaptation of motion sensitive neurons during continuous visual motion stimulation that is followed by an increase in activity when motion direction changes. The similarities between these two bistable motion illusions, Enigma and the wagon wheel illusion, show spontaneous reversals from clockwise to counter-clockwise rotation and vice versa. This supports our interpretation of assuming similar physiological mechanisms regarding the spontaneous reversals phenomenon. The gradual decrease of the reversal rate within the same inspection period may similarly result from directional adaptation or tiring of the observers.

Eye movements have also been ruled out as a factor for the wagon-wheel illusion (Sterzer et al., 2002), which is another well-known reversing phenomenon in the domain of motion. Instead, transient fMRI-activation was found in area hMT+/V5 correlated with sudden changes in perceived motion direction. It would be interesting to check whether a similar correlation holds also for the Enigma illusion.

Table 1 based on a survey by Strüber and Stadler (1999) summarizes the rate of reversals and mean duration for various static bistable phenomena. Results for the Enigma figure (first column) and the wagon wheel illusion (second column) are given for comparison. Results for the dynamic and static percepts are in the same order of magnitude, although durations for the Enigma illusion are consistently longer and reversals fewer than for the other illusions. However, there is excellent agreement with the mean duration of 4.7 s obtained for the wagon wheel illusion.

We have no explanation for the directional bias (clockwise > counter-clockwise) at the beginning of a trial or the slight bias for clockwise rotation over the entire inspection period. Handedness is not likely to be a factor as a comparison between right-handed and left-handed subjects in a small sample of 5 vs. 2 observers showed no difference. No evidence of handedness was found either by MacKay (1957) who studied "complementary motion" in a radial ray pattern and reported an even greater directional bias of 75% for clockwise vs. 25% for counter-clockwise rotation. In an informal observation, one of the authors (S.G.) noticed little or no effect of focused attention on reversal rate.

Table 1: Mean number of spontaneous reversals and mean duration (in s) for each percept in various static bistable illusions. Data for the Enigma illusion (this study) and wagon-wheel illusions (from Sterzer et al., 2002) are given for comparison. Results have been adjusted for 30 s of observation (from Strüber & Stadler, 1999).

	Enigma Illusion	**Wagon-wheel Illusion**	**Necker Cube**
Mean number of reversals	6.4	6.4	8.2
Mean duration of one percept	4.7	4.7	3.7

	Rock´s Chef/Dog	**Schröder's Staircase**	**Rubin´s Vase/Faces**	**Maltese Cross**
Mean number of reversals	9.1	11.7	13.3	10
Mean duration of one percept	3.3	2.6	2.3	3

Experiment 2: Adaptation to real rotation

Here we asked whether the direction of illusory motion could be influenced by prolonged adaptation to physical rotation prior to viewing the Enigma figure. In this way we hoped to find out whether real and illusory motion perception interact within the same neuronal inventory.

Methods

Subjects

Six naïve subjects (mean age 26 yrs; SD = 2.5) participated in the experiment.

Stimuli

For motion adaptation a black-and-white sector disk (Kleiner, 1878) spinning either clockwise or counter-clockwise was displayed on the face of the monitor. The disk had the same radius as the outer ring of the Enigma figure (5.65 deg). Michelson contrast was 98.4 % and there were a total of 62 sectors. Speed of rotation was 12 deg/ s (0.03 rps). This speed was chosen because it yielded the longest motion aftereffect. Fixation was in the middle of the disk.

Procedure

Adapting time was 30 s. Immediately after adaptation to the sector disk, the Enigma figure was displayed for 15 s, during which period subjects reported the beginning as well as the direction of the apparent rotation by key press. There were 4 measurements for each of the 3 rings in each adapting direction. The total number of test periods was 144 (4 repetitions x 3 rings x 2 adapting directions x 6 subjects). The time interval between successive trials was 1 min.

The mean duration of the resulting motion aftereffect measured under these conditions was 9.2 s (SD = 3.2). Since the first reversal of the illusory rotation in Experiment 1 occurred on average after 6.8 s (2.1 s initial delay plus 4.7 s mean duration), any influence of the preceding adaptation to the real motion should be reflected in a shift of the initial direction bias towards the motion aftereffect.

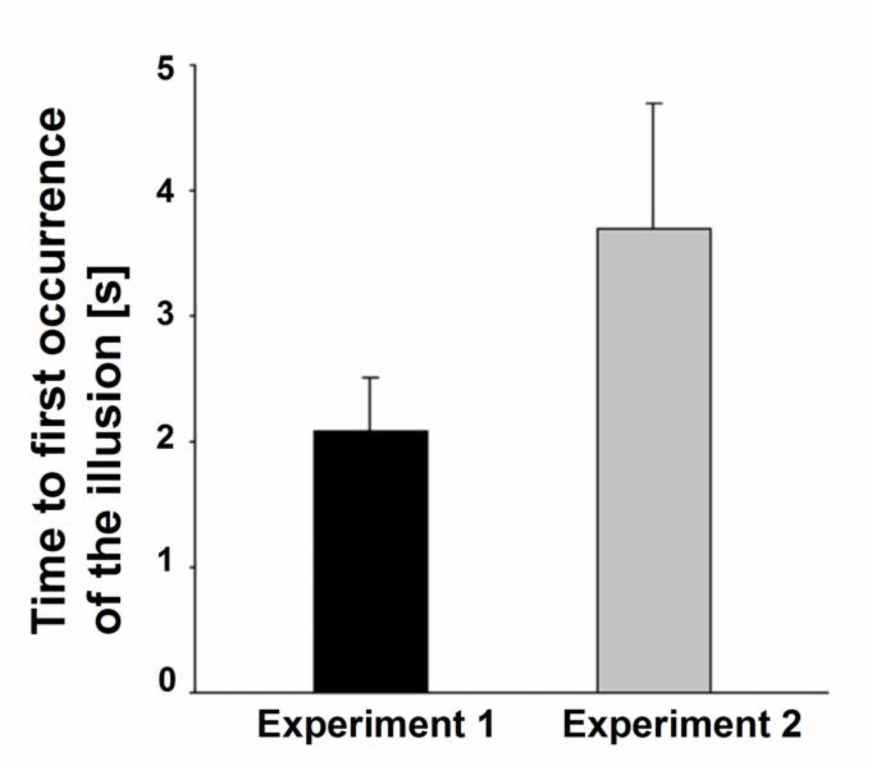

Figure 3: Time lag for first perceiving illusory rotation on the rings of the Enigma figure without and with adaptation to real motion. Data are averages from 105 (Experiment 1) and 144 (Experiment 2) trials. The bars give the standard error.

Results

Mean time required for perceiving the rotary motion after adaptation to real motion was 3.7 s (SD = 2.4 s), which is significantly longer than the time lag for the motion onset (2.1 s) found in Experiment 1 (Figure 3). There are no significant differences between the onset delays observed with clockwise adaptation and counter-clockwise adaptation (t_{71} = 0.61, p = n.s.). However, there was a major shift of the response bias at the beginning of a trial. After adapting to clockwise rotation, 31.9% of the responses were clockwise and 68.1% counter-clockwise. In comparison, after adapting to counter-clockwise rotation, 80.6 % of the initial responses were clockwise and 19.4 % counter-clockwise. These results are significantly different from the 64.8 % to 35.2 % ratio found without adaptation (Figure 4). The relative preference for clockwise direction is present even after adaptation.

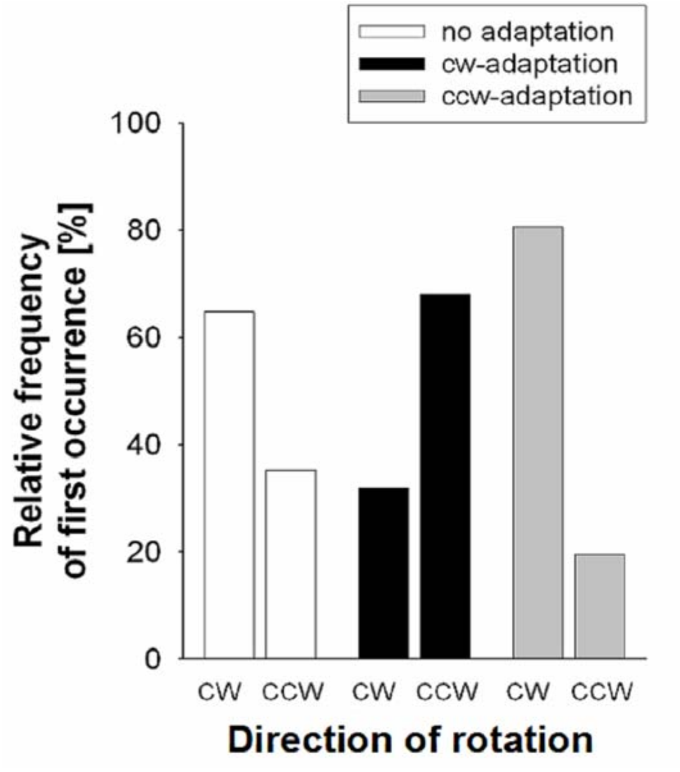

Figure 4: Relative frequency of first occurrence of clockwise and counter-clockwise rotation without and with adaptation to real motion in one or the other direction (see inset). Data represent 105 trials for "no adaptation" and 72 trials for each direction of "adaptation".

Discussion

Results show that the motion aftereffect resulting from adaptation to a rotating sector disk delays the onset of apparent motion in the Enigma illusion from 2.1 s to 3.7 s and also changes the directional bias towards the motion aftereffect. Specifically, previous adaptation to clockwise motion resulted in a 32.9% increase for counter-clockwise responses, while adaptation to counter-clockwise adaptation resulted in a 15.8% increase for clockwise responses. Thus, clockwise adaptation had an effect that was twice as strong as counter-clockwise adaptation, consistent with the initial directional bias found in Experiment 1.

We do not think that this result can be accounted for by a change of attention. It is true that the motion aftereffect attracts attention (Huk, Ress & Heeger, 2001). However, all subjects could readily distinguish between the global motion aftereffect that became immediately visible in the pre-adapted area of the Enigma figure and the apparent rotation on the three rings that emerged a few seconds thereafter.

From earlier observations we know that the motion aftereffect typically is strongest during the first 4 s after offset of the adapting stimulus, whereafter it rapidly declines and disappears. This is about the same time (3.7 s) that we measured for the onset of the Enigma illusion following adaptation to the sector disk. We therefore cannot rule out that the strong motion aftereffect masked and captured the weaker rotary motion on the rings delaying its onset and shifting the directional bias. On the other hand, the motion aftereffect might have interfered with the illusory motion because it has access to the same neural circuitry that mediates the Enigma illusion. This assumption would be consistent with the finding by Sterzer et al. (2002) that both real motion and illusory motion in the wagon-wheel figure produce activity in the same cortical area, MT+/V5 (occipito-temporal junction). PET-activation in motion sensitive cortical areas recorded in response to the Enigma figure (Zeki, Watson & Frackowiak, 1993) would also favor a neuronal interpretation. Meanwhile, it has been shown that in addition to motion, attention-generated activity needs also to be taken into account (Huk et al., 2001).

Experiment 3: T-junctions

To probe for an explanation of the Enigma illusion, we here asked whether and to what extent the illusory rotation requires orthogonal rays impinging on a closed annulus. Fermüller et al. (1997) report that in a large quadrant of the original Enigma figure (their Figure 8a) illusory motion in both directions continued to be seen within the segment. We extended this observation by reducing the segment to one eighth of a circle and still observed motion. Therefore, a closed annulus is not necessary for eliciting the Enigma illusion. Furthermore, Fermüller et al. (1997) used a linear grating pattern with six horizontally oriented gray bands intersecting the grating lines at right angles (their Figure 8b). Under these conditions illusory streaming motion was still present on the bands. Thus, curvature is not a requirement either. This is confirmed by the grainy motion seen in the undulating street pattern of DeRays (1976), as illustrated in Figure 5.

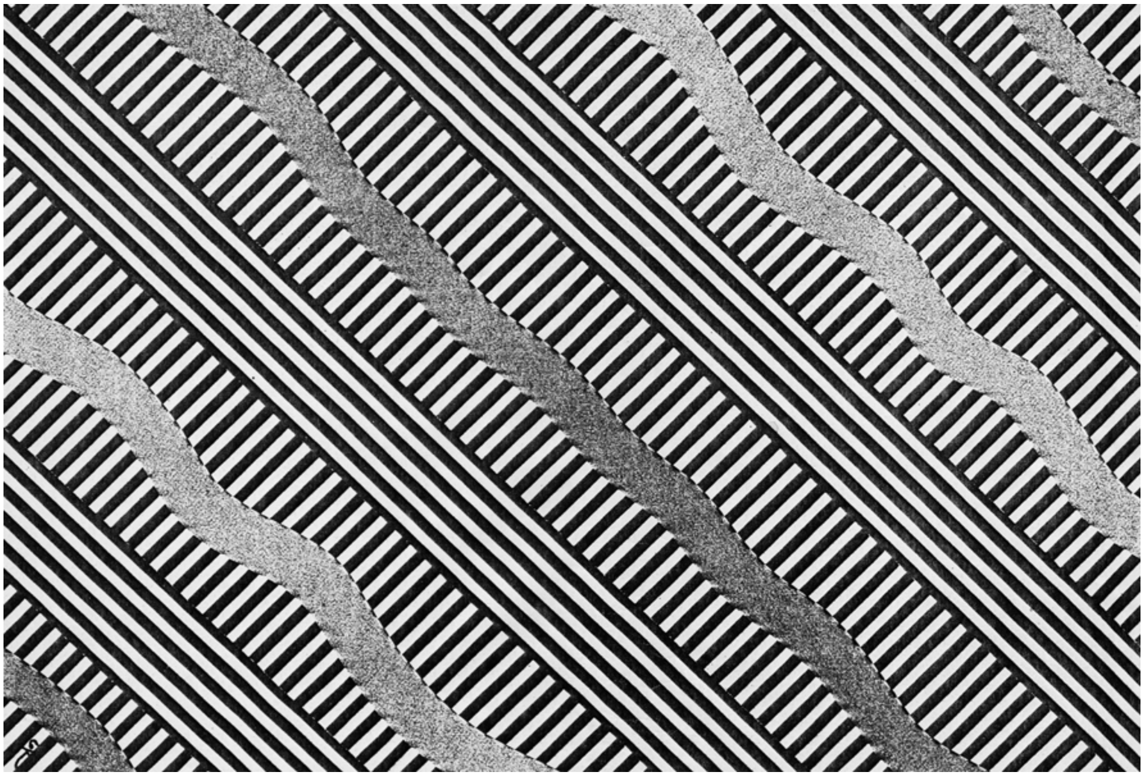

Figure 5: Street pattern by De Rays. Note the illusory motion of the grainy “dust” on the undulating streets.

All these patterns have in common that the inducing lines impinge at right or near-right angles onto the narrow interspace on which the illusory motion is seen. We therefore asked whether a 90 deg angle is critical for eliciting the illusory motion. The hypothesis was that T-junctions might be crucial for obtaining the illusory motion. To test for the effect of T-junctions, we superimposed a straight, bicolored bar comparable to the outer ring of the Enigma figure onto a black-and-white grating and systematically changed the angle between the bar and the grating lines.

Methods

Subjects

Eleven naïve subjects (mean age 30 yrs; SD = 4.8) participated in the study.

Stimuli

Six stimuli were presented, each composed of a black- and-white vertical grating and a bar with two shades of purple superimposed onto it. The grating had a spatial frequency of 1.7 cpd similar to the outermost set of radial lines in the Enigma figure and subtended 19.3 (height) x 29 deg (width). The black lines were again 1.5 times as wide as the white interspaces. The intersecting bar was 19.3 deg long and 1.4 deg wide. Fixation was 3.8 deg away from the center of the bar and orthogonal to it. The angle between the bar and the grating lines was randomly varied in steps of 18 deg from 90 deg (orthogonal) to 0 deg (parallel).

Procedure

Subjects were seated 40 cm away from the stimulus. The task was to rank-order the six different stimuli according to strength of the illusory motion seen on the chromatic bar. We used print-outs on paper, laid out in a random sequence, so that stimuli could be viewed and compared simultaneously. The results for all 11 subjects were then assigned to a scale ranging from 0 to 5 points. The pattern with the strongest illusory motion was assigned 5 points, the pattern with the weakest illusory motion was assigned 0 points, for each subject. This arbitrary scale was expressed as a percentage of the total.

Results

All subjects reported fast streaming motion streaks shuttling back and forth on the bar, comparable to the illusory motion on the 45 deg sector mentioned earlier. Figure 6 plots the strength of this motion as a function of the angle between the chromatic bar and the grating lines. Illusory motion increases linearly with increasing angle. The determination coefficient of the regression line was $R^2 = 0.99$ and the Bartlett Chi square was $\chi^2_1 = 13.98$ ($p < 0.001$).

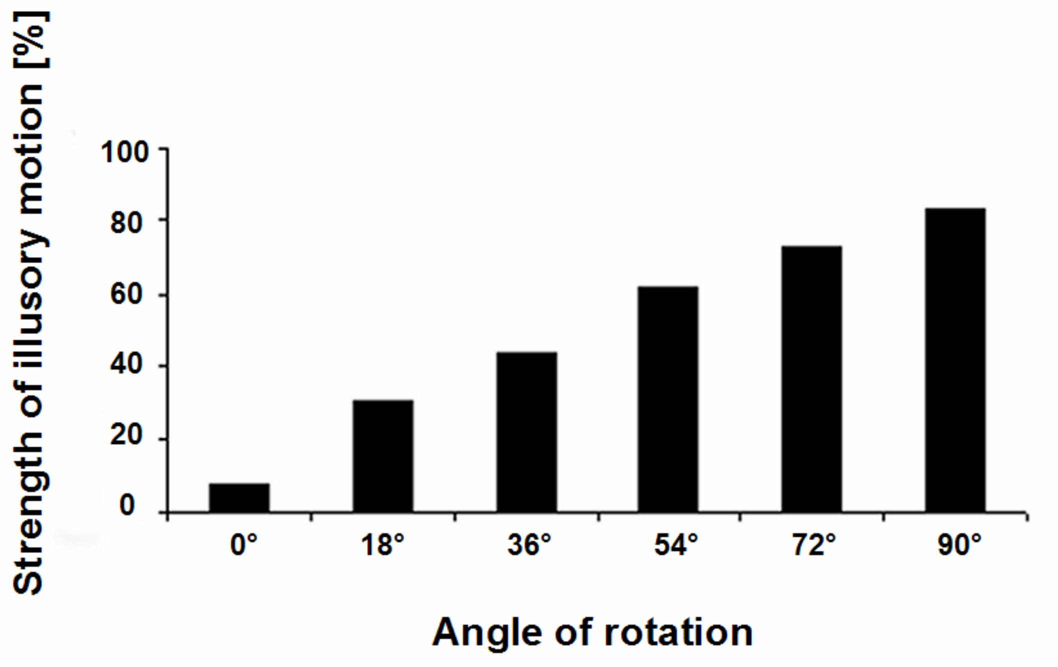

Figure 6: Strength of illusory motion as a function of the angle between a chromatic bar and the grating lines. Stimuli were rank-ordered according to strength and assigned to a scale ranging from 0 to 5 points. The results of 11 subjects were then cumulated and expressed as a percentage of the total (Σ = 55).

Discussion

Results show that T-junctions are a strong factor in eliciting illusory motion. Whereas the illusory motion was judged most salient (83.7%), when bar and gratings lines were oriented at right angles, it was least salient (7.3%), when the chromatic bar was oriented parallel to the grating. In fact, many subjects reported that in the latter case there was almost no motion. The progressive decrease in strength may depend on the reduction in figure-ground segregation and depth-ordering that may also affect the illusion. However, even these two factors cannot explain, how orientation signals from the terminators of the grating lines are transformed to produce rotary (and reversing) motion on the bar.

End-stopped neurons as a candidate mechanism for generating orthogonal motion have recently been shown to lack orientation specificity (Pack, Livingstone, Duffy & Born, 2003) and therefore no longer qualify for an explanation. We are therefore back to MacKay (1957, 1961), who described “complementary” afterimages, similar to the streaming motion in the Enigma figure, in radial, concentric, and grating patterns. He hypothesized that “the system tends to favor the direction at right angles to the regular contours, suggesting a theoretical model of form-perception in which directions at right angles are treated by the system as competitive” (MacKay, 1957). Visual neurons suitable for this task remain to be identified.

Conclusion

The perceived reversal of illusory rotation in Leviant’s Enigma figure with time follows an oscillatory pattern, irrespective of the retinal eccentricity of the rings. Initial rotation in the clockwise direction outweighed by far rotation in the counter-clockwise direction;

clockwise rotation also lasted longer than counter-clockwise rotation. Our findings demonstrate that this directional bias is influenced by previous adaptation to real rotation suggesting that the same higher-level processes that subserve the perception of real motion may also mediate illusory motion.

Our study shows a strong influence of T-junctions in line with previous results by Hamburger and Spillmann (2005). This dependency on angle rules out a low-level origin. A locus in the cortex is also evident from the PET-study by Zeki et al. (1993), who found activation in response to the Enigma illusion in motion sensitive cortical areas; and from the fMRI-study by Sterzer et al. (2002) reporting transient fMRI-activation in the same area correlated with directional motion reversals. Thus, combining psychophysics and brain imaging in future studies may provide us with better insight into the nature of this illusory motion phenomenon.

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Chapter 10 –

A new motion illusion: the Rotating-Tilted-Lines illusion[10]

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[10] This work was published in a slightly different form: Gori, S., & Hamburger, K. (2006). A new motion illusion: The Rotating-Tilted-Lines illusion. *Perception, 35,* 853-857.

A new static motion illusion, the Rotating-Tilted-Lines illusion, is introduced and it is discussed in the context of various other static motion illusions, such as the Pinna-Brelstaff illusion, the Rotating Snakes illusion, and the Enigma illusion. This new phenomenon is closely related to the Pinna-Brelstaff illusion but appears to be simpler and could therefore serve as a valuable research tool in upcoming studies on apparent motion perception.

Introduction

Visual illusions are not just entertaining; moreover, they are non invasive means for investigating human brain mechanisms. While they show us where our visual system fails, they can tell us how it works. Therefore, we here introduce a new motion illusion that could represent the simplest pattern that elicits illusory motion due to self-motion. It may be instrumental for future research to better understand motion processing in the brain.

A new motion illusion: the *Rotating-Tilted-Lines-Illusion*

Figure 1 represents the new *Rotating-Tilted-Lines-Illusion*. In its simplest form (Figure 1a) this new illusion arises in a circular pattern of 120 black, radial lines tilted by 45 degrees to the right and presented on a white background (ECVP 2005 Best Visual Illusion Contest, presented in: Martinez-Conde, Pérez & Martinez, 2005). When one approaches the stimulus pattern, the radial lines appear to rotate in counter-clockwise direction, whereas when one recedes from it, they appear to rotate clockwise. If the lines are tilted to left the illusory effects occurs in the opposite direction as a function of the self-motion. The length of the lines is not critical in this illusion. Only if the lines are too short to perceive their tilt anymore, the illusion disappears. These observations suggested that the tilt of the lines is the most important factor – the illusory effect disappears if the lines are arranged radially – as direction-selective neurons need to be taken into account for the illusory rotation (Morgan, 2002; Gurnsey, Sally, Potechin & Mancini, 2002). Furthermore, we created a more complex version of this illusion. The 'ring' of tilted lines is now embedded in a context of an equal number of lines oriented in the opposite direction representing the background (Figure 1b). Here, the illusory rotation is stronger and there may occur some residual counter rotation in the surround. Finally, in Figure 1c the tilted radial lines of Figure 1a were elongated, having only a serpent shape (as the surround in Figure 1b) without a ring of lines (this pattern is somewhat similar to *MacKay's ray figure*). Again, while approaching and receding from the pattern counter-clockwise and clockwise rotation is perceived depending on the direction of self-motion and the orientation of the lines. But, the rotation perceived is completely different from the 'complementary afterimage' described by MacKay (1957). His subjects reported spontaneous illusory rotation that could be in clockwise or in counter-clockwise direction. In contrast, the direction of perceived motion in our illusion is a function of the direction of a subject's self motion. This new kind of illusion also works perfectly well if the stimulus is moved instead of the observer's body. Informal observations in 40 subjects (age range 19 – 70 years) revealed that everybody was able to perceive the phenomena described above while moving towards or away from these patterns.

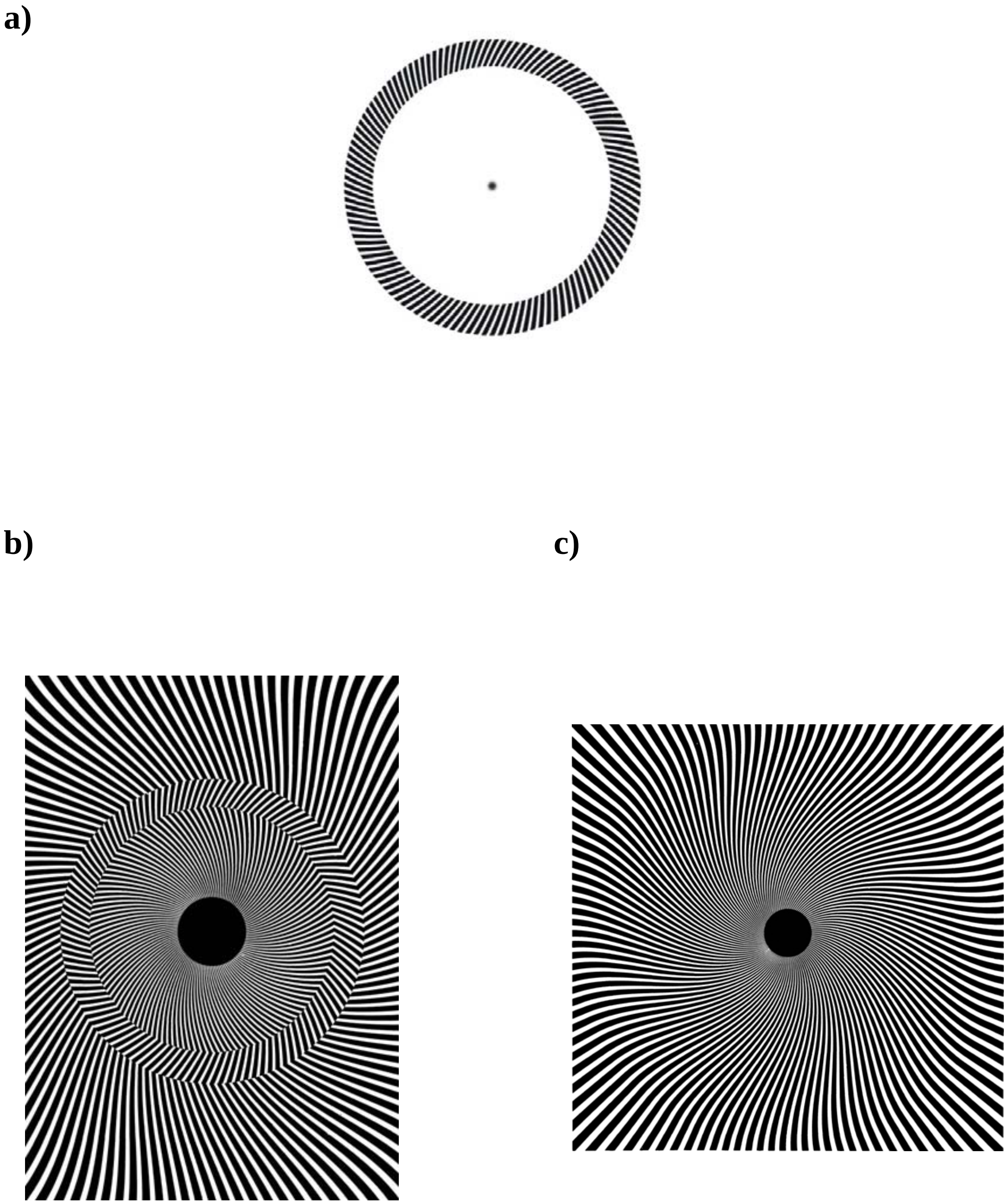

Figure 1: a) The simplest version of motion illusion that requires self-motion. 120 black radial lines are tilted by some degrees to one side. When one approaches the stimulus pattern, the radial lines appear to rotate in a counter-clockwise direction, whereas when one recedes from it, they appear to rotate clockwise. b) A more complex version of the previous illusion. In this version the illusory rotation is stronger and there may be some residual counter rotation in the surround. c) The tilted radial lines are elongated and have a serpent shape. Here, the same kind of counter-clockwise and clockwise rotation can be perceived as in the previous patterns. In this form the pattern might remind us of the MacKay rays (MacKay, 1957).

Combining two motion illusions

An additional aim was to create a new pattern that could elicit two different kinds of illusory motion; a spontaneous one and one due to self-motion. In Figure 2 the two designated illusory effects are combined. The tilted line pattern of Figure 1a is superimposed onto the colored rings of the *Enigma-Figure* created by Isia Leviant in 1981 (Leviant, 1996). The effect of perceived clockwise and counter-clockwise rotation is still present while approaching the pattern and receding from it (or moving the pattern towards or away from the eye). In the first case, the direction of motion is opposite the inclination of the lines (backward), in the second it is forward. Viewed statically streaming motion on the colored rings appears like in the *Enigma-Illusion*. There, the observer perceives a streaming or spinning motion on the colored rings in one or the other direction, whereas the direction of perceived motion changes frequently (Gori, Hamburger & Spillmann, 2005). This streaming motion in *Enigma* is still present (although slightly weaker) when the ciliar muscles of the eye are paralyzed (Zeki, 1994; Mon-Williams & Wann, 1996; Hamburger & Spillmann, 2005) or in a long-lasting stabilized afterimage (Hamburger & Spillmann, 2005). Which of the two combined illusory effects is perceived in Figure 2 depends on the mode of presentation, i.e., constant vs. variable observation distance.

As a side note, with static presentation of the stimulus pattern, one additionally may perceive a shimmer or jitter of the tilted radial lines as reported by MacKay (1957, 1958) and Gregory (1993, 1995, 2002a, 2002b). In contrast to the streaming motion in *Enigma* this effect does not occur with paralyzed ciliar muscles (Mon-Williams & Wann, 1996; Hamburger & Spillmann, 2005) or in a long-lasting stabilized afterimage (Gregory, 2002a; Hamburger & Spillmann, 2005). These results suggest cortical mechanisms for the *Enigma-Illusion* but a more low-level processing of the jitter in *MacKay's ray* figure.

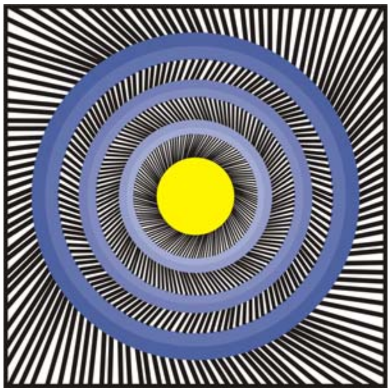

Figure 2: The illusory motions of the Enigma-Illusion and the Pinna-Brelstaff-Illusion become united in a single pattern (see also Figure 2c of chapter 8 for a larger representation). Fixating the center of the static patterns leads to spinning motion on the three rings, while approaching and receding from it leads to rotation of the tilted radial lines in clockwise or counter-clockwise direction.

Discussion and Conclusion

(i) The new *Rotating-Tilted-Lines-Illusion* presented in the first part (Figures 1a – c) appears to be the basic pattern or, at least, the simplest figure known so far that elicits illusory rotary motion caused by self-motion. Similar, but more complex phenomena have been reported by Pinna and Brelstaff (2000) and later on by Kitaoka (Kitaoka, 2000; Kitaoka, Pinna & Brelstaff, 2001) in several forms. However, their inducing patterns are different from ours as they use micropatterns (tiles) with dark and bright edges (or stimulus elements) that are subject to the aperture effect. In their cases, the polarity of stimulus elements (alternating black and white elements of a certain orientation; high luminance contrast) seemed to be the important parameter for the occurrence of the illusions. Gurnsey et al. (2002) found that not the precise geometrical structure of the micropatterns is critical, but the low-frequency orientation structure in the display, using complex Gabor patches. The luminance relationship of the static elements seems to be the main factor also eliciting illusory motion in the Rotating Snakes by Kitaoka (2000). Physiological evidence for the importance of luminance contrast are presented by Conway, Kitaoka, Yazdanbakhsh, Pack and Livingstone (2005) studying the directional selective neurons in the visual cortex of macaque during observation of the Rotating Snakes. In comparison, the illusory rotation in the pattern presented here is obtained by just tilting the black lines that compose the ring. No micropatterns are used here. Moreover, the illusory motion is even present at lower luminance contrasts. This last finding challenges the idea that the luminance relationship of the elements could be a good explanation for our new illusion. We suggest that the illusory motion derives from a difference in motion vector based on the sequential change of orientation of the lines. The enhanced rotation observed in the complex version of our pattern may additionally arise from the difference in phase and orientation of the abutting lines. As a side note, another way to enhance the illusory effect is to present a smaller circle of lines tilted in the other direction inside of Figure 1a. Then we obtain the same effect as in the Pinna-Brestaff Illusion without using micropatterns.

We are planning to investigate the hypothesis described above by systematically varying the angle at which the grating lines abut each other. We suggest that our simplest version of the illusion could be a candidate for single-cell recording studies, exploring how direction-selective neurons are involved in this “failure” of our brain to interpret the reality. Moreover, future brain imaging studies could benefit from this new illusion endorsing recent fMRI studies investigating the Pinna-Brelstaff illusion (Budnik, Speck, Kaller, Hamburger, Pinna & Hennig, 2005) and the Spinning-Disks illusion (Williams, Zanker & Ashida, 2005) and find out whether real motion as well as illusory motion are processed within the same brain areas. Utilizing our simpler forms of rotary motion illusion allows for better experimental controls and might reduce the number of possible artifacts (noise) in investigating processing mechanisms for illusory motion in the brain because of its simplicity.

(ii) With the combination of illusions (Figure 2) we demonstrate that a single pattern can elicit two different kinds of rotary motion. Combining two different illusory effects may not be a novel finding, but here the mode of presentation is crucial for the different effects to occur. With static presentation the *Enigma-Illusion* arises, whereas with dynamic presentation the illusory counter rotation of the lines is perceived. Each may require different mechanisms of processing in the visual system and different explanations. This pattern shows us that we need to distinguish different ‘classes’ of motion illusions – by mode of presentation and maybe by processing mechanisms in the visual system and cortex as well –, instead of subsuming them all under the simple term of ‘motion illusion’.

(iii) Last but not least, we would like to stimulate researchers’ and naïve observers’ thoughts with our new illusions.

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III Conclusion

We presented deep insights and elaborate discussions to each topic in the discussion sections of each chapter. Therefore, we want to abjure to repeat them here again.

In summary, with an elaborate series of different psychophysical experiments and theoretical approaches presented here, we provide the reader and the field of Vision Sciences with further knowledge about the human visual system, from low- to higher-level processes in the visual cortex (from early as the retina and LGN to V5/MT, MST). To realize this aim, we utilized a great variety of illusory phenomena and limitations of the visual system. Additionally, we were also able to provide new visual illusions for future research on the human or monkey visual system, such as the weaves or the Rotating-Tilted-Lines illusion.

Future research

A major task of this series of studies and the upcoming ones is to establish a new classification system for visual illusions in the near future. Classical works on categorizing illusions have mainly been based on phenomena (e.g., Luckiesh, 1922; Boring, 1942; Tolanski, 1964; Gregory, 1968, 1997). Rather than a phenomenologically based classification system, we are trying to identify the neural processes underlying these phenomena and employ them as better variables for categorization. Such a new classification system could be implemented in diagnostics of lesions ranging from the retina to the striate and extra-striate cortex.

This thesis takes a step forward.

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Giessen, 21. Dezember 2006 Kai Hamburger