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Geometric-optical illusions at isoluminance

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Abstract

The idea of a largely segregated processing of color and form was initially supported by observations that geometric-optical illusions vanish under isoluminance. However, this finding is inconsistent with some psychophysical studies and also with physiological evidence showing that color and luminance are processed together by largely overlapping sets of neurons in the LGN, in V1, and in extrastriate areas. Here we examined the strength of nine geometric-optical illusions under isoluminance (Delboeuf, Ebbinghaus, Hering, Judd, Müller-Lyer, Poggendorff, Ponzo, Vertical, Zöllner). 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 effective as the luminance versions (both for high and low contrast). The magnitudes of the illusion effects were highly correlated across subjects for the different conditions. In two additional experiments we determined that the strong illusions observed under isoluminance were not due to individual deviations from the photometric point of isoluminance or due to chromatic aberrations. Our findings show that our conscious percept is affected similarly for both isoluminance and luminance conditions, suggesting that the joint processing for chromatic and luminance defined contours may extend well beyond early visual areas.

Keywords: Geometric-optical illusions; Isoluminance; Luminance contrast; Magnocellular pathway; Parvocellular pathway

1. Introduction

Among the illusions with the longest history in vision science is the class of geometric-optical illusions that are constructed from lines and simple geometric forms. These illusions are typically presented achromatically, as black lines on white background (Fig. 1). Isoluminant variants of these illusions have been used for a long time to investigate the factors that contribute to these illusions (for a review, see Cavanagh, 1991). Very early studies with isoluminant geometric-optical illusions have focused on the question whether irradiance, i.e., the apparent increase of brighter surfaces in size, may contribute to the illusion (Lehmann, 1904; Liebmann, 1927). More recently, attempts have been made to link the geometric-optical illusions to the physiology of early visual processing (Li & Guo, 1995; Livingstone & Hubel, 1987, 1988; Puts, Pokorny, & Smith, 2004).

While some studies have found that geometric-optical illusions break down under isoluminance (Lehmann, 1904; Liebmann, 1927; Livingstone & Hubel, 1987), others showed that most illusions are present under isoluminance as well (Cavanagh, 1986, 1989; Gregory, 1977, 1979; Li & Guo, 1995), as summarized in Table 1. The finding that geometric-optical illusions persist under isoluminance is consistent with physiological findings showing that color and luminance are processed together by the same parvo retinal ganglion cells (De Valois & De Valois, 1988) and that neurons in V1 and V2 respond to oriented chromatic contrast (e.g., Friedman, Zhou, & von der Heydt, 2003; Gegenfurtner & Kiper, 1992; Johnson, Hawken, & Shapley, 2001; Lennie, Krauskopf, & Sclar, 1990; for review, see Gegenfurtner, 2003). Based on this physiological evidence and the prior psychophysical work one may expect that geometric-optical illusions occur at isoluminance. However, the study with the largest number of illusions

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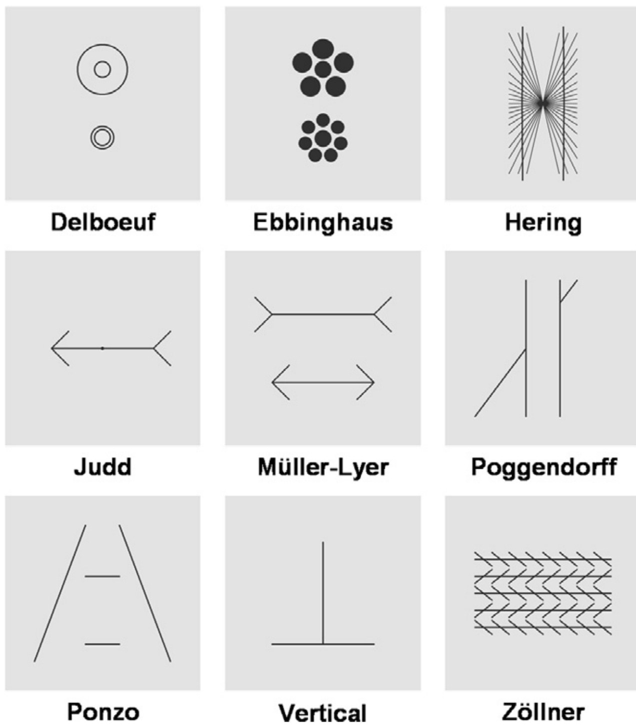


Fig. 1. The classical geometric-optical illusions investigated.

tested so far has found just the opposite (Livingstone & Hubel, 1987). We tried to resolve this issue by investigating a whole range of illusions using a large number of observers. Since the stimuli in these and in the earlier experiments mainly consist of thin lines, chromatic aberrations are a serious concern. Therefore we performed additional experiments with blurred stimuli to reduce any potential effects of chromatic aberrations.

Unlike previous studies, we (i) used a large number of nine geometric-optical illusions (Delboeuf, Ebbinghaus, Hering, Judd, Müller-Lyer, Poggendorff, Ponzo, Vertical, Zöllner; for comparison to other studies see Table 1) that are investigated (ii) under high and low luminance contrast and two isoluminant chromatic contrast conditions (reddish—greenish and greenish-yellow—purplish), varying along physiologically meaningful axes ($L-M$ axis, and $S-(L+M)$); (iii) use a large number of subjects to compute correlations between the different conditions; and (iv) control for chromatic aberration by using blurred stimuli. Each contrast condition was investigated in a series of three psychophysical experiments. In the first experiment we investigated the two luminance contrast conditions (low and high contrast) and the two isoluminance conditions ($L-M$ and $S-(L+M)$ axis) under photometric isoluminance for a large number of 20 subjects. In Experiment 2 we repeated the first experiment using subjective isoluminance values for each subject and also tested several discrete contrast values between the points of photometric and subjective isoluminance in repeated sessions. In Experiment 3 we used low-pass filtered (blurred) stimuli to control for chromatic aberration. The nine geometric-optical illusions investigated here show illusions of size, length, orientation, curvature, and position. These illusions were chosen because they are among the oldest and most prototypical examples which allows for a comparison to previous studies. We investigated the illusory effects using a paradigm where subjects could adjust for each illusion the length, size, orientation, curvature or position of the critical stimulus parameter. This allowed us to quantify the strength of the illusions under each condition. Overall, we have found that all illusions persist under all conditions tested. In almost all cases the illusions presented under the different conditions of isoluminance or luminance were of equal strength and highly correlated across subjects.

2. Experiment 1—Photometric isoluminance

In this experiment we investigated geometric-optical illusions under photometric isoluminance. We tested 20 subjects with nine illusions shown in four conditions (high and low achromatic contrast and photometric isoluminance in two chromatic directions).

2.1. Method

2.1.1. Subjects

Twenty naïve student subjects (10 females, 10 males) participated in the experiment. In this and the 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). All participants were right-handed. The age ranged between 20 and 48 years.

Table 1
Overview of studies of geometric-optical illusions under isoluminance: stimuli and findings showing that illusions exists (X) or not (O); empty cells refer to illusions that have not been tested

	Delboeuf	Ebbinghaus	Hering	Judd	Müller-Lyer	Münsterberg	Poggendorff	Ponzo	Vertical	Zöllner
Lehmann (1904)					O	O	O			O
Liebmann (1927)					O	O	O			
Gregory (1977)					X	O		X		X
Livingstone and Hubel (1987)			O		O		O	O		O
Cavanagh (1989)									X	X
Li and Guo (1995)	X				X			X		X
This study	X	X	X	X	X		X	X	X	X

2.1.2. Color space

The stimulus chromaticities in all experiments were defined in the DKL color space (Derrington, Krauskopf, & Lennie, 1984; Krauskopf, Williams, & Heeley, 1982). The DKL color space is a second stage cone-opponent color space that reflects the preferences of retinal ganglion cells and LGN neurons. It is spanned by an achromatic luminance axis, the L + M axis, and two chromatic axes, the L − M axis, and S − (L + M) axis. The two chromatic axes define an isoluminant plane. These three so-called cardinal axes intersect at the white point. The L + M axis is determined by the sum of the signals generated by the long wavelength sensitive cones (L-cones) and the middle wavelength sensitive cones (M-cones). The L − M axis is determined by the differences in the signals as generated by the L-cones and the M-cones. Along the L − M axis the L- and M-cone excitations co-vary at a constant sum, while the S-cone excitation does not change. Colors along the L − M axis vary between reddish and bluish-greenish. The S − (L + M) axis is determined by the difference in the signals generated by the short wavelength sensitive cones (S-cones) and the sum of the L- and M-cones. Along the S − (L + M) axis only the excitation of the S-cones changes and colors vary between yellow-greenish and purple.

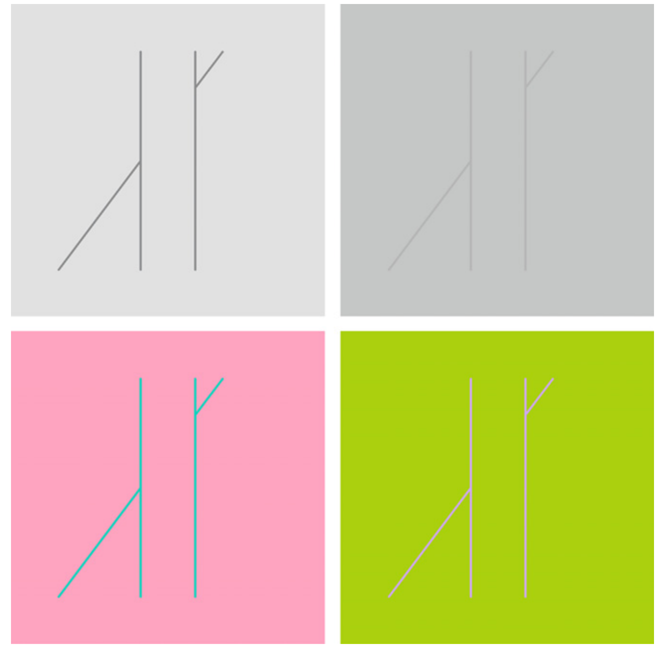


Fig. 2. Four different luminance conditions exemplified with the Poggendorff illusion. Fifty percent luminance contrast condition (dark gray/light gray; upper left), 10% luminance contrast (gray; upper right), isoluminance with L − M color contrast (lower left), and isoluminance with S − (L + M) color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

2.1.3. Stimuli

Nine different visual illusions were tested in all experiments (Fig. 1): Delboeuf (Delboeuf, 1892); Ebbinghaus (e.g., Wundt, 1898); Hering (Hering, 1861); Judd (Judd, 1899); Müller-Lyer (Müller-Lyer, 1889); Poggendorff (Burmester, 1896; Zöllner, 1860); 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/). All stimuli subtended 17 deg of the visual field and had a constant line width of 4 pixels, corresponding to 0.14 deg. A smaller line width of 1 pixel (0.035 deg) was used for the radial lines of the Hering illusion. Stimuli were presented in a classical luminance contrast condition (50% contrast; dark gray lines on light gray background), a low luminance contrast condition (10% contrast, medium gray lines on slightly lighter background), and two isoluminance conditions along the cardinal axes of DKL color space (L − M, reddish lines on bluish-greenish background and S − (L + M), purplish lines on yellow-greenish background). Sample stimuli for high and low luminance contrast and for the isoluminant color contrast conditions are depicted in Fig. 2.

2.1.4. Procedure

Subjects were instructed to adjust the length (Judd, Müller-Lyer, Ponzo, Vertical), size (Delboeuf, Ebbinghaus), orientation (Zöllner), curvature (Hering), or position (Poggendorff) in the particular stimulus 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 of 1 pixel (0.035 deg) at a time were achieved by pressing a key just once. Observers were instructed to adjust the point of subjective equality from two directions (ascending and descending). The initial value of the adjustable parameter was randomly varied in each trial. Possible adjustments ranged from −1.4 deg (−40 pixel), corresponding to a physical enhancement of the illusory effect, to +2.8 deg (+80 pixel), corresponding to the expected compensation of the illusory effect. When subjects perceived the stimuli to have equal length, size, orientation, etc., they pressed the space bar to confirm 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. Each stimulus was presented four times in randomized order. Stimuli were presented on a gamma corrected 21″ Iiyama Vision Master Pro 513 CRT monitor with a resolution of 1154×768 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.

Stimuli were presented in four conditions of luminance and isoluminance which were randomly intermixed in each session.

Condition 1: In the high luminance contrast (50%) condition the background was achromatic light gray (78.2 cd/

m[2]) 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 (56.9 cd/m^2), whereas a slightly darker gray was used for the stimuli.

Condition 3: In the L – M photometric isoluminance condition pure chromatic contrast along the cardinal L – M axis of the DKL color space (Derrington et al., 1984; Krauskopf et al., 1982) was used. The luminance of the stimulus was 52.4 cd/m^2. The stimuli were drawn with bluish-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: In the S – (L + M) photometric isoluminance condition, pure chromatic contrast along the cardinal S – (L + M) axis of the 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.

2.2. Results

Subjects compensated for the illusory effect by adjusting the stimulus elements in the direction opposite to the illusory effect. All subjects were affected by all illusions under all four contrast conditions. Results are shown in Fig. 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 consistent over conditions: those subjects who adjusted low or high values in one condition adjusted similar values in the other condition (Fig. 4).

Illusory effects under all conditions were significantly different from zero. Even though an ANOVA for repeated measures revealed some significant differences across conditions (all values are Greenhouse–Geisser corrected; Delboeuf: $F_{1.842} = 9.005$, $p = .001$; Ebbinghaus: $F_{2.787} = 5.370$, $p = .003$; Hering: $F_{2.391} = 7.749$, $p = .001$; Judd: $F_{2.751} = 1.579$, $p = .208$; Müller-Lyer: $F_{2.546} = 2.134$, $p = .117$; Poggendorff: $F_{2.595} = 1.390$, $p = .258$; Ponzo: $F_{2.397} = 1.219$, $p = .310$; Vertical: $F_{2.478} = 6.421$, $p = .002$; Zöllner: $F_{2.745} = 7.254$, $p = .001$), these differences were not present anymore in the Bonferroni-corrected *t*-tests. Significant differences just occurred for the Hering illusion. For example, here the luminance condition was significantly stronger than the low luminance and the isoluminant conditions. However, these differences were small compared to the overall strength of the illusion, which were present under all conditions. Within subject variability of the illusory effects was small. The smallest variability occurred in the Judd illusion (average *SD* 0.11 deg across all conditions), the largest variability occurred in the Vertical illusion (average *SD* 0.36 deg across all conditions). Gender analysis did not reveal any significant differences in illusion strength between females and males across the different conditions. Therefore, gender differences were not further investigated in the other experiments.

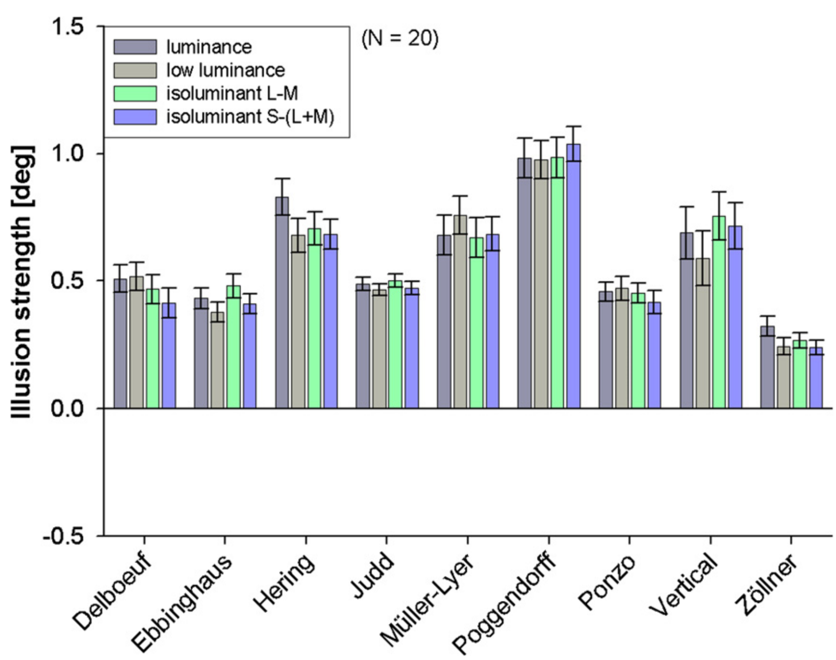


Fig. 3. Results for the different geometric-optical illusions at luminance contrast and photometric isoluminance ($N = 20$). Error bars denote the SEM. Illusory effects occur with similar strength under all conditions. Subjects were very consistent across conditions (Pearson's correlation coefficient varied between $r = .645$ and $r = .968$ with a median of $r = .850$).

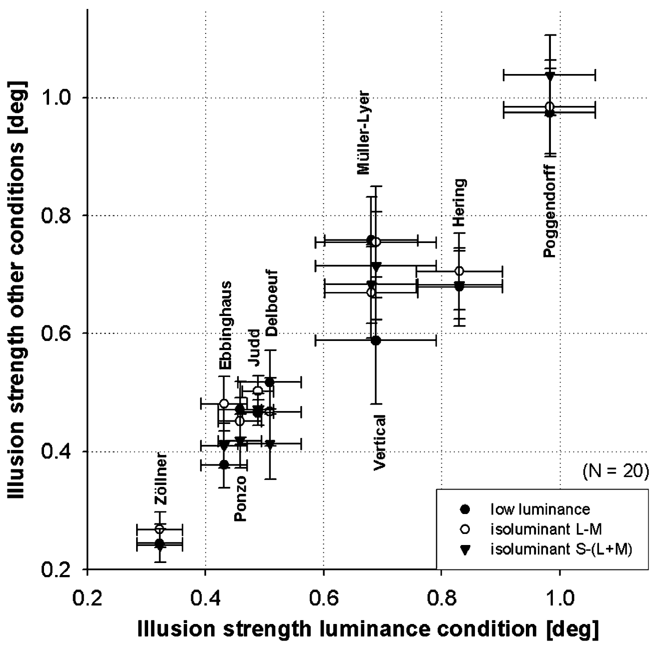


Fig. 4. Correlations between the luminance condition and the other conditions tested (low luminance, isoluminance L − M, isoluminance S − (L + M)). Horizontal error bars denote the SEM in the luminance condition and vertical error bars denote the SEM in the other conditions. High correlations between 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.

3. Experiment 2—Subjective isoluminance

Since individual observers vary to some degree in their subjective point of isoluminance, it is possible that the settings in Experiment 1 could have been at least partly due to residual luminance effects caused by these deviations. We therefore measured the point of subjective isoluminance individually for each subject. Isoluminant stimuli were then presented based on these measured values. We tested 10 subjects with nine illusions shown in four conditions, similar to Experiment 1.

3.1. Method

3.1.1. Subjects

Ten 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.

3.1.2. Stimuli

The same stimuli as in Experiment 1 were used.

3.1.3. 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 stimulus color and the other part was filled with the background color. Subjects had to adjust the subjective luminance of the stimulus colors until the border between the two parts of the disc became least visible. 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 subjective value of isoluminance used in the main experiment.

3.2. Results

Results for the subjective isoluminance experiment are shown in Fig. 5. Again, all subjects were affected by all illusions, and illusions occurred robustly under subjective isoluminance.

Next we computed the individual correlations between the values measured in the two luminance conditions to the values measured under the conditions of subjective isoluminance (L − M and S − (L + M)). Most conditions (25 out of 36; nine illusions × two luminance conditions × two isoluminant conditions) correlated highly with each other and were significant with a median value of $r = .836$. We also computed correlations between the two isoluminance conditions. The lowest and only insignificant correlation for isoluminance L − M vs. isoluminance S − (L + M) occurred for the Ebbinghaus illusion ($r = .590$, $p = .072$). All other correlations were significant, with the highest correlation found for the Vertical illusion ($r = .932$, $p < .001$). The median of correlations was $r = .812$.

An ANOVA for repeated measures did not reveal any significant differences of illusion strength across conditions except for Hering (all values are Greenhouse–Geisser corrected; Delboeuf: $F_{2.477} = .589$, $p = .598$; Ebbinghaus: $F_{2.153} = .650$, $p = .544$; Hering: $F_{2.335} = 4.212$, $p = .024$; Judd: $F_{2.470} = .943$, $p = .422$; Müller-Lyer: $F_{1.587} = 1.980$, $p = .179$; Poggendorff: $F_{2.192} = 1.909$, $p = .172$; Ponzo: $F_{2.144} = 2.007$, $p = .159$; Vertical: $F_{2.375} = .104$, $p = .929$; Zöllner: $F_{2.438} = 1.144$, $p = .345$).

Since subjective isoluminance settings can be quite variable, it is not entirely clear whether they actually improve upon the photometric settings. Note that the photometric setting is based on the luminance sensitivity curve which has been obtained by averaging over a large number of observers to reduce variability (e.g., Stockman & Sharpe, 1998, 2000). There is no ideal solution to this problem, but as an additional precaution we repeated Experiment 2 using five different isoluminance values between subjective and photometric isoluminance. Three female subjects from Experiment 2, aged between 20 and 22, participated

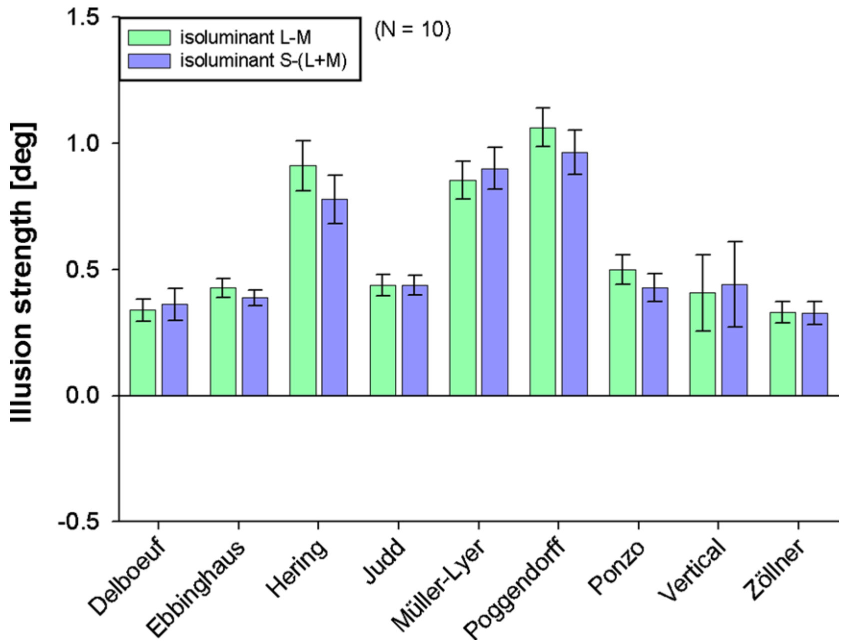


Fig. 5. Results for the different geometric-optical illusions at subjective isoluminance ($N = 10$). Error bars denote the SEM. Illusory effects occur with similar strength under all conditions.

in this multi-session experiment. Between experimental sessions there was a break of at least one day. The results are shown in Fig. 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 without any significant differences in illusion strength for the five different luminance contrast conditions (from photometric to subjective isoluminance).

It has frequently been reported that some geometric-optical illusions such as the Zöllner illusion (Judd & Courten, 1905) or the Müller-Lyer illusion (Judd, 1902; Köhler & Fishback, 1950a, 1950b; Schiano & Jordan, 1990) become greatly reduced or even vanish with repeated exposure. We did not find such an effect; all subjects taking part in more than just one of the experiments did not show any attenuation of illusory effects.

4. Experiment 3—Low-pass filtered (blurred) stimulus edges

Chromatic aberration can introduce luminance artifacts into nominally isoluminant stimuli (Flitcroft, 1989; Marimont & Wandell, 1992). 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 ran an experiment using low-pass filtered images (blurred edges).

4.1. Method

4.1.1. 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 chosen to allow for a comparison between high contrast and blurred edges.

4.1.2. Stimuli

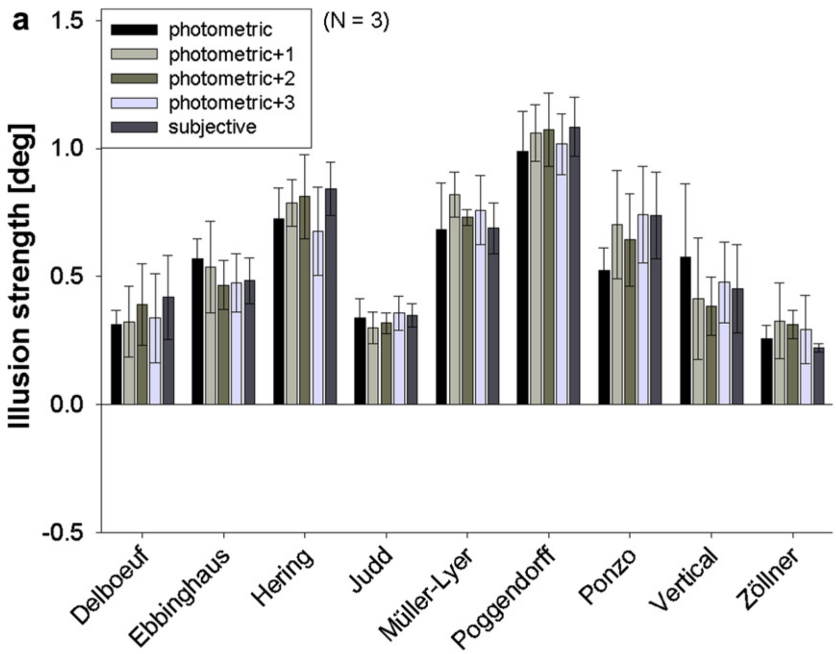
The same stimuli as in Experiment 1 were used in this experiment. Stimuli were blurred with a discrete approximation of a Gaussian filter (binominal filter with an order of $n = 20$). The standard deviation of the filter was $\sigma = \sqrt{(n/4)} = 2.24$ pixels corresponding to a visual angle of 0.078 deg or 4.696 min. The order of the binomial filter was chosen to reduce high spatial frequency components above 4 cyc/deg. The chosen filter reduces the amplitude at 4 cyc/deg to 2.5% of the mean value (0 frequency), which should greatly reduce potential effects of chromatic aberration (see Cavanagh & Anstis, 1991).

4.1.3. 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.

4.2. Results

Results for Experiment 3 are shown in Fig. 7. All illusions were present with blurred stimuli. A comparison of the mean illusory effects in Experiment 1 (Fig. 3) with those in Experiment 3 (Fig. 7) did not reveal any major differences, just small effects for the Hering and Zöllner illusion. For each illusion the strength of the illusory effect was similar across all conditions.



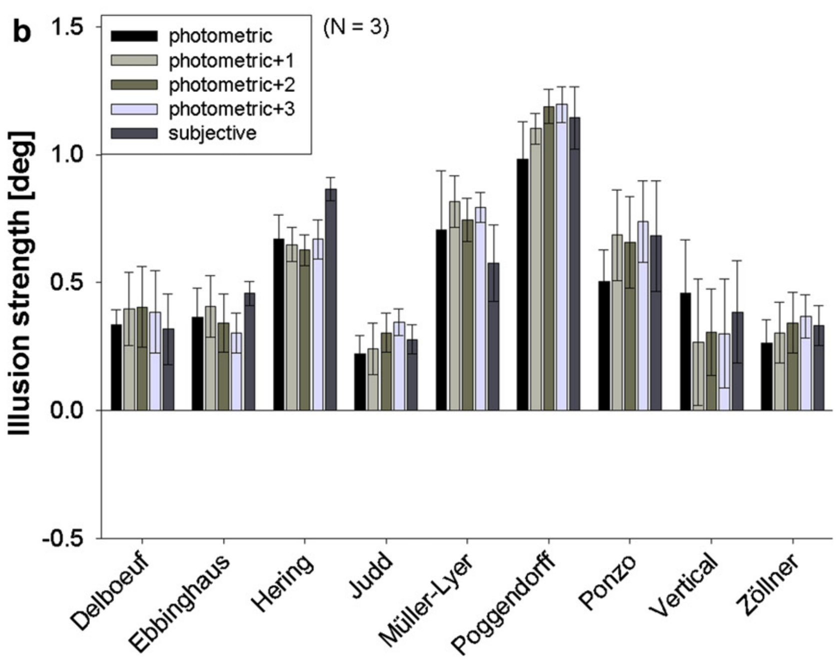


Fig. 6. (a) Results for the different geometric-optical illusions in the L – M color contrast condition at five different luminance values varying from photometric to subjective isoluminance ($N = 3$). Error bars denote the SEM. Illusory effects occur with similar strength under all conditions. (b) Results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

We also computed the individual correlations between the values measured in the four conditions. Most conditions (42 out of 54, nine illusions × six pairs) were significantly correlated. The lowest significant correlation was obtained in the Hering illusion ($r = .674$, $p = .046$ for isoluminance L – M vs. isoluminance S – (L + M)), whereas the highest correlation was obtained in the Ponzo illusion ($r = .993$, $p < .001$ for isoluminance L – M vs. isoluminance S – (L + M)). All other significant correlations were in between these two. For three illusions (Ebbinghaus, Hering, and Zöllner), not all conditions correlated significantly. In particular, three correlations were moderate but insignificant ($r > .580$, $p < .010$; Ebbinghaus luminance vs. isoluminance L – M, isoluminance L – M vs. isoluminance S – (L + M); Hering low luminance vs. isoluminance L – M) and some correlations were far from 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

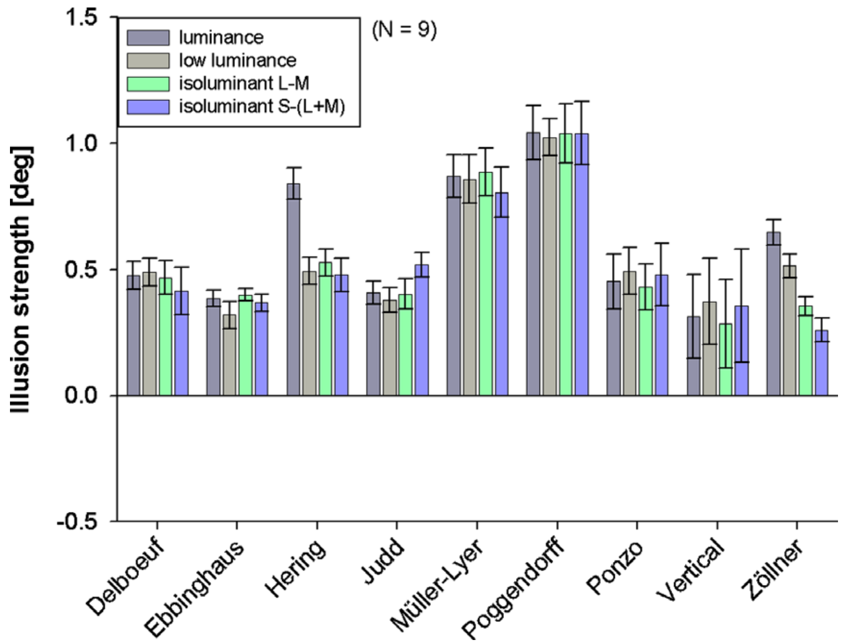


Fig. 7. Results for the low-pass filtered geometric-optical illusions at luminance contrast and photometric isoluminance ($N = 9$). Error bars denote the SEM. Illusory effects occur with similar strength under all conditions.

S − (L + M); and all combinations but that for luminance vs. low luminance in the Zöllner illusion).

An ANOVA for repeated measures revealed significant differences for Hering, Judd, and Zöllner (all values are Greenhouse–Geisser corrected; Delboeuf: $F_{1.830} = 1.022$, $p = .378$; Ebbinghaus: $F_{1.810} = 1.872$, $p = .191$; Hering: $F_{2.096} = 19.753$, $p = <.001$; Judd: $F_{2.522} = 6.664$, $p = .004$; Müller-Lyer: $F_{1.722} = .778$, $p = .461$; Poggendorff: $F_{2.899} = .026$, $p = .993$; Ponzo: $F_{2.056} = .867$, $p = .441$; Vertical: $F_{2.062} = .569$, $p = .582$; Zöllner: $F_{1.821} = 18.343$, $p = <.001$). In the following t-tests just differences between conditions in Hering and Zöllner remained. However, these differences were of minor interest, since the illusion strengths were in all cases significantly different from zero.

5. Discussion

We investigated nine geometric-optical illusions under conditions of isoluminance compared to low and high luminance contrast. The present study extends earlier ones in several ways by (i) testing further geometric-optical illusions; (ii) investigating isoluminant variations along the S − (L + M) axis; (iii) using a large number of subjects to compute correlations between the different conditions; and (iv) control for chromatic aberration using blurred edges. All subjects showed the illusory effects under each of the four luminance and isoluminance conditions and across all three experiments using different presentations (photometric isoluminance, subjective isoluminance, five discrete steps from photometric to subjective isoluminance, low-pass filtered stimuli). Individual adjustments were highly consistent in all experiments. Even though few significant differences between illusory strengths were obtained, they did not reveal any systematic differences (except Hering in Experiment 1, and Hering and Zöllner in Experiment 3). 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 purely chromatic contrast elicited an illusory effect as strong as in the luminance conditions. The present study is the study with the largest number of geometric-optical illusions and the most systematic variations investigated so far (cf. Table 1).

5.1. Comparison to earlier studies

It has been claimed that geometric-optical illusions are mediated by the magnocellular system and break down under isoluminance when only the parvocellular system is stimulated (Hubel & Livingstone, 1987; Livingstone & Hubel, 1987, 1988). This idea was based on the assumption of a totally independent processing of different features such as color, luminance, and form in different anatomical pathways. However, numerous studies have now demonstrated that subcortical pathways combine early in the cortex and cannot be mapped to independent functional streams (Felleman & Van Essen, 1991; Lamme & Roelfsema, 2000; Sincich & Horton, 2005). For example, Johnson et al. (2001) reported that many neurons in V1 of the macaque monkey respond robustly to an oriented contrast defined by isoluminant color or luminance modulation (color-luminance cells).

But why did these and other studies (Lehmann, 1904; Liebmann, 1927) report geometric-optical illusions to vanish under isoluminance? Most likely, the lines were too thin to be resolved by the chromatic system. Contrast sensitivity for chromatic gratings declines strongly with increasing spatial frequencies (Kelly, 1983). Cavanagh (1986,1989) found that geometric-optical illusions occur at full strength under conditions of isoluminance with large stimuli (8 deg) and bold lines of about 30 arc min.

More recently Li and Guo (1995) investigated four geometric-optical illusions (Delboeuf, Müller-Lyer, Ponzo, and Zöllner) under conditions of isoluminance along the L − M axis. In agreement with the present study they found that the four illusions they tested occur with equal strength under conditions of isoluminance and luminance contrast. They suggest that geometric-optical illusions of length, size, and orientation are mediated by the parvocellular system.

5.2. Effects of blur and contrast

In Experiment 3 we used a low-pass filtering to reduce potential effects of chromatic aberration. Results were similar to those obtained in the previous two experiments. Consequently, the illusions we found for isoluminant stimuli are unlikely to be caused by luminance artifacts due to chromatic aberration. A comparison of Experiment 1 and Experiment 3 revealed some differences in illusion strength for the Hering and Zöllner illusions, but they were not systematic in nature.

It has been shown that the Poggendorff illusion increases when the lines are highly blurred, while moderate amounts of blur (*SD* of the Gaussian filter below 6 arc min) had no effect on the illusory bias (Morgan, 1999). In our experiments blurring did not reduce any illusory effects. This is in agreement with the finding by Morgan (1999), because the standard deviation of the filter we used (4.7 arc min) was below the range where Morgan found an effect.

It has also been claimed that high contrast borders are necessary for geometric-optical illusions to occur. For example, Li and Guo (1995) have found that the Zöllner illusion disappeared at 15% contrast. In our experiments, all nine illusions occurred robustly even at a low luminance contrast of 10%. Li and Guo (1995) used a slightly smaller width of the lines (6.3 arc min compared to 8.4 arc min in the present study), which may account for the difference. Our results are in line with Zanker and Abdullah (2004) who used shaded areas adjacent to the main line in the Müller-Lyer illusion and the Judd illusion to influence the three-dimensional interpretation of the stimuli. With this partial reduction of line contrast they did not find any reduction in the illusory effect.

5.3. Correlations between conditions

Overall, subjects in our experiments were highly consistent within and across conditions. We found that 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 with low-pass filtered stimuli. The fact that there were very high correlations between the conditions substantiates the hypothesis that the illusory phenomena tested here are mediated by the same neural mechanisms. Since neurons in the magnocellular layers of the LGN have an exceedingly low sensitivity to these chromatic stimuli (e.g., Schiller, Logothetis, & Charles, 1991), these results strengthen the hypothesis that these illusions are mediated mainly by the activity of neurons in the parvo- and koniocellular layers of the LGN.

5.4. Use of stimuli that differentially activate only the S-cones

With few exceptions (Gregory, 1977) previous studies of geometric-optical illusions at isoluminance used isoluminant stimuli that vary along the L − M axis. Gregory (1977) used different combinations of red and blue figures with either green, red, or contrasting blue backgrounds. He found the Müller-Lyer, Orbison, Ponzo, and Zöllner illusion to be essentially unchanged for all including zero luminance ratios. Here we used stimuli that vary along the S − (L + M) axis of DKL color space and differentially activate only the S-cones. The signals that excite the S-cones (S on) are processed by a special class of bistratified retinal ganglion cells (Dacey & Lee, 1994) and are mediated a separate functional channel in primate LGN, the koniocellular pathway (for a review, see Hendry & Reid, 2000). Our findings that geometric-optical illusions occur also and with equal strength for stimuli changing only along the S − (L + M) axes suggest that geometric-optical illusions are mediated not only by the parvocellular, but also by the koniocellular pathway.

6. Summary

The present study shows that geometric-optical illusions under isoluminance are as strong as when presented at luminance contrast, consistent with the joint processing of oriented color and luminance contrast in early visual areas. Furthermore, the results show that our conscious percept is affected 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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