# What kinds of contours bound the reach of filled-in color?

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Is a retinal representation of an edge necessary to constrain the reach of color filling-in? If so, then color filling-in should not be constrained by illusory contours, because they do not exist at a retinal level. Alternatively, if color filling-in is constrained by contours at a perceptual level of neural representation, regardless of whether there is a retinal representation, then color filling-in should be constrained by illusory contours. To address this question, a variety of real luminance edges and illusory contours were presented under conditions designed to cause color filling-in. The results showed that illusory contours bounded the reach of color filling-in. A neural representation of a contour may first exist at a retinal level or a cortical level; in either case, the contour exists at a perceptual level and bounds color filling-in.

Keywords: color perception, filling-in, S-cones, featural completion, modal completion, illusory contour

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## Introduction

Filling-in occurs when a visual feature located in one region of visual space is perceived to spread into a nearby region where it is not actually present. In 1668, Mariotte made the first known demonstration of filling-in, fixating an object in monocular vision such that it projected exactly on the optic nerve (Walls, 1954). As a result, the object disappeared from perception and the area was filled-in by its surroundings. Brewster wrote the first scientific description, though he concluded with something mysterious: the optic nerve was called "The Divine Artificer," and the phenomenon was included in his "Letters on Natural Magic" (Brewster, 1832).

In dim light, below cone threshold, the fovea is blind due to the absence of rods, but this usually is not noticed unless one fixates a star and observes its disappearance. This filling-in perhaps was known to Phoenician sailors who first navigated by the stars, but the first scientific description was written by Arago in 1858 (Walls, 1954).

The filling-in phenomenon occurs in many other situations. Pessoa, Thompson, and Noe (1998) suggest that filling-in and perceptual completion are expressions used by visual scientists to describe the same phenomenon. In order to better understand the similarities and dissimilarities among the many kinds of filling-in, they present a taxonomy of the phenomenon with two general dimensions in the classification scheme: (i) amodal completion versus modal completion and (ii) boundary completion versus featural completion. Amodal completion refers to filling-in of an object that is occluded, i.e., not entirely visible; in modal completion, the completed parts display the same type of attributes (e.g., color) as the rest of the figure. Boundary completion refers to illusory contours, and featural completion refers to the attributes of the surface of an object (e.g., color, texture, brightness).

Another classification divides filling-in events into three main groups (Komatsu, 2006). The first group includes deficits of visual inputs when some region of the visual field is deprived of visual stimulation and the region is filled-in perceptually by the surroundings; the classical examples are the blind spot and scotomas. In both cases, several studies suggest that neural activity in V1 mediates this type of filling-in (Fiorani, Rosa, Gattas, & Rocha-Miranda, 1992; Matsumoto & Komatsu, 2005; Spillmann & Werner,

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1996; Tong & Engel, 2001). The second group includes steady fixation and stabilized retinal images, such as Troxler's effect (Krauskopf, 1963; Troxler, 1804). Troxler's effect occurs when steady fixation causes a region in the periphery to be filled-in by its surroundings. Stabilization of the retinal image is the extreme case of this type of filling-in, using a device that eliminates movement of the retinal image caused by involuntary eye movements. In both cases, visual features in the surround occupy the part of the visual field corresponding to the object; neural activity in V1 is posited to mediate this filling-in (Hsieh & Tse, 2006, 2010; Mendola, Conner, Sharma, Bahekar, & Lemieux, 2006). The third group includes neon color spreading (Bressan, Mingolla, Spillmann, & Watanabe, 1997; Grossberg & Mingolla, 1985; Redies & Spillmann, 1981; van Lier, 2002; van Tuijl, 1975; Varin, 1971), the Craik–O'Brien–Cornsweet effect (Cornsweet, 1970; Craik, 1966; Grossberg & Todorovic, 1988), and the phantom illusion (Kitaoka, Gyoba, & Sakurai, 2006; Rosenbach, 1902; Tynan & Sekular, 1975). The third group essentially includes all the events that cannot be included in the first two groups. Recent studies show neural activity correlating with filling-in in V1 for neon color spreading and the phantom illusion (Meng, Remus, & Tong, 2005; Sasaki & Watanabe, 2004). For the Craik–O'Brien–Cornsweet effect, correlated responses have been found from LGN to higher level areas (Anderson, Dakin, & Rees, 2009; Boyaci, Fang, Murray, & Kersten, 2007; Cornelissen, Wade, Vladusich, Dougherty, & Wandell, 2006; De Weerd, Gattass, Desimone, & Ungerleider, 1995; Perna, Tosetti, Montanaro, & Morrone, 2005; Rossi & Paradiso, 1996; for review: Hsieh & Tse, 2010; Komatsu, 2006; Paradiso et al., 2006; Pessoa et al., 1998; Spillmann, 2009b).

In the specific case of color, a classical example of filling-in is the Boynton Illusion (Mollon, 1995), in which an achromatic area between a black squiggly contour and a yellow region is perceptually filled-in by the yellow. The light in the yellow and achromatic areas differs in only S-cone stimulation. In this case, the squiggly line serves as a luminance contour that bounds the area filled-in by color. According to Mollon (1995), the Boynton Illusion demonstrates the poor spatial resolution of one subsystem of color vision: " the colour signals from the short-wave cones give only inexact information about spatial position, and it seems that signals from abundant longer-wavelength cones are used to decide the exact position of an edge" (pp. 132–133). Thus, perceptual bleeding of the color occurs across the true yellow/achromatic edge to produce a uniform yellow area up to the luminance contour (Eskew & Boynton, 1987; Gregory, 1977; Pessoa et al., 1998).

The explanation of color filling-in defined solely by an S-cone decrement compared to its achromatic surround offered by Mollon (1995) posits that the excitation of middle- and/or long-wavelength cones by a physical contour at the retinal level is sufficient to constrain color filling-in. This explanation, however, does not address whether a neural representation of the contour at *only* a higher level of the visual system also may be sufficient to constrain color filling-in. In other words, is a retinal representation of the contour *necessary* to constrain color filling-in? Illusory contours are not represented at the retinal level but do exist at a cortical level of visual processing (Peterhans & von der Heydt, 1991; von der Heydt & Peterhans, 1989; von der Heydt, Peterhans, & Baumgartner, 1984). If a retinal representation of the contour is necessary to constrain color filling-in, then color filling-in should not be limited by illusory contours. Alternatively, if color filling-in is constrained by contours at a perceptual level, then illusory contours should be effective edges for limiting the spread of filled-in color.

While neon color spreading implicitly involves color filling-in bounded by a contour not physically present, there are important differences between neon color spreading and the color filling-in studied here. In neon color spreading, a faint illusory color spreads from small physical chromatic regions over a much larger area bounded by illusory contours. A clear difference in perceived color is maintained between the physical chromatic regions and the larger area perceived with the spread illusory color. In contrast, for the color filling-in considered here, the color, defined solely by an S-cone decrement compared to its achromatic surround, spreads to the illusory contour and the physical chromatic edge disappears from perception. The colored area appears uniform: the physical chromatic region and the area containing the spread illusory color are indistinguishable. Other differences between these two kinds of color filling-in are presented in the Discussion section (Bressan et al., 1997; Redies & Spillmann, 1981; van Lier, 2002).

A variety of real luminance edges and illusory contours were investigated here. Real contours had a luminance-contrast edge (Figure 1a). Illusory contours were of three kinds: a Kanizsa square formed by black solid "pacmen," a Kanizsa square from "bull's-eye pacmen," and horizontally phase-shifted vertical lines (Figure 1b). A yellow square, defined solely by an S-cone decrement compared to its achromatic surround, was presented simultaneously within these contours. The percentage of stimulus presentations with perceived filling-in and the time required to fill-in were measured. The results showed that all contours, real and illusory, bounded the extent of filling-in.

# Illusory contours constrain filling-in

## Methods

### *Observers*

Ten observers participated in the study. All had normal or corrected-to-normal acuity and normal color vision as assessed with the Neitz anomaloscope. The observers participated in practice sessions before data collection

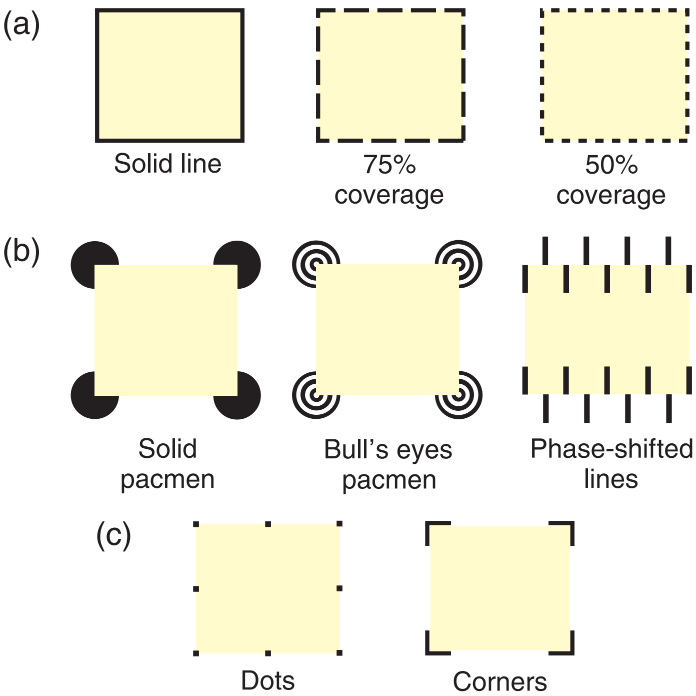


Figure 1. Different contours used in the experiment: (a) real luminance-contrast contours (solid, 75% coverage, and 50% coverage); (b) illusory contours of a Kanizsa square formed from solid "pacmen," a Kanizsa square formed from "bull's-eye pacmen," and horizontally phase-shifted vertical lines; and (c) control conditions that define the shape of the square using eight dots or only the corner edges of the solid "pacmen."

was initiated. Each observer then completed a total of ten sessions. The ten observers were naive as to the purpose of the study except for one graduate student participant. Each observer gave informed consent. This research protocol was approved by an Institutional Review Board at the University of Chicago.

### *Apparatus and calibration*

Stimuli were generated on a Macintosh computer and presented on a 21-in. color monitor (NEC AccuSync, 1280 by 1024 pixels, 75 Hz). The 1,024 light levels for each gun were linearized with a radiometer (International Light IL-1700) and stored in a lookup table. The chromatic calibration was completed with a PR-650 SpectraScan Spectrophotometer (Photo Research).

### *Stimuli and procedure*

In this experiment, different kinds of real and illusory contours were presented in separate sessions. For the real contours (Figure 1a), different forms of a luminance-contrast edge were presented: full square outer edge (left), 75% coverage of the square edge (middle), or 50% coverage (right). For the illusory contours (Figure 1b), the contour resulted from a Kanizsa square formed from solid "pacmen" (left), a Kanizsa square from "bull's-eye pacmen" (middle), or horizontally phase-shifted vertical lines (right). In addition, there were two control conditions (Figure 1c): one for shape information using eight dots (one at each corner and one at the midpoint of each side, left) and one for the solid "pacmen" of the Kanizsa square that had only the corner edges that were part of the "pacmen" (right). In all conditions, the edges bounded a square 2 deg in width.

For all stimuli, a yellow square was presented simultaneously with the contours. The chromaticity of the yellow square was defined solely by an S-cone decrement from its achromatic surround. The achromatic surround had L/(L + M) and S/(L + M) chromaticities of 0.665 and 1.0 (MacLeod & Boynton, 1979), respectively, making it metameric to equal-energy-spectrum (EES) "white." The luminance was 8.5 cd/m$^2$. The yellow square had L/(L + M) and S/(L + M) chromaticities of 0.665 and 0.7, respectively.

All stimuli were presented in three different conditions. In one condition, the yellow square was physically abutting the contour. In the other two conditions, the yellow region was smaller, leaving an achromatic gap for filling-in of either 4 min of arc or 6 min of arc between it and the contour. Each condition was repeated 2 times in each session, and each session was repeated 10 times. Therefore, each stimulus was presented 20 times.

In all sessions, the observers were dark adapted for 2 min before the experiment began. During presentation of the stimuli, observers fixated the center of the stimulus. The task was to indicate via a button press whether the yellow appeared to be touching the contour (thus a filled-in color). One second before the presentation of each stimulus, the observer heard a beep to indicate the beginning of a trial. All stimuli were presented for 8 s. This duration was determined from pilot experiments, which revealed that if filling-in did not occur within 8 s, it had a very low probability of occurring with a longer stimulus presentation. von der Heydt, Friedman, and Zhou (2003) registered filling-in as late as 7 s. The interval between successive presentations was 5 s. The proportion of times that the yellow color was perceived to touch the contours and the time required for filling-in were measured.

## Results

### *Measurements of filling-in*

When the yellow square abutted the contours (a control), observers perceived the yellow square to be touching the contour in 100% of the trials in every condition (white bars, Figure 2). This was expected but gives a baseline with which to compare results from other conditions.

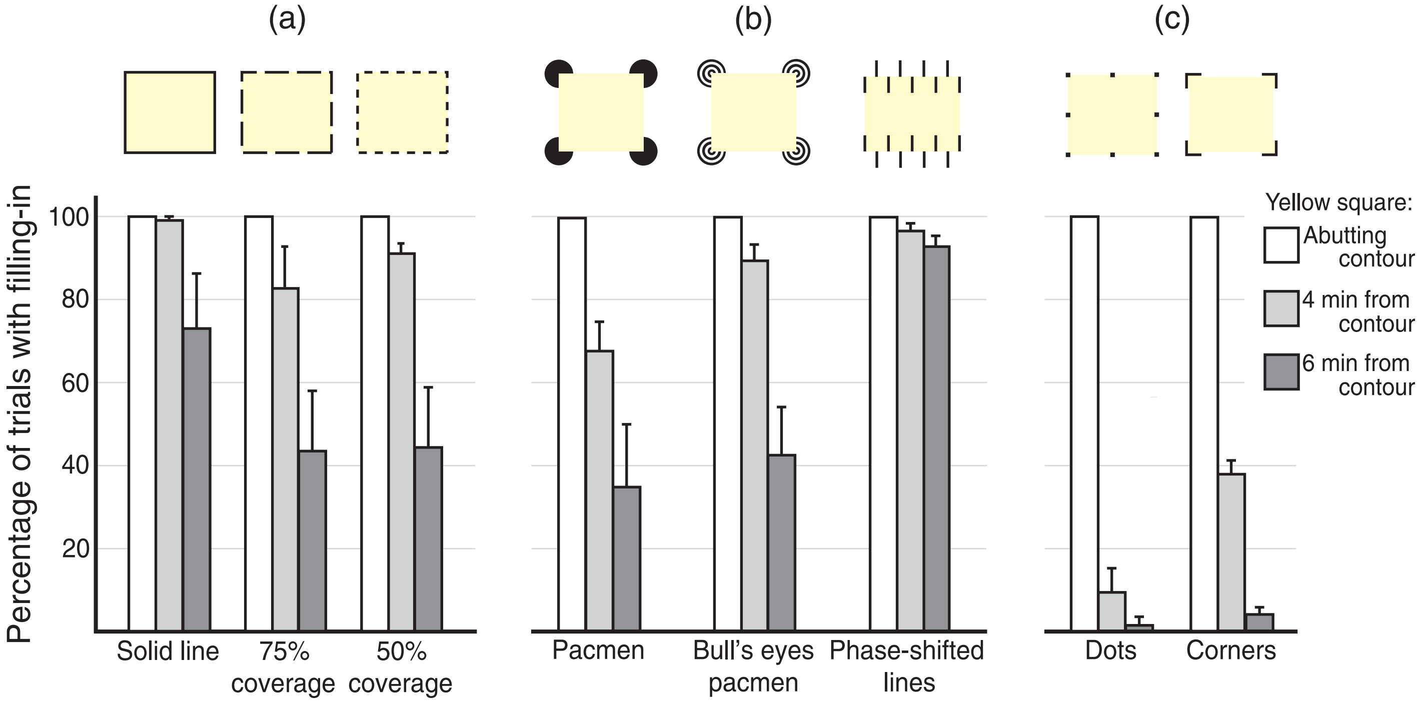


Figure 2. Percentage of trials with perceived filling-in (a) with real contours, (b) with illusory contours, and (c) in control conditions. White bars show results (all at 100%) for the condition in which the yellow region abutted the contour. Light (dark) gray bars are results with the yellow region 4 (6) min of arc from the contour.

### *Real contours*

The proportion of times that filling-in occurred with real contours is shown in Figure 2a. Compared to conditions that gave only shape information but had no contours (Figure 2c), the proportion of times filling-in occurred with any type of real contour was significantly greater ($p < 0.05$, Tukey HSD test), for both the 4 min of arc or 6 min of arc gap. For the real contours, the proportion of trials with perceived filling-in decreased significantly when the yellow region was farther away from the border (compare light gray to dark gray bars in Figure 2a; $p < 0.05$, Tukey HSD test).

The response time measurements for filling-in for the real contours are shown in Figure 3a. For all the real contours, the time to filling-in was greater when the yellow region was 4 or 6 min of arc from the contour compared to when the yellow region was abutting the contour (compare white bars to light and dark gray bars for solid line, 75% or 50% coverage; $p < 0.05$, Tukey HSD test). Therefore, the time to fill-in increased when the color information was presented away from the border.

### *Illusory contours*

The proportion of times that filling-in occurred with illusory contours is shown in Figure 2b. Compared to either control condition (Figure 2c), the proportion of times filling-in occurred with any type of illusory contours was significantly greater ($p < 0.05$, Tukey HSD test). For the illusory contours, the proportion of trials with perceived filling-in decreased significantly when the yellow region was farther away from the border for the Kanizsa square formed from solid "pacmen" ($p < 0.05$, Tukey HSD test) and the Kanizsa square formed from "bull's-eye pacmen" ($p < 0.05$, Tukey HSD test), but not for the horizontally phase-shifted vertical lines (compare light gray to dark gray bars, Figure 2b).

The response time measurements for filling-in for the illusory contours are shown in Figure 3b. For the illusory contours, there was no significant difference among the times to fill-in depending on the distance from the border, for all three conditions (compare light gray to dark gray bars, Figure 3b).

Response time measurements for filling-in for the two control conditions (Figure 3c) are not shown (indicated with an X in the graph) because too few or no trials resulted in perceived filling-in to estimate the time.

In summary, observers reported that a filled-in color from a chromatic light into an equiluminant achromatic surround was bounded by illusory contours. This strongly suggests that illusory as well as real edges bound the reach of filled-in color. A possible alternative explanation, however, is that observers reported filling-in because they could not

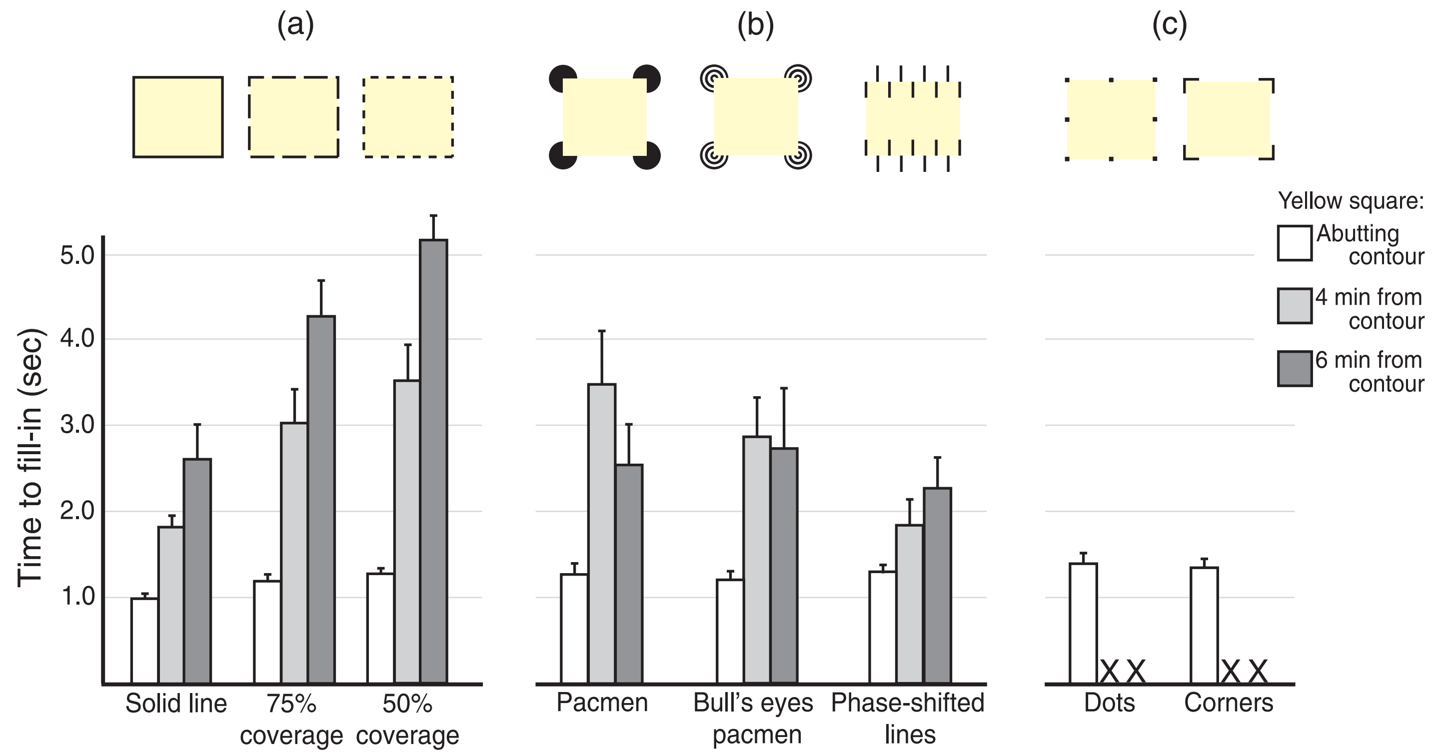


Figure 3. Time to fill-in (s) (a) for real contours, (b) for illusory contours, and (c) in control conditions. White bars indicate the time to report a "filled-in" percept when the yellow region abutted the contour. Light (dark) gray bars are results with the yellow region 4 (6) min of arc from the contours. The symbol X indicates that too few or no trials resulted in perceived filling-in to estimate the time.

accurately localize the position of the illusory contours. To test this possibility, two further experiments were designed to measure (1) observers' ability to localize illusory contours and (2) the frequency of perceived filling-in when the chromatic light that normally filled-in had a slightly higher luminance than its achromatic surround. If the results in the previous experiment were due to poor localization of illusory contours, then the frequency of filling-in with a luminance increment in the chromatic area should be similar to the results above because the added luminance-contrast edge still would reach the poorly localized illusory contour. On the other hand, if the illusory contours in the experiment above bounded the reach of filling-in, then the added luminance-contrast edge between the chromatic and achromatic regions should reduce perceived filling-in to the illusory edge because the added luminance edge would limit the reach of the filled-in color.

# Localization of illusory contours

This experiment was designed to determine the precision of observers' perceived location of illusory contours.

## Observers

Three naive observers participated in this experiment, one of whom also participated in the previous experiments.

## Stimuli and procedure

The three kinds of illusory contours from the main experiment (Figure 1b) were presented in separate sessions.

Two luminance-defined horizontal lines, each one 10 min of arc long with thickness of 1 min of arc, were added, with one on either side of the stimulus (see Figure 4, inset); the yellow square was not presented so the entire interior area was achromatic. The horizontal lines were presented at 9 different vertical positions, equally spaced in a range from 4 min of arc above to 4 min of arc below the illusory contour. Each position was repeated 10 times in each session.

The observer's task was to indicate via a button press whether the horizontal lines appeared to be above or below the illusory contour. When the observer pressed the button, the next stimulus was presented on the screen. Each observer ran three sessions for each kind of illusory contour, for a total of 9 sessions.

## Results

The psychometric function for each observer's ability to localize the illusory contour is shown in Figure 4. Observers were able to localize the position of the illusory contour over 90% of the time within 2 min of arc, for each of the three kinds of illusory contour. This is better resolution than the smallest gap of 4 min of arc used in earlier experiments.

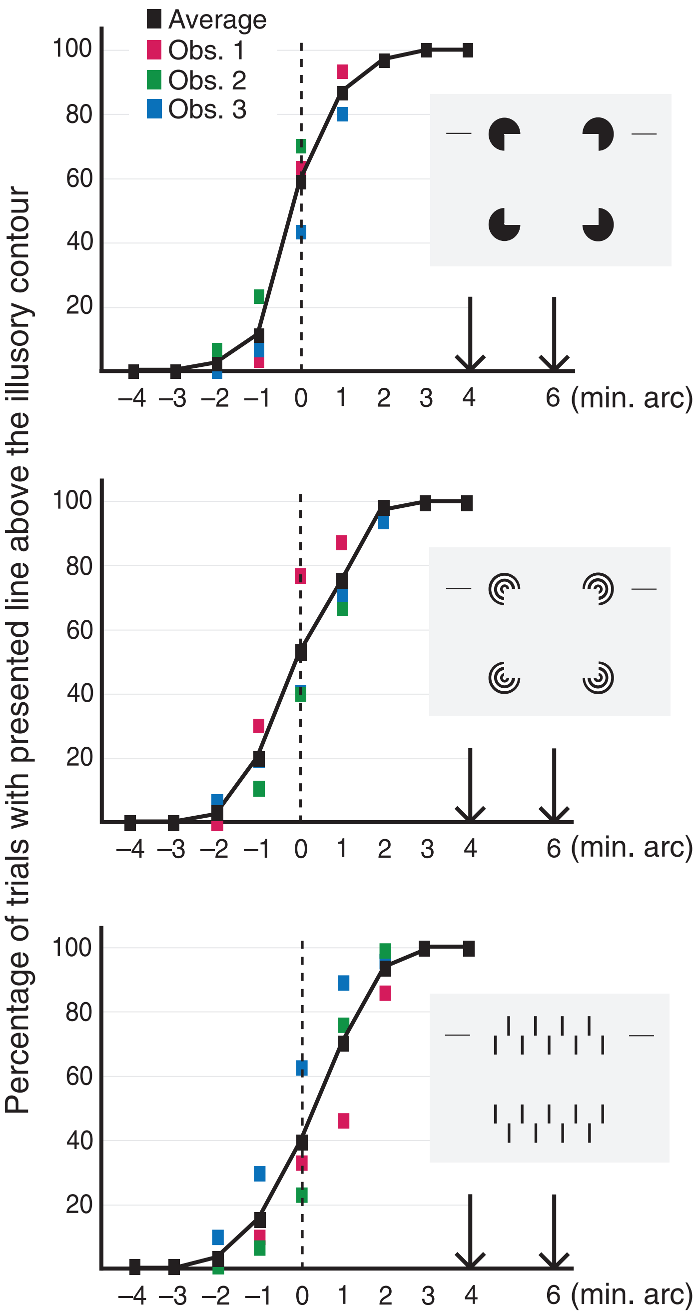


Figure 4. The psychometric function for discriminating the location of the illusory contour for a Kanizsa square formed from solid "pacmen" (top panel), for a Kanizsa square formed from "bull's-eye pacmen" (middle panel), and for horizontally phase-shifted vertical lines (bottom panel). Results for three observers as well as their averages (black squares) are shown in each panel. The arrows indicate the distances between the yellow square and the contour in the previous experiment.

# Higher luminance chromatic region

This experiment measured the frequency of perceived filling-in when the "yellow" chromatic region, which normally filled-in within the equiluminant achromatic surround, had a slightly higher luminance than the achromatic surround. This created a luminance-contrast edge at the border of the yellow region and this edge should reduce filling-in, unless the illusory contours are poorly localized and perceived to be located at the added luminance edge. If illusory-contour localization is indeed poor, then the frequency of filling-in should not be affected by the added luminance-contrast edge, which still would be perceived to reach a poorly localized illusory contour.

The methods were the same as in the first experiment.

## Observers

Three observers participated in this experiment, one of whom also participated in the previous experiment.

## Stimuli and procedure

The yellow square was presented at three levels of incremental Michelson luminance contrast: 5%, 7%, and 11%. Each luminance contrast was presented in a separate session. Each observer ran 10 sessions at each luminance-contrast level.

## Results

The proportion of times that filling-in occurred when the chromatic light contained a luminance-contrast edge is shown in Figure 5 for 4 min of arc separation between the yellow region and the contours. The frequency of filling-in for the three illusory contours was sharply reduced with either 5% or 7% luminance contrast, compared to the equiluminant condition without luminance contrast. Statistical analysis shows that there is no overlap of the 95% confidence intervals. Note that the shading of the bars in this figure represents the magnitude of luminance contrast, not the distance from the contour as in previous figures. Filling-in was completely abolished (0% filling-in) at 11% luminance contrast (indicated by Xs in Figures 5a and 5b). Furthermore, with 6 min of arc separation perceived filling-in

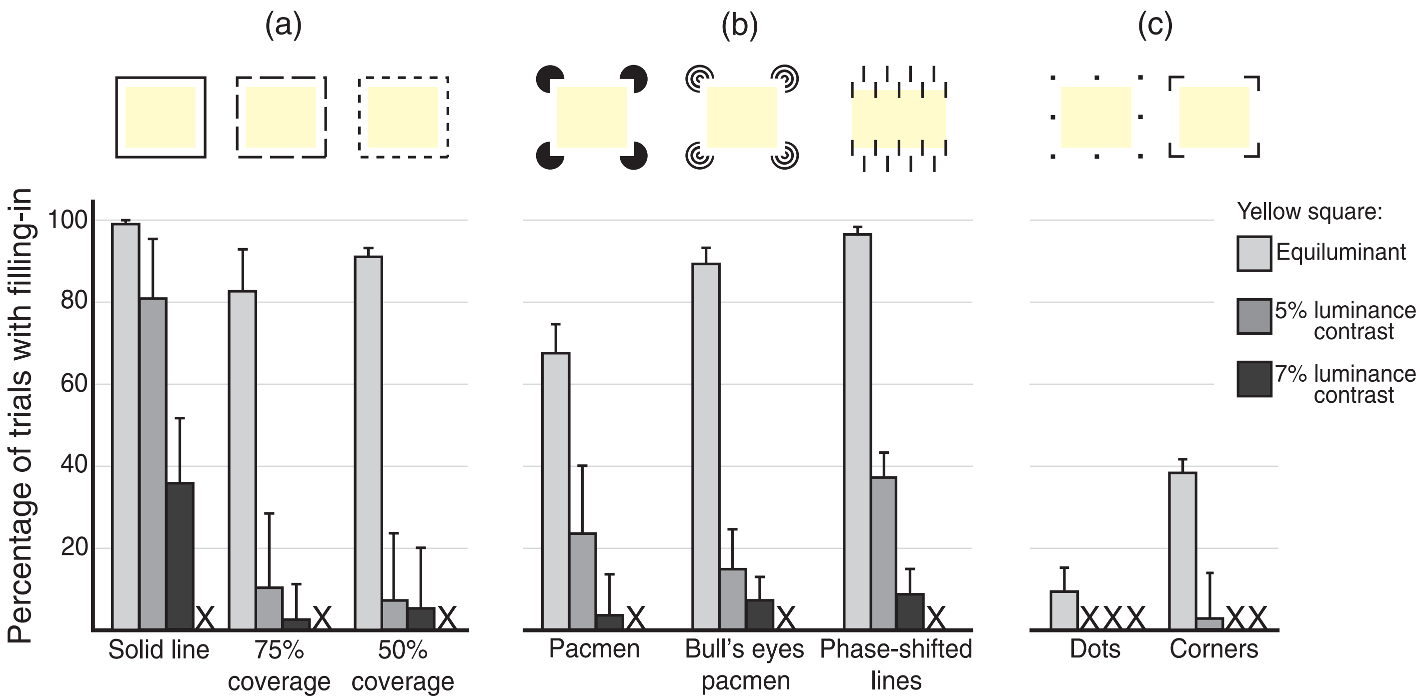


Figure 5. Percentage of trials with perceived filling-in when the yellow region had greater luminance than its achromatic surround and was presented 4 min of arc from the border, for (a) real contours, (b) illusory contours, and (c) control conditions. Light gray bars (equiluminant condition) are replotted from Figure 2 when the yellow region was equiluminant to its achromatic surround and was presented 4 min of arc from the border. Dark gray (black) bars show results when the yellow region had 5% (7%) luminance contrast. The symbol X indicates no trials (0%) with perceived filling-in when the yellow region had 5%, 7%, or 11% luminance contrast.

*never* occurred for any type of contour at any nonzero luminance contrast (data not shown).

In summary, the results showed that perceived filling-in in the first experiment could not be explained by poorly localized illusory contours.

## Discussion

The present study shows that filled-in color from a chromatic light into an equiluminant achromatic surround is bounded by illusory contours as well as by real luminance edges. The color filling-in discussed here does not consider all possible chromatic lights into an equiluminant achromatic surround but only a chromatic light defined solely by an S-cone decrement compared to its achromatic surround.

According to Mollon (1995), the type of color filling-in seen in the Boynton Illusion occurs because signals from the short-wave cones give only inexact information about spatial position, so longer wavelength cones establish the position of an edge. The study here is the first to show that color filling-in defined solely by an S-cone decrement compared to its achromatic surround is bounded also by illusory contours; excitation of middle- or long-wavelength cones is not necessary to bound the reach of filled-in color. Illusory contours are thought to be first represented at a cortical level, so these results implicate a cortical representation that determines the extent of color filling-in (Bakin, Nakayama, & Gilbert, 2000; Friedman, Zhou, & von der Heydt, 2003; Komatsu, 2006; Peterhans & von der Heydt, 1989, 1991; Spillmann, 2009b; Spillmann & De Weerd, 2003; von der Heydt & Peterhans, 1989; von der Heydt et al., 1984).

As previously mentioned, neon color spreading might be considered an example of color filling-in bounded by illusory contours. In neon color spreading, colored parts of a repeated shape are aligned to form the contour of an illusory figure, and the color of the parts spreads faintly across the illusory figure (Bressan et al., 1997; Komatsu, 2006; van Lier, 2002). Though both are examples of color filling-in, neon color spreading and the filling-in presented here have important differences between them. For example, neon color spreading depends on the presence of depth stratification compatible with transparency overlay. Without it, neon color spreading vanishes (Nakayama, Shimojo, & Ramachandran, 1990). In addition, in the absence of an illusory contour (i.e., presenting a real luminance contour), the effect persists, but its extent is reduced (Watanabe & Takeichi, 1990). In the filling-in investigated here, the illusory contour is perceived without depth or transparency, and the filled-in color is bounded by both illusory and real contours. Further, in neon color spreading, the physical chromatic regions make up only a small fraction of the entire area perceived to be colored, and there is a clear perceived difference in color between the physical chromatic regions and the areas with the faint filled-in color. The color filling-in studied here, on the other hand, results in a uniform chromatic percept up to the border since the physical chromatic region appears identical in color to the area containing the filled-in color. This is the kind of color filling-in discussed by Mollon, which is consistent with independent determinations by the visual system of the boundary of a chromatic region and the color of that region. In this case, the retinal image of the chromatic border in the stimulus fades and no difference is seen between the "real" stimulus-color area and the filled-in color region (Bressan et al., 1997; Nakayama & Shimojo, 2009; Pinna & Grossberg, 2005; Spillmann, 2009a).

Note that the contours are necessary for filling-in to occur in the study presented here. Filling-in can occur with blurred color fields that do not have a clear contour (Kanai, Wu, Verstraten, & Shimojom, 2006), but in the present study, filling-in does not occur using only dots or corners to delineate the location or shape of a boundary (Figure 1c). One speculative theory to account for this finding is that the presence of the outer contour diminishes the neural response to the inner equiluminant (yellow/achromatic) edge, which in turn allows the color to spread out to the outer contour. Weakening of the inner equiluminant edge could result from adaptation to the outer contour, which lowers sensitivity to the nearby inner equiluminant contour (Anderson & Winawer, 2005; Cornsweet, 1970; De Valois, Webster, & De Valois, 1986; De Weerd, Desimone, & Ungerleider, 1998; Grossberg & Mingola, 1985; Paradiso & Nakayama, 1991; Redies & Spillmann, 1981; Spillmann, Otte, Hamburguer, & Magnussen, 2006). Alternatively, the outer contour may not affect the neural representation of the inner equiluminant contour; instead, higher levels of the visual system may interpret the color as extending to the more salient outer edge. This would be consistent with a symbolic theory of filling-in (for review, see Komatsu, 2006; Pessoa et al., 1998; Spillmann, 2009b).

Most current explanations of filling-in phenomena are based on the idea that a neural representation of contours bounds feature spreading (e.g., color, texture, brightness; Kanai et al., 2006; Sasaki & Watanabe, 2004; Spillmann & De Weerd, 2003; von der Heydt et al., 2003). An experiment by Spillmann et al. (2006) supports this view. They determined a minimum region around the blind spot that must be stimulated to evoke perceived filling-in of the blind spot. For color filling-in, the minimum width was 0.05 degree of visual angle; for texture filling-in, the minimum was 0.2 degree. If the stimulation was narrower than these values, perceived filling-in was partial. The present study is also consistent with the idea that color filling-in is determined by a neural representation of a real contour or an illusory contour. Moreover, the experiment with a higher luminance chromatic region shows that when a luminance-contrast edge is introduced at the boundary of the chromatic light, the color filling-in is sharply reduced or abolished.

The proportion of trials with perceived filling-in decreased significantly for the illusory contours when the yellow region was farther away from the border (for the Kanizsa square formed from solid "pacmen" and the Kanizsa square formed from "bull's-eye pacmen," Figure 2b) but not for the horizontally phase-shifted vertical lines (compare light gray to dark gray bars, Figure 2b). A possible explanation is that neural representations for these illusory contours occur at different stages of visual processing. The illusory contours constructed from the horizontally phase-shifted vertical lines are represented as early as V1 (Grosof, Shapley, & Hawken, 1993; Mendola, Dale, Fischl, Liu, & Tootell, 1999), while the illusory contours of the Kanizsa square constructed from the "pacmen" are represented in V2 (Peterhans & von der Heydt, 1989, 1991; von der Heydt & Peterhans, 1989; von der Heydt et al., 1984). In addition, electrophysiological experiments with phase-shifted line stimuli have been studied in V1 and V2, and both areas responded in an orientation-specific manner to this type of illusory contour (Sheth, Sharma, Rao, & Sur, 1996).

Color filling-in also occurs when a retinally stabilized image undergoes perceptual fading. Hsieh and Tse (2006) suggest that the filled-in color in this case is not solely determined by the background. Instead, it can be a mixture between the background and foreground colors, even when the two colors are presented to different eyes, thus implying that color mixing during filling-in, at least in part, is a cortical phenomenon. According to the authors, it is commonly believed that information about the apparently vanished color is lost and replaced by the color arising from the surround. They challenge this view with fMRI measurements from observers who fixate blue disks on a red background and perceive a purple field and background. The results imply that the color filled-in, in this specific retinally stabilized image, is a process of "feature mixing," not "feature replacement" (Hsieh & Tse, 2010). The "feature mixing" was found also with psychophysical methods over different domains such as luminance and motion and for different cases of neon color spreading (Hsieh & Tse, 2009). It is not possible to address whether the perceived color filling-in here is a "feature mixing" or a "feature replacement" process because with our stimuli the yellow stimulus covers the vast majority of the total area. However, the present study implies that either real or illusory contours may delineate the boundaries within which "feature mixing" or "feature replacement" occurs.

Some neurons that respond to modulation along the *s* axis in V1 also respond to spatiotemporal luminance contrast (Horwitz, Chichilnisky, & Albright, 2005). Specifically, these neurons increase their response to *s*-modulated stimulation in the presence of luminance contrast regardless of the polarity of this luminance contrast. The basic filling-in phenomena studied here bears some similarity to the interaction observed in these neural response properties. Adding a luminance-contrast or illusory edge caused perceived yellow in a region that previously appeared achromatic. Thus, the filled-in yellow was a result of the interaction between the S-cone decrement and the luminance or illusory edge. Further, the nonlinear polarity-insensitive properties of the aforementioned neurons could cause responses to the horizontally phase-shifted vertical lines as well as luminance edges. These neural response properties may aid in signaling the presence of *s* modulation at well-localized luminance or illusory contours.

In sum, filled-in color from a chromatic light into an equiluminant achromatic surround is bounded by illusory contours as well as by real luminance edges. This suggests that the neural representation of the contour, which may exist first at a retinal level or first at a cortical level, must exist at a perceptual level to bound the reach of filled-in color.

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