Contrast magnitude and polarity effects on color filling-in along cardinal color axes

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Color filling-in is the phenomenon in which the color of a visual area is perceived as the color that is only presented in an adjacent area. In a stimulus with multiple edges, color filling-in can occur along any edge and in both centripetal and centrifugal directions when maintaining steady fixation. The current study aimed to investigate the role of chromatic contrast magnitude and polarity along the two chromaticity cardinal axes and the interaction of the axes in the color filling-in process. In Experiment 1, the color filling-in process was examined using stimuli with three different regions and two edges. The three regions had chromaticities that varied only in one of the chromaticity axes. In Experiment 2, the regions along both edges differed in chromaticity along both axes. The results showed that the contrast magnitudes and polarity relationship of the two edges worked together to determine the filled-in direction and time course of the filled-in percepts. Further, the results pointed to a common mechanism mediating the color filling-in process along the two cardinal axes, and the two axes did not act independently in this process.

Introduction

Perceptual filling-in is a phenomenon in which a visual area is perceived to possess a feature that is presented only in the adjacent area (Gerrits & Vendrik, 1970; Walls, 1954). Filling-in can occur with a variety of visual features, such as luminance, color, texture, and motion (De Weerd, Gattass, Desimone, & Ungerleider, 1995; Friedman, Zhou, & von der Heydt, 1999; Murakami, 1995; Paradiso & Hahn, 1996; Ramachandran & Gregory, 1991) and can be observed in different forms, such as modal completion, neon color spreading, filling-in at the blind spot, and filling-in from steady fixation (Ramachandran, 1992; Sakaguchi, 2006; van Tuijl & Leeuwenberg, 1979). In the current study, we focused on color filling-in during steady fixation.

A classical example of filling-in during steady fixation is the Troxler effect, in which a peripheral field gradually fades, is filled in with the background feature, and finally becomes invisible when maintaining steady fixation (De Weerd, Desimone, & Ungerleider, 1998; Spillmann & Kurtenbach, 1992). Some factors have been reported to affect the occurrence of filling-in during steady fixation, and edge representation is thought to be one of the most important factors (Friedman et al., 1999). It has been suggested that an edge forms the boundary that stops perceptual filling-in, and edge adaptation leads to edge representation fatigue and further breaks the boundary for filling-in to occur (Ramachandran & Gregory, 1991). On the other hand, eye movement that prevents edge adaptation can break the filling-in percept. However, stabilizing the retinal image that boosts edge adaptation facilitates filling-in, supporting the importance of edge representation in filling-in (Krauskopf, 1963). In addition, a stronger edge representation caused by a larger feature difference in luminance, orientation, spatial frequency, or color between edges makes filling-in more difficult (Sakaguchi, 2001).

Prior studies of filling-in from steady fixation have focused on investigation of the situations in which filling-in occurs or is broken or stopped as well as the possible mechanisms underlying the filling-in phenomena. In most cases, filling-in from steady fixation is studied using a simple stimulus with one edge along a small target area that is placed in the periphery against a large uniform or textured background. For these stimuli, it is typical that the background feature (e.g., color or texture) fills in to the target area. In a more complex stimulus with more than two regions and multiple edges, multiple filled-in percepts with both centripetal and centrifugal directions can be observed.

For instance, using an equiluminant stimulus configuration consisting of a central disk surrounded by two concentric rings, Hamburger, Prior, Sarris, and Spillmann (2006) reported multiple filled-in percepts, including the inner ring filled in with the color of the central disk and the outer ring, the central disk filled in with the color of the inner ring, and a step-wise filling-in from the inner ring to the central disk and then from the outer ring to the whole stimulus. However, it is unclear what mechanism determines the direction of filling-in for such a complex stimulus.

It has been proposed that edge integration, as an evolution from retinex theory (Land & McCann, 1971), plays an important role in the filling-in process by combining contrast information, including magnitude and polarity along multiple edges. Edge integration has been successfully used to account for the effect of local and distal edge contrast on perceived brightness, which is believed to involve a brightness filling-in process (Rudd, 2001; Rudd & Arrington, 2001; Rudd & Zemach, 2007; Vladusich, Lucassen, & Cornelissen, 2006). However, few studies have systematically investigated the effects of chromatic contrast and polarity in color filling-in. Previous color filling-in studies only examined a few chromaticities that belonged to different color categories (Hamburger et al., 2006; Sakaguchi, 2001). Furthermore, these chromaticities were typically defined in a CIE color space (Hsieh & Tse, 2009; Kim & Francis, 2011; van Lier, Vergeer, & Anstis, 2009). Such a color space is difficult to link to the underlying physiological mechanisms of chromatic processing. In the current study, we systematically manipulated color contrast magnitude and polarity in a cone-based chromaticity space (MacLeod & Boynton, 1979). In the MacLeod and Boynton chromaticity space, the horizontal axis [$l = L/(L + M)$] represents variation in relative L- versus M-cone stimulation at equiluminance, and the vertical axis [$s = S/(L + M)$] represents variation in S-cone stimulation. Anatomical and physiological studies have identified two distinct visual pathways for chromatic processing, i.e., the parvocellular (PC) and koniocellular (KC) pathways (Creutzfeldt, Lee, & Valberg, 1986; Hendry & Reid, 2000; Martin, White, Goodchild, Wilder, & Sefton, 1997). Physiological recordings (Derrington, Krauskopf, & Lennie, 1984; Lee, Pokorny, Smith, Martin, & Valberg, 1990) have indicated that PC and KC cells show preferred responses to $L/(L + M)$ and $S/(L + M)$ signals, respectively. Studies have shown that border representation depends mainly on the activities of the L and M cones (Tansley & Boynton, 1976, 1978), and S cones only provide a small contribution to border representation (Boynton, Eskew, & Olson, 1985). Given these distinct characteristics between S cones versus L and M cones, the color filling-in process along the s axis may exhibit a different pattern from

that along the l axis. No prior investigation has been conducted to examine the filling-in process along the two cardinal axes parametrically. By measuring color filling-in while varying l or s systematically, we can investigate the color filling-in processes in the inferred PC and KC pathways. Therefore, the aims of the current study were twofold: (a) to examine the role of chromatic contrast magnitude and polarity along the l or s axis as determinants of the color filling-in percepts and to measure the time course of the percepts and (b) to investigate whether the two cardinal axes act differently and independently in the color filling-in process.

Methods

Observers

Five observers (four females and one male, age 20–60 years) participated in the experiments with the l inner-outer field pairs (see Stimuli section) and one additional observer (male, age 19 years) participated in the experiments with the s inner-outer field pairs. All observers had normal color vision assessed by the Neitz OT anomaloscope. All observers, except for the authors (DC and XZ), were naïve as to the purpose and design of the experiments. The study protocols were approved by the Institutional Review Board at The University of Illinois at Chicago and were in compliance with the Declaration of Helsinki.

Apparatus

The visual stimuli were generated using an iMac computer and presented on a NEC 17" CRT color monitor with a refresh rate of 75 Hz. The CRT was calibrated by measuring the spectral outputs of the red, green, and blue guns using a Photo Research PR-670 spectrophotometer. The linearity of each gun was established by measuring the light outputs at 1,024 light levels using an International Light radiometer/photometer (IL-1700).

Stimuli

The stimulus configuration is shown in Figure 1a. An annular field (A) with an inner diameter of 12° and an outer diameter of 16° was surrounded by a circular inner field (I, 12° in diameter) and a rectangular outer field (O, 36.6° × 27.4°, which extended to the full size of the CRT monitor). A black cross (0.14°) in the center of the inner field served as the fixation mark.
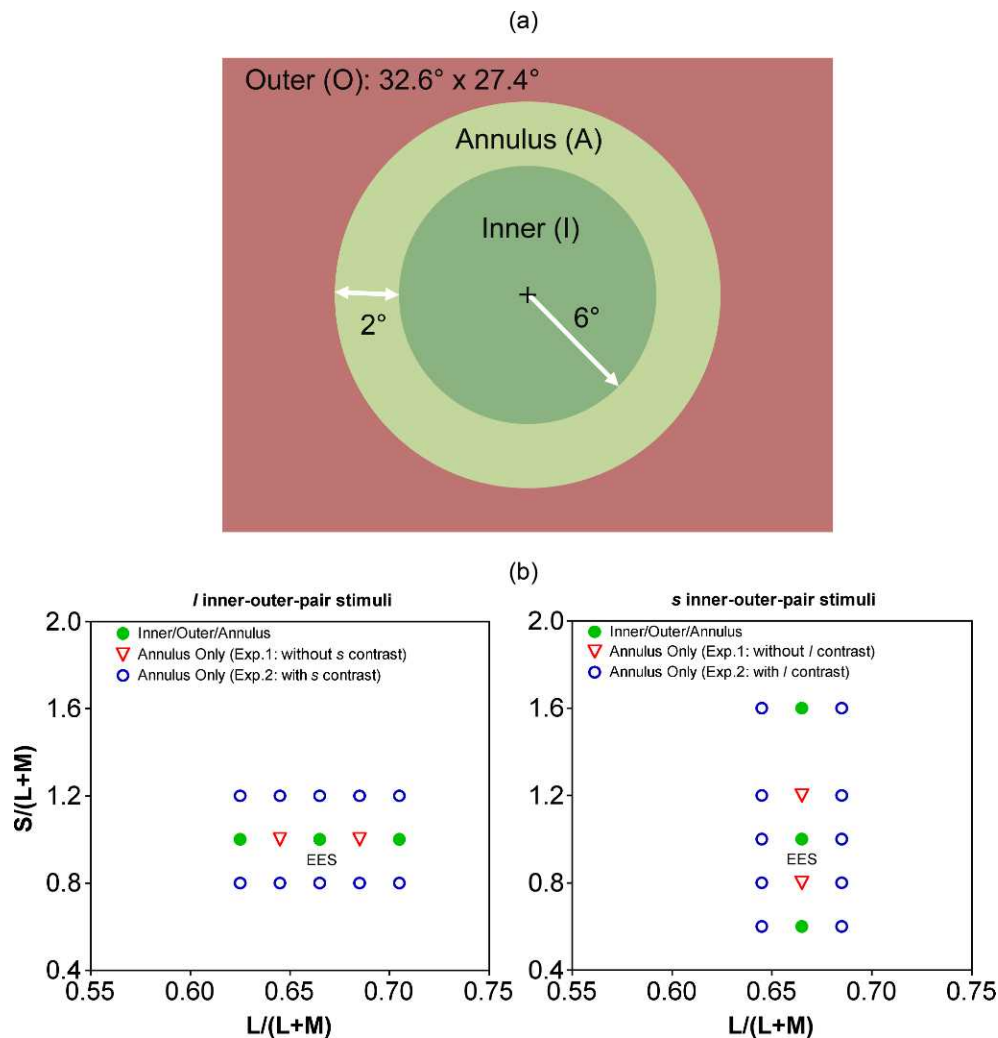
Figure 1. (a) Schematic diagram of the stimulus configuration. The stimuli consisted of a rectangular outer field (O) extending to the edges of the display monitor with a size of 36.6° × 27.4°, an annulus (A) 2° in width, and an inner circular field (I) with a 6° radius. The three fields were equiluminant at 13.0 cd/m² and differed in chromaticity. A black cross of 0.14° was presented at the center of the stimuli as the fixation mark. (b) Stimulus chromaticities used in the two experiments plotted in a MacLeod and Boynton (1979) chromaticity space.

The three fields (the inner, annular, outer fields) were equiluminant at 13.0 cd/m² and differed in chromaticity. A heterochromatic flicker photometry (12.5 Hz) procedure was used to establish equiluminance for each observer. The stimulus chromaticity was defined in the MacLeod-Boynton chromaticity diagram (MacLeod & Boynton, 1979), in which an equal energy spectrum light had $l = 0.665$ and $s = 1.0$.

The first experiment varied chromaticity only along the l axis (l contrast stimuli) or the s axis (s contrast stimuli). For the l contrast stimuli, the s chromaticities of all three fields were fixed at 1.0. The l chromaticities of the inner and outer field were 0.625 ("green"), 0.665 ("white"), or 0.705 ("red"), leading to six l inner-outer field pairs ("red"-"green," "green"-"red," "red"-"white," "white"-"red," "green"-"white," and "white"-"green") (see Figure 1b for the chromaticities plotted in

MacLeod-Boynton [1979]). The annulus l chromaticity was chosen from 0.625, 0.645, 0.665, 0.685, or 0.705 (Figure 1b). For each l inner-outer field pair, the two chromaticities used in the inner and outer fields were not used in the annulus, leading to three annulus chromaticities tested. For the s contrast stimuli, the l chromaticities of all three fields were fixed at 0.665 (Figure 1b). The inner and outer fields had an s chromaticity of 0.6 ("yellow"), 1.0 ("white"), or 1.6 ("purple"), leading to six s inner-outer field pairs ("purple"-"yellow," "yellow"-"purple," "purple"-"white," "white"-"purple," "yellow"-"white," and "white"-"yellow"). The annulus s chromaticity was chosen from 0.6, 0.8, 1.0, 1.2, or 1.6 (Figure 1b). Similarly, for each s inner-outer field pair, the two chromaticities used in the inner and outer fields were not used in the annulus, leading to three annulus

chromaticities tested. In total, 36 chromaticity combinations were tested in this experiment, 18 for each axis.

For each type of contrast stimuli, the chromaticity arrangement in the three fields led to patterns with the same or opposite contrast polarities between the inner edge (the edge between the inner field and annulus) and the outer edge (between the annulus and outer field). For the same polarity pattern, the outer field chromaticity was larger than the annulus chromaticity, which was, in turn, larger than the inner field chromaticity (i.e., $l_O > l_A > l_I$ for the l contrast stimuli, or $s_O > s_A > s_I$ for the s contrast stimuli), or the chromaticities decreased monotonically from the outer to the inner field (i.e., $l_O < l_A < l_I$, or $s_O < s_A < s_I$). For the opposite polarity pattern, the chromaticity changed nonmonotonically from the outer field to the inner field (i.e., $l_O < l_A > l_I$ or $l_O > l_A < l_I$ for the l contrast stimuli; $s_O < s_A > s_I$ or $s_O > s_A < s_I$ for the s contrast stimuli).

In Experiment 2, the inner and outer fields had the same chromaticities as in Experiment 1. In other words, the inner and outer fields differed only in l chromaticity (l inner-outer field pairs) or s chromaticity (s inner-outer field pairs). However, the annulus differed from the inner and outer fields in both l and s chromaticities. For the l inner-outer field pairs, the annulus had the same l chromaticities as the l contrast stimuli in Experiment 1 and had s chromaticity of 0.8 or 1.2. For the s inner-outer field pairs, the annulus had the same s chromaticities as the s contrast stimuli in Experiment 1 and had l chromaticity of 0.645 or 0.685. In total, 72 chromaticity combinations (36 for the l inner-outer field pairs and 36 for the s inner-outer field pairs) were tested in this experiment.

Procedure

During the experiment, observers rested their head on a chin rest that was 57 cm from the monitor. Each session consisted of one pair of inner-outer chromaticity combinations with each annulus chromaticity tested twice in a randomized order. Each l or s inner-outer field pair stimulus was repeated five times on different days, leading to 10 trials for each chromaticity combination in the three fields for each observer. The order of the sessions was randomized.

For each trial, observers pressed a button on a gamepad sensed by the computer to initiate the presentation of the stimulus, which lasted for 25 seconds. Observers were instructed to maintain fixation at the center cross without blinking while reporting percepts continuously by pressing and holding designated buttons on the gamepad. There were six possible filled-in percepts: (a) the annulus assumed the color of the inner field (I → A); (b) the annulus assumed the

color of the outer field (O → A); (c) the inner field assumed the color of the annulus (A → I); (d) the outer field assumed the color of the annulus (A → O); (e) the inner field color spread onto the whole screen (I → A + O); and (f) the outer field color spread onto the whole screen (O → A + I). These percepts were predetermined based on pilot experiments in which other filled-in percepts occurred very rarely. Observers were instructed not to press any buttons if they did not perceive filling-in. The computer recorded the time to filling-in and duration for each percept. Observers were allowed to rest as long as they desired between trials and then pressed the initiation button to start the next trial once they were ready to continue. Each session lasted about 10–15 minutes. Observers were given enough practice experience to be familiar with the tasks.

Data analysis

We calculated the frequency of each filled-in percept, the time it took for the percept to occur (time to filling-in) and percept duration. The observers could report the same percept multiple times during a single trial, namely, the same filled-in percept could disappear then reappear, probably due to eye movements that affected fixation. To simplify the analysis, we focused on the first filled-in percepts and subsequent filled-in percepts that were different from the first filled-in percepts and occurred shortly (within 1.5 s) after the disappearance of the first percepts. We analyzed how the l or s contrast magnitude and polarity between the two edges affected filled-in percept frequency, time to filling-in, and percept duration. Percept frequency distributions were compared among conditions using multinomial logistic regression with the likelihood ratio chi-square and p value reported. The time to filling-in and percept durations between conditions were compared using t tests. A Michaelis-Menten saturation function model was fitted to assess the association between contrast magnitude and time to filling-in or percept duration.

Results

Experiment 1: Color filling-in with the *l* or *s* contrast stimuli

Overview

Overall, color filling-in was reported among 83% of the trials for the l contrast stimuli and 85% of the trials for the s contrast stimuli. For stimuli having the same contrast polarities, the majority of filling-in occurred in a direction from a higher color saturation field into a
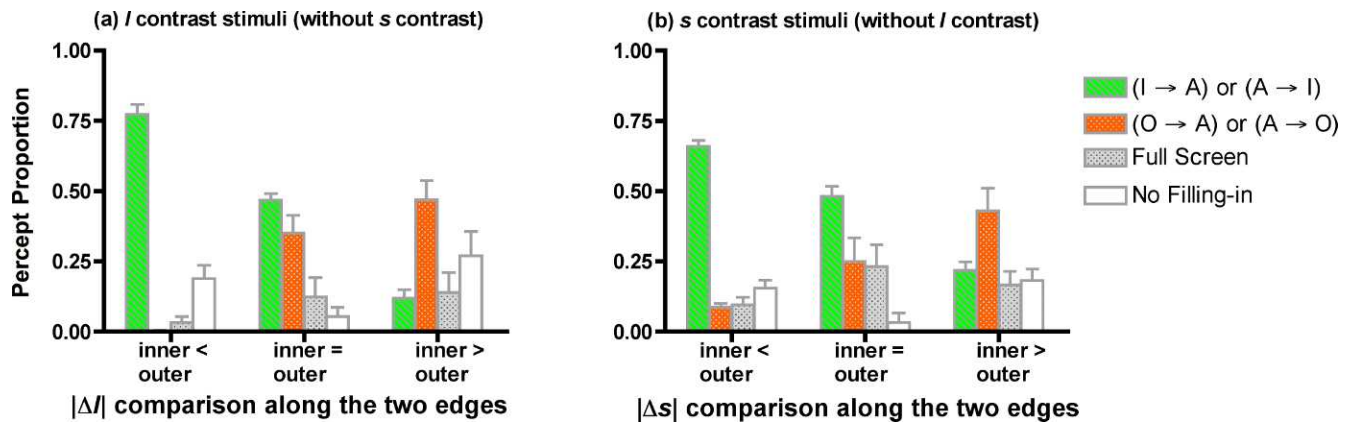
Figure 2. Relative frequency proportions of filled-in percepts for the *l* contrast stimuli (a) or the *s* contrast stimuli (b) under different inner-outer contrast magnitude relations: The inner edge had either a smaller (inner < outer), equal (inner = outer), or larger (inner > outer) contrast magnitude than the outer edge. The proportions are the averages across observers ($n = 5$) and error bars show the SEM.

lower saturation field (on average, 81% among those trials reporting filling-in for each inner-outer pair). Here, the color saturation was defined as the absolute difference between the *l* or *s* chromaticities in the inner, annular, or outer field and equal energy white (EEW) chromaticity ($l_W = 0.665$ and $s_W = 1.0$, i.e., $|l - l_W|$ for the *l* contrast stimuli or $|s - s_W|$ for the *s* contrast stimuli). On the other hand, for the stimuli having opposite contrast polarity (i.e., the inner or outer field had to be "white"), the filling-in occurred mainly between the "white" field and the annulus, but the filling-in direction could be either way (on average, 68% among the trials reporting filling-in). In sum, the filling-in direction depended on the color difference as well as the contrast polarity. The following provides a more detailed analysis of the effect of contrast magnitude and polarity on the filled-in percepts and their time courses.

Contrast magnitude effect

The outer-edge contrast magnitude was computed as $\Delta l_O = l_O - l_A$ or $\Delta s_O = s_O - s_A$ for the *l* or *s* contrast stimuli, respectively. Similarly, the inner-edge contrast magnitude was computed as $\Delta l_I = l_A - l_I$ or $\Delta s_I = s_A - s_I$. Comparing the absolute contrast magnitudes of the inner and outer edges, we divided the data into three contrast conditions for the *l* or *s* contrast stimuli: (a) the inner contrast magnitude was smaller than the outer contrast magnitude ($|\Delta l_I| < |\Delta l_O|$ or $|\Delta s_I| < |\Delta s_O|$); (b) the inner and outer contrasts had the same magnitudes ($|\Delta l_I| = |\Delta l_O|$ or $|\Delta s_I| = |\Delta s_O|$); and (c) the inner contrast magnitude was larger than the outer contrast magnitude ($|\Delta l_I| > |\Delta l_O|$ or $|\Delta s_I| > |\Delta s_O|$). Because we were interested in the relationship of the contrast magnitudes between the two edges in determining the edge at which the filling-in would occur, we grouped the filled-in percepts into four categories: (a)

color spreading along the inner edge (I → A or A → I); (b) color spreading along the outer edge (O → A or A → O); (c) color filling-in to the full screen (I → A + O or O → A + I); and (d) no filling-in. For both *l* and *s* contrast stimuli, frequencies of different filled-in percepts depended on the relationship of the contrast magnitudes between the two edges with color filling-in more likely to occur along the edge that had a smaller contrast magnitude (the *l* contrast stimuli: $\chi^2 = 35.64$, $p < 0.001$, see Figure 2a; the *s* contrast stimuli $\chi^2 = 53.62$, $p < 0.001$, see Figure 2b). When the inner edge had a smaller contrast magnitude than the outer edge, color filling-in along the inner edge (I → A and A → I) dominated (77% of the trials for the *l* contrast stimuli and 68% for the *s* contrast stimuli). On the other hand, when the outer edge had a smaller contrast magnitude than the inner edge, color filling-in along the outer edge (O → A and A → O) occurred most frequently (47% of the trials for the *l* contrast stimuli and 45% for the *s* contrast stimuli) than other filling-in percepts. When the two edges had the same contrast magnitude, filling-in occurred along both edges in closer frequencies but was more likely along the inner edge (the *l* contrast stimuli: 47% and 35% for color spreading along the inner edge and outer edge, respectively; the *s* contrast stimuli: 42% and 25% for spreading along the inner edge and outer edge, respectively).

Time to filling-in and duration of the filled-in percepts also showed dependency on the contrast magnitude. We examined how time to filling-in and duration for filled-in percepts that occurred along each edge varied with the contrast magnitude of that edge. To equate the contrast magnitude in the *l* and *s* axes, we scaled chromatic contrast in terms of chromatic detection threshold units. Using an identical stimulus configuration, the averaged detection threshold was 0.002 in the *l* axis (Cao & Lu, 2012) or 0.041 in the *s*
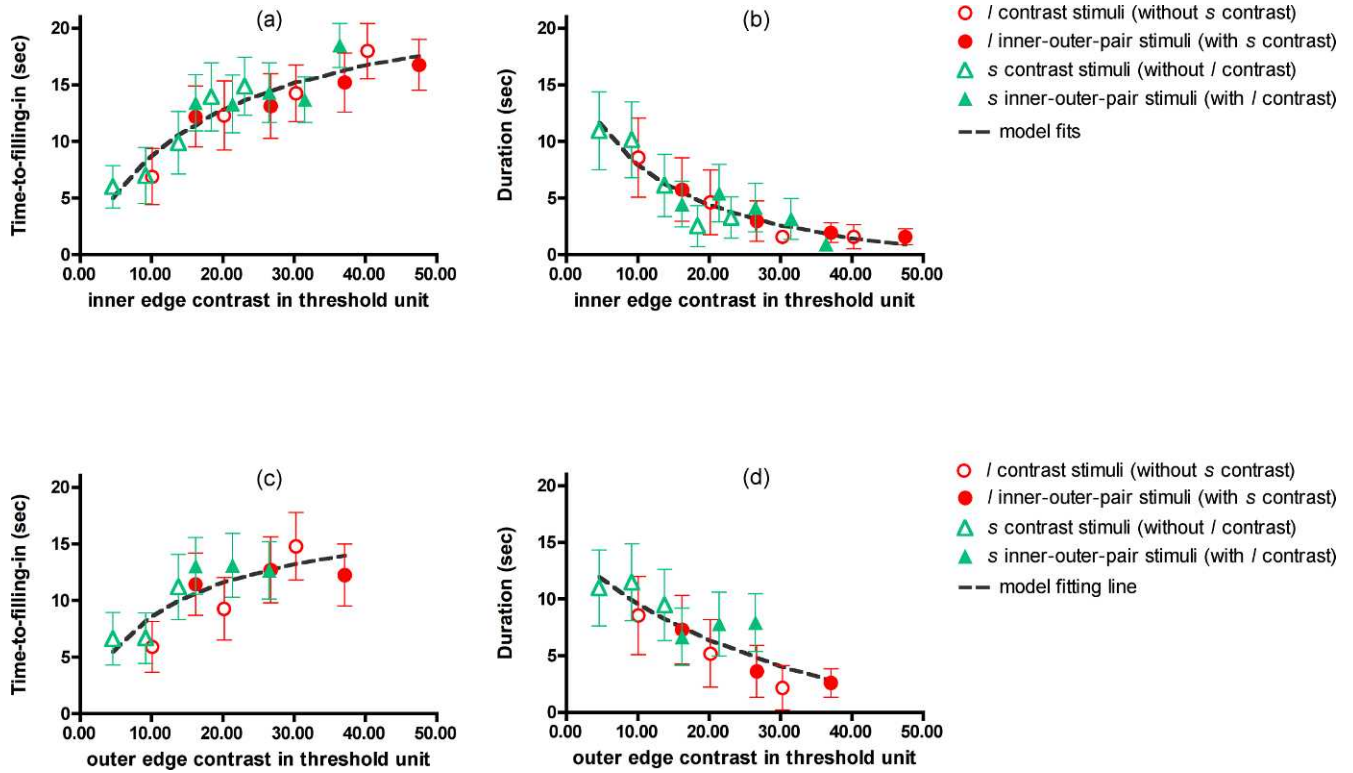
Figure 3. Average time to filling-in and percept duration results and model fits as a function of the inner edge contrast (a and b) or outer edge contrast (c and d).

axis (unpublished data measured from two observers in the current experiment; using a different stimulus configuration, *s* chromatic discrimination had a similar threshold [Cao, Zele, Smith, & Pokorny, 2008]). Figure 3 depicts the time to filling-in and duration as a function of chromatic contrast magnitudes expressed in threshold units. Clearly, with an increasing contrast magnitude, the time to filling-in increased and duration decreased in both axes. The dependence of time to filling-in (T) on contrast magnitude (C, in threshold units) can be described by a Michaelis-Menten saturation function:

$$T = T_0 + T_{max}C/(C + C_{satT}) \qquad (1)$$

where T_0 represents time to filling-in at zero contrast, T_{max} represents the maximum time to filling-in, and C_{satT} is the contrast level (in threshold units) at which T reaches half of T_{max}. Similarly, the percept duration is described as

$$D = D_0 - D_{max}C/(C + C_{satD}) \qquad (2)$$

where D_0 represents duration at zero contrast, D_{max} represents the maximum duration, and C_{satD} is the contrast level (in threshold units) at which D reaches half of D_{max}.

For filling-in along the inner edge, the fitted values obtained by minimizing the residual sum of squares were $T_0 = 0.0$ s, $T_{max} = 24.13$ s, $C_{satT} = 17.74$, $D_0 =$

17.59 s, $D_{max} = 20.08$, and $C_{satD} = 11.61$; the overall variance (R^2) for all four conditions (the *l* contrast stimuli and the *s* contrast stimuli in Experiment 1, the *l* inner-outer field pair with *s* contrast and the *s* inner-outer pair with *l* contrast in Experiment 2) explained by the model was 86.3% for time to filling-in or 89.2% for percept duration. For the filling-in along the outer edge, the fitted values were $T_0 = 0.9$ s, $T_{max} = 17.73$ s, and $C_{satT} = 13.12$ ($R^2 = 67.5\%$); $D_0 = 14.43$ s, $D_{max} = 24.25$, and $C_{satD} = 40.0$ ($R^2 = 75.8\%$). Note the identical model described time courses of filling-in in both color axes, suggesting a similar mechanism mediating color filling-in in the *l* and *s* axes.

Contrast polarity effect

Because percepts I → A, O → A, and A → I were the three major filled-in percepts reported, we focused on these three percepts in the following analysis. We examined the percept frequency for those conditions with the same contrast magnitudes but different polarities. For instance, for the *l* contrast stimuli, the magnitudes of outer and inner edges were 0.2 and 0.6, respectively (e.g., $|\Delta l_O| = 0.2$ and $|\Delta l_I| = 0.6$), the polarity could be the same (e.g., $\Delta l_O = 0.2$ and $\Delta l_I = 0.6$, or $\Delta l_O = -0.2$ and $\Delta l_I = -0.6$) or opposite ($\Delta l_O = 0.2$ and $\Delta l_I = -0.6$, or $\Delta l_O = -0.2$ and $\Delta l_I = 0.6$). Figure 4a shows the overall effect of contrast polarity on the
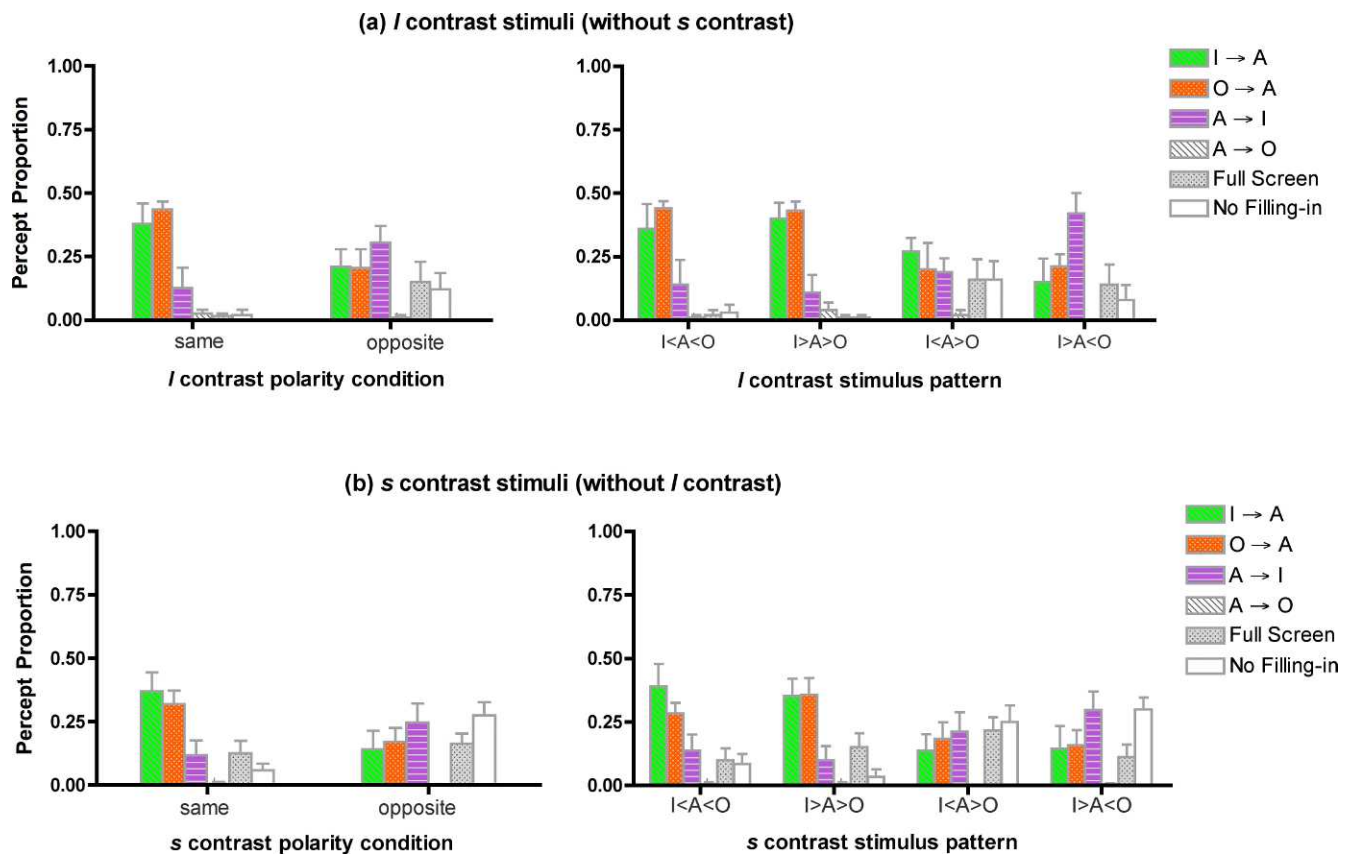
Figure 4. Filled-in percept proportion for different contrast polarity conditions for (a) *l* contrast stimuli and (b) *s* contrast stimuli. The left panels depict the proportions for the two different contrast polarity conditions between the two edges: same versus opposite polarity. The right panels show the same data in more detail for each of the two same polarity patterns and two opposite polarity patterns.

filled-in percept frequency distribution with the contrast magnitude matched between the same and opposite polarities for the *l* contrast stimuli ($\chi^2 = 13.66$, $p < 0.0005$, Figure 4a). Specifically, compared with the opposite polarity, the same polarity increased the likelihood of the annulus being filled in with the adjacent color but decreased the likelihood for the annulus color filling-in to the inner field (same vs. opposite polarity: 81.5% vs. 51.5% for I → A and O → A; 12.5% vs. 30.5% for A → I; see Figure 4a, left panel). Furthermore, the two different kinds of same polarity patterns ($l_O < l_A < l_I$ and $l_O > l_A > l_I$) showed a similar frequency distribution for the filled-in percepts whereas the two different opposite polarity patterns ($l_O < l_A > l_I$ and $l_O > l_A < l_I$) exhibited different frequency distributions with percept A → I being more dominant in the $l_O > l_A < l_I$ pattern than in the $l_O < l_A > l_I$ pattern (see Figure 4a, right panel). The *s* contrast stimuli showed similar results (see Figure 4b).

To examine the polarity effect in more detail, we replotted the frequency of the three main percepts separately as a function of the contrast magnitude along the corresponding edge with positive contrasts for the same polarities between two edges and negative contrasts

for the opposite polarities (Figure 5). The results showed an inverted V-shape pattern for each percept, indicating that filling-in frequency decreased with increasing contrast magnitude. For percepts I → A and O → A, the function peaked at 0.02 for the *l* contrast stimuli or 0.2 for the *s* contrast stimuli, suggesting that an identical contrast polarity increased the filling-in frequency compared with an opposite polarity condition. In contrast, for percept A → I, an opposite polarity facilitated filling-in to occur more often. The contrast polarity effect was further examined in relation to the relative contrast magnitudes between the two edges. We separated the conditions in which the inner contrast magnitude was smaller or larger than the outer contrast magnitude. For the *l* contrast stimuli, when the inner contrast magnitude was smaller than the outer contrast magnitude, the same polarity led to I → A as the dominant filled-in percept (70%). In contrast, for an opposite polarity pattern, the filled-in percept A → I occurred most frequently (52%) compared to the other percepts, and I → A was the second most frequent percept (38%). The frequencies were significantly different in these two polarity conditions ($\chi^2 = 30.86$, $p < 0.001$). When the inner contrast magnitude was larger than the
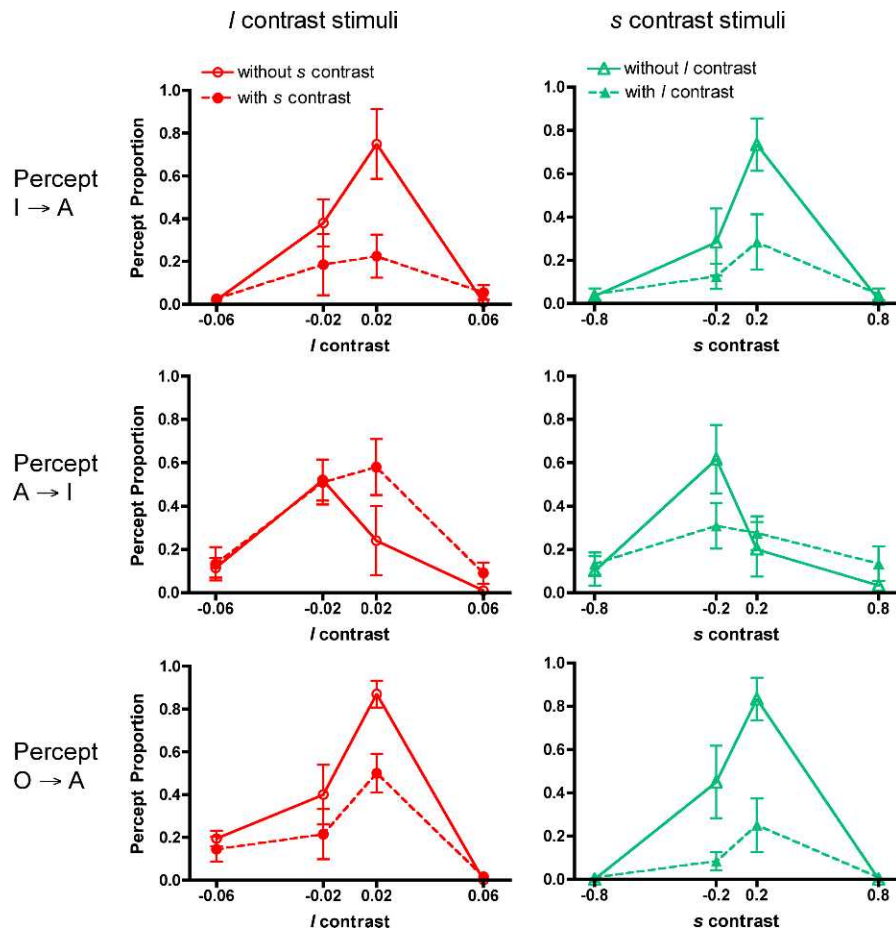
Figure 5. Relative frequency proportions of the main filled-in percepts along the inner edge (I → A, top panels; and A → I, middle panels) and outer edge (O → A, bottom panels) as a function of contrast magnitude at the corresponding edge. Positive and negative contrast values represent the conditions when the two edges have the same versus opposite contrast polarity. The left panels show data for the *l* contrast stimuli in Experiment 1 and for the *l* inner-outer pair stimuli in Experiment 2. The right panels show data for the *s* contrast stimuli in Experiment 1 and for the *s* inner-outer pair stimuli in Experiment 2.

outer contrast magnitude, the frequencies were also significantly different in these two polarity conditions ($\chi^2 = 55.63, p < 0.001$). However, the filled-in percept O → A was the dominant percept regardless of the polarity relationship of the contrasts although a stronger dominancy was shown with the same polarity pattern (same vs. opposite polarity: 83% vs. 45%). Similar results were observed for the *s* contrast stimuli. When the inner contrast had a smaller absolute magnitude, percept I → A was dominant in the same polarity condition, but percept A → I was dominant in the opposite polarity condition. On the other hand, percept O → A was the dominant percept when the outer edge had a smaller absolute magnitude regardless of polarity conditions.

The time course for the three major filled-in percepts changed with the polarity patterns of the *l* or *s* chromaticities. It took a shorter time for each filled-in percept to be completed in the same polarity condition than in the opposite polarity condition (see Table 1). Filled-in percepts (I → A and A → I) lasted

significantly longer in the same than in the opposite polarity condition (see Table 1).

We further analyzed the sequential filling-in immediately (within 1.5 s) following the three types of filled-in percepts. For the *l* contrast stimuli, sequential filling-in was more likely to occur in the same polarity condition than in the opposite polarity condition when the first percepts were I → A or O → A (same vs. opposite polarity: 38% vs. 22%, $\chi^2 = 10.09, p = 0.002$) but not for the first percept A → I (same vs. opposite polarity: 16% vs. 19%, $\chi^2 = 0.25, p = 0.62$). However, for the *s* contrast stimuli, sequential filling-in was rarely reported (8% of trials).

Experiment 2: Color filling-in with both *l* and *s* contrasts

We first compared the frequencies of different filled-in percepts between Experiments 1 and 2. For the *l*

	l contrast stimuli without s contrast			s contrast stimuli without l contrast		
	Same polarity	Opposite polarity	p	Same polarity	Opposite polarity	p
Time to filling-in						
I → A	4.37 (1.27)	8.96 (0.41)	< 0.001	4.92 (1.40)	8.63 (1.57)	0.002
O → A	5.04 (1.15)	10.91 (1.05)	< 0.001	6.59 (1.49)	9.60 (2.26)	0.007
A → I	5.86 (1.66)	12.21 (1.56)	< 0.001	5.53 (1.70)	10.80 (2.18)	0.009
Duration						
I → A	11.35 (3.15)	7.36 (2.86)	0.028	14.07 (3.01)	6.43 (3.02)	0.044
O → A	12.21 (3.37)	6.44 (2.37)	0.062	12.03 (3.33)	9.88 (0.71)	0.151
A → I	11.93 (7.47)	5.05 (1.73)	< 0.001	14.62 (5.87)	8.56 (3.15)	< 0.001

Table 1. Average time to filling-in/duration (seconds).

inner-outer field pairs that differed only in l chromaticity in the inner and outer fields, having a different s chromaticity in the annulus from the two adjacent fields changed the frequency distribution of filled-in percepts significantly ($\chi^2 = 43.88$, $p < 0.001$, see Figure 6a). In particular, the presence of s contrast increased the likelihood of A → I or no filling-in while it reduced the likelihood of I → A or O → A (without s contrast vs. with s contrast: 17% vs. 36% for A → I; 17% vs. 26% for no filling-in; 28% vs. 14% for I → A; 25% vs. 16% for O → A). Similarly, for the s inner-outer pairs that differed only in s chromaticity in the inner and outer fields, having an l contrast changed the frequency distribution of the filled-in percepts ($\chi^2 = 203.90$, $p < 0.001$, Figure 6b). The most pronounced change was that no filling-in occurred for the majority of trials (65%) with the presence of l contrast (vs. 22% in Experiment 1). This may be due to having both s and l contrasts, making the overall contrast too high for filling-in to occur, and the two edges always having opposite contrasts along either the s axis or l axis. In addition, unlike in Experiment 1, percepts I → A and O → A tended to occur less frequently than percept A → I in Experiment 2.

The same models as in Experiment 1 (Figure 3) could describe the dependence of time to filling-in and

duration on contrast magnitude. The contrast magnitudes in the l and s axes were pooled with a quick-pooling function:

$$C_{l,s} = (C_l^Q + C_s^Q)^{1/Q} \qquad (3)$$

where C_l and C_s are contrast magnitudes (in threshold units) in the l and s axes, respectively, and Q is the quick-pooling parameter. The fitted Q was 0.89 for filling-in along both the inner and outer edges (see Table 2 for goodness-of-fit statistics, R^2). Figure 3 indicates the models with common parameters as the l contrast stimuli or s contrast stimuli accounted for the data reasonably well.

In the presence of both l and s differences, different polarity along two edges resulted in different frequency distributions of filled-in percepts (the l inner-outer pairs: $\chi^2 = 36.08$, $p < 0.001$, Figure 7a; the s inner-outer pairs: $\chi^2 = 17.64$, $p = 0.003$, Figure 7b). However, unlike in Experiment 1 in which the dominant filled-in percept changed with the polarity condition (Figure 4a and 4b), in this experiment, the A → I percept was dominant in both polarity conditions (same vs. opposite: l inner-outer pairs, 34% vs. 30%, Figure 7a; s inner-outer pairs, 20% vs. 36%, Figure 7b). The filling-in frequency for the percepts I → A and O → A as a function of contrast had a similar pattern to that in Experiment 1 with the
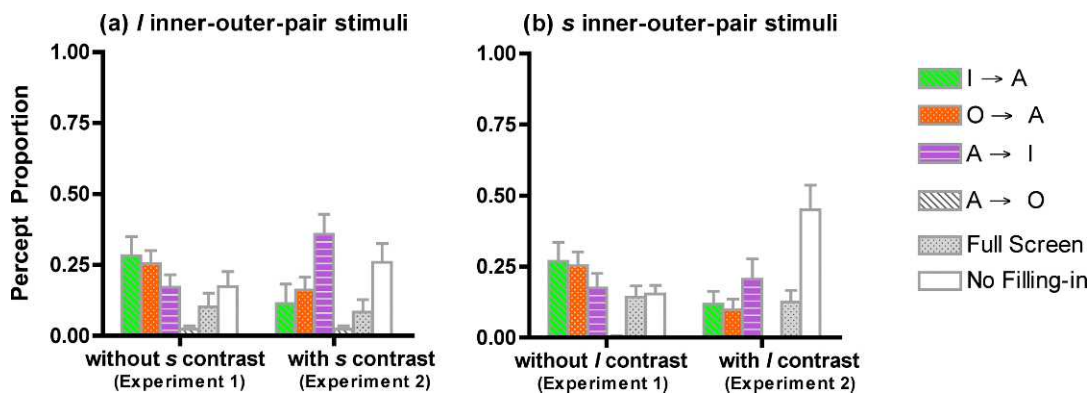

Figure 6. Overall proportion for each filled-in percept in Experiment 1 versus in Experiment 2 for (a) l inner-outer pair stimuli and (b) s inner-outer pair stimuli.

	Q = 0.89		Q = 1	
	Inner edge	Outer edge	Inner edge	Outer edge
Time to filling-in (T)	86.3%	67.5%	85.2%	64.6%
Duration (D)	89.2%	75.8%	89.7%	78.0%

Table 2. Model goodness of fit (R^2).

overall frequency at an intermediate contrast magnitude reduced (Figure 5). For the percept A → I, however, having a contrast from the second chromatic axis increased the likelihood of the percept to occur when the two edges had the same polarities, particularly for the *l* inner-outer pair stimuli (Figure 5).

Furthermore, for the *l* inner-outer field pairs, the polarity relationship between the two edges did not alter the dominant filled-in percept when the inner edge had a smaller contrast (with A → I as the dominant percept: 58% vs. 51% for same vs. opposite polarity) or when the outer edge had a smaller contrast (O → A as the dominant percept: 50% vs. 22% for same vs. opposite polarity). For *s* inner-outer pairs, when the inner edge had a smaller contrast, I → A and A → I were the main filled-in percepts regardless of polarity conditions (I → A: 28% vs. 13% for same vs. opposite polarity; A → I: 28% vs. 31% for same vs. opposite polarity). In contrast, when the outer edge had a smaller contrast, O → A was the main filling-in percept in the same polarity condition but not in the opposite polarity condition (25% vs. 8%).

Discussion

We systematically investigated the roles of chromatic contrast magnitude and polarity relationships between two edges in a complex stimulus configuration as determinants of color filled-in percepts. Prior studies using a stimulus consisting of one edge between the target and surround have shown that the larger the difference between two areas, the harder it was for filling-in to occur because a larger difference between the areas forms a stronger boundary between them, making filling-in more difficult to occur. For example, Sakaguchi (2001) showed that a larger difference in luminance, orientation, spatial frequency, or color between the target and surround areas delayed the time to filling-in from surround to the target area. Our study further showed that in the presence of two edges both the contrast magnitude at a given edge as well as the contrast polarity relationship between the two edges controlled filling-in frequency and direction. Specifically, color filling-in was more likely to occur along the edge that had a smaller contrast magnitude, and the time course of filling-in depended on the contrast magnitude. Meanwhile, when two edges had similar contrast magnitudes, color spreading was equally likely along either of the edges. This result further suggested the importance of edge representation and the interaction of two edges in the color filling-in process.

Because the two color cardinal axes contribute to edge representation differently, with S cones having much less contribution than L and M cones, we would expect that the filling-in process along the *s* axis would be different from that along the *l* axis. We found that the percept frequency distributions with the *l* contrast and *s* contrast stimuli were comparable (Figure 2). In addition, the dependence of filling-in time courses on *l* and *s* contrast magnitudes could be described by the same function when chromatic contrasts were scaled by chromatic detection threshold units. Simple reaction
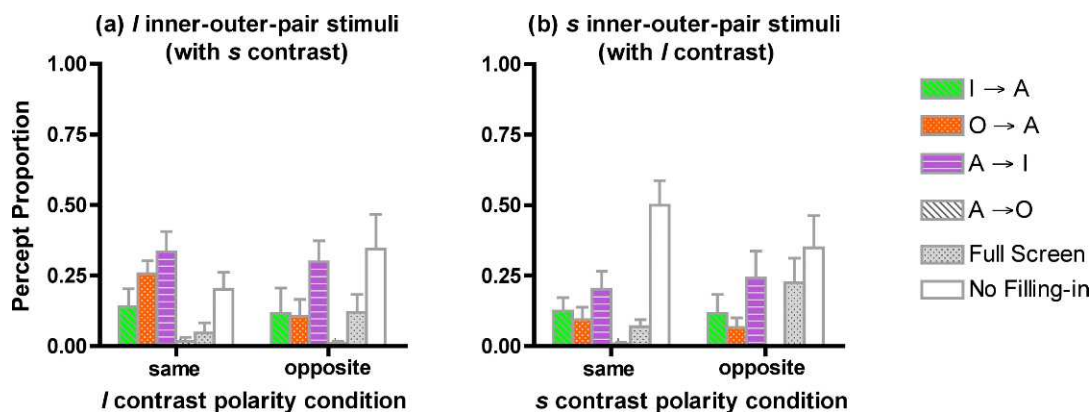

Figure 7. Filled-in percept proportions for different contrast polarity conditions for (a) *l* inner-outer pair stimuli and (b) *s* inner-outer pair stimuli.

times to chromatic contrast in threshold units also indicated that the two axes have similar temporal properties (Medina & Díaz, 2006). In a texture filling-in study, Stürzel and Spillmann (2001) showed a linear relationship between time to filling-in ("fading time") was linearly related to target salience estimates using a texture pattern defined by orientation, shape, and order contrast. The mathematic function we used (Equation 1) has an initial linear portion, followed by a nonlinear segment. It is likely that in Stürzel and Spillmann's study, the contrast was not large enough to reach the nonlinear segment. In our case, we treated contrast magnitude (in threshold units) linearly. It is possible the salience estimate was not linearly related to stimulus contrast, as Stürzel and Spillmann showed. In the presence of both l and s contrasts (Experiment 2), when l and s contrasts in threshold units were summed, the time to filling-in and percept duration could be described by the same function as the l contrast or s contrast stimuli (Figure 3). Putting this together, results from both experiments indicated that a common mechanism may mediate color filling-in in the inferred PC and KC pathways, and the chromatic signals from the two pathways were summed first before the neural mechanism for filling-in was active.

An important finding of the current study is that varying the l or s contrast polarity relationship of the two edges changed the frequency distribution of the filled-in percepts. When the polarities were the same (i.e., a monotonic arrangement of chromaticities, I > A > O or O > A > I) along one of the cardinal axes without contrast along the other axis, the annulus was predominantly filled with either the outer color (O → A) or the inner color (I → A) within a few seconds. Further, a stimulus pattern with the same polarity led to more sequential filling-in for the l contrast stimuli. These results are consistent with the directional filling-in theory (Arrington, 1996). When the polarities were opposite instead, color filling-in from the annulus to the inner field (A → I) was more frequently reported, and it typically required more than 10 s to complete. Meanwhile, the same polarity facilitated filling-out from the inner field to the annulus when the inner edge had a smaller cone contrast and filling-in from the outer field to the annulus when the outer edge had a smaller cone contrast. These results indicated that a same contrast polarity from a distal edge facilitated filling-in along a given edge, but an opposite polarity from a distal edge may partially block filling-in (Rudd, 2010; Rudd & Arrington, 2001; Rudd & Popa, 2007; Rudd & Zemach, 2007; Vladusich et al., 2006). These findings further suggested that color filling-in depended on the contrast characteristics of the local edge as well as the distal edges, consistent with the edge integration theory (Arrington, 1996; Rudd & Arrington, 2001; Vladusich et al., 2006).

Compared to the experiment with chromaticity varying only along one axis, the presence of contrasts from both axes changed the filled-in percept frequencies. These results suggested that the two cardinal axes do not act independently in the color filling-in process. The interaction between the two cardinal axes has been reported by many other studies, including on chromatic contrast matching (Webster & Mollon, 1991, 1994), chromatic discrimination (Danilova & Mollon, 2010, 2012; Eskew, Newton, & Giulianini, 2001; Krauskopf, Williams, Mandler, & Brown, 1986; Newton & Eskew, 2003), color image classification (Hansen & Gegenfurtner, 2005), or wavelength discrimination (Mullen & Kulikowski, 1990). When the contrast magnitudes are pooled, the same function can describe the time course of the filling-in. It is likely that the interaction between the two cardinal axes in color filling-in is different from those observed with different approaches (Eskew, 2009). In the case of color filling-in, we found that the signals from both axes were summed in a linear fashion (Q = 0.89 in Equation 2; in fact, setting Q = 1 did not change the model's goodness of fit, see Table 2). This is consistent with physiological studies that showed V1 neurons use linear summation of the inputs from two axes (Komatsu, 1998; Lennie, Krauskopf, & Sclar, 1990). Note that for the l inner-outer field pairs, the s contrast always had opposite polarities along the two edges. Similarly, having different l chromaticity in the annulus led to opposite polarities along the two edges for the s inner-outer field pairs. Therefore, adding a separate contrast from a different axis had two effects: namely, increasing contrast magnitudes (by a linear summation mechanism) and producing opposite polarities along the edges. Consequently, Experiment 2 showed more no filling-in than Experiment 1.

Using the identical stimulus configuration, chromatic discrimination measurements indicated that the inner adapting field outweighed the outer field for the "red"-"green" and "green"-"red" pairs, but the "white" field always dominated in other pairs in determining chromatic discrimination along the l axis (Cao & Lu, 2012). Here, we did not observe inner field dominance in color filling-in; that is, the "red"-"green" and "green"-"red" pairs had similar filling-in patterns. However, when the inner or outer field was "white," it appears that filling-in was more likely to occur along the edge that consisted of a "white" field, suggesting the importance of "white" in color filling-in as we suggested in a chromatic discrimination experiment (Cao & Lu, 2012). Due to some normalization processing to the lights in the natural environment (Walraven & Werner, 1991), the visual system may have an intrinsic representation of neutral color (Webster & Leonard, 2008). Chromatic discrimination functions measured in a dark surround showed a V shape with a minimum at EEW, also suggesting

intrinsic normalization toward EEW (Smith, Pokorny, & Sun, 2000). This intrinsic representation of white may explain why the "white" adapting field is important in determining color filling-in as well as chromatic discrimination.

A fundamental question concerns which neural mechanisms mediate color filling-in or, generally, perceptual filling-in. Researchers have proposed different theories regarding neural mechanisms underlying filling-in phenomena. Among these theories, two competing theories have been considered more often than others. These opposing theories are referred to as symbolic versus isomorphic. The fundamental difference between these two theories is whether neural activation in the early visual cortex changes when filling-in occurs. The symbolic theory surmises that neural activation of the early visual cortex does not change when filling-in is perceived, and the perceived color spreading is due to a reconstruction of color information along the borders in higher visual areas (Komatsu, 2006; von der Heydt, Friedman, & Zhou, 2003). On the other hand, the isomorphic theory assumes a retinotopic spread of neural activation in the early visual cortex from the border to the interior of a region when filling-in occurs, and a two-dimensional point-wise representation of visual features is activated in the early visual cortex (Komatsu, 2006; von der Heydt et al., 2003). Evidence supporting these theories comes from various studies. von der Heydt et al. (2003) reported that during steady fixation, the edge cells' responses to the contrast border gradually decreased, suggesting an edge adaptation process. In the same study, they also reported that the activities of surface cells in the V1 and V2 areas did not change when filling-in occurred, which seems to suggest no neural activation spread in the early visual cortex during filling-in, which therefore supports the symbolic theory. On the other hand, other studies found neural activations correlating to the filling-in percepts in V1, V2, or V3 when examining other types of filling-in, such as the Craik-O'Brien-Cornsweet illusion and blind spot filling-in, which supports the isomorphic theory (Meng, Remus, & Tong, 2005; Sasaki & Watanabe, 2004). Our study was not designed to assess the two hypotheses. The results from our study probably can provide some insight on the two theories. The effect of polarity on filled-in percepts and the occurrence of stepwise sequential filling-in imply the importance of retinotopic representation. It has been suggested that a reconstruction of color information from the higher visual areas does not need to take a stepwise process whereas stepwise spreading is necessary for retinotopic neural activation spreading (Hamburger et al., 2006). In this sense, our results are more consistent with the isomorphic theory.

References

Arrington, K. F. (1996). Directional filling-in. *Neural Computation, 8*(2), 300–318.

Boynton, R. M., Eskew, R. T., Jr., & Olson, C. X. (1985). Blue cones contribute to border distinctness. *Vision Research, 25*(9), 1349–1352.

Cao, D., & Lu, Y. (2012). Chromatic discrimination: Differential contributions from two adapting fields. *Journal of the Optical Society of America, A, 29*(2), A1–A9.

Cao, D., Zele, A. J., Smith, V. C., & Pokorny, J. (2008). S-cone discrimination for stimuli with spatial and temporal chromatic contrast. *Visual Neuroscience, (25)*, 349–354.

Creutzfeldt, O. D., Lee, B. B., & Valberg, A. (1986). Colour and brightness signals of parvocellular lateral geniculate neurons. *Experimental Brain Research, 63,* 21–34.

Danilova, M. V., & Mollon, J. (2010). Parafoveal color discrimination: A chromaticity locus of enhanced discrimination. *Journal of Vision, 10*(1):4, 1–9, http://www.journalofvision.org/content/10/1/4, doi:10.1167/10.1.4. [PubMed] [Article]

Danilova, M. V., & Mollon, J. D. (2012). Cardinal axes are not independent in color discrimination. *Journal of the Optical Society of America, A, 29*(2), A157–A164.

Derrington, A. M., Krauskopf, J., & Lennie, P. (1984). Chromatic mechanisms in lateral geniculate nucleus of macaque. *Journal of Physiology (London), 357,* 241–265.

De Weerd, P., Desimone, R., & Ungerleider, L. G.

(1998). Perceptual filling-in: A parametric study. *Vision Research, 38*(18), 2721–2734.

De Weerd, P., Gattass, R., Desimone, R., & Ungerleider, L. G. (1995). Responses of cells in monkey visual cortex during perceptual filling-in of an artificial scotoma. *Nature, 377*(6551), 731–734.

Eskew, R. T. (2009). Higher order color mechanisms: A critical review. *Vision Research*, 49(22), 2686–2704.

Eskew, R. T., Newton, J. R., & Giulianini, F. (2001). Chromatic detection and discrimination analyzed by a Bayesian classifier. *Vision Research, 41*(7), 893–909.

Friedman, H. S., Zhou, H., & von der Heydt, R. (1999). Color filling-in under steady fixation: Behavioral demonstration in monkeys and humans. *Perception, 28*(11), 1383–1395.

Gerrits, H. J., & Vendrik, A. J. (1970). Simultaneous contrast, filling-in process and information processing in man's visual system. *Experimental Brain Research, 11*(4), 411–430.

Hamburger, K., Prior, H., Sarris, V., & Spillmann, L. (2006). Filling-in with colour: Different modes of surface completion. *Vision Research, 46*(6–7), 1129–1138.

Hansen, T., & Gegenfurtner, K. R. (2005). Classification images for chromatic signal detection. *Journal of the Optical Society of America, A, 22*(10), 2081–2089.

Hendry, S. H., & Reid, R. C. (2000). The koniocellular pathway in primate vision. *Annual Review of Neuroscience, 23,* 127–153.

Hsieh, P. J., & Tse, P. (2009). Feature mixing rather than feature replacement during perceptual filling-in. *Vision Research, 49*(4), 439–450.

Kim, J., & Francis, G. (2011). Color selection, color capture, and afterimage filling-in. *Journal of Vision, 11*(3):23, 1–18, http://www.journalofvision.org/content/11/3/23, doi:10.1167/11.3.23. [PubMed] [Article]

Komatsu, H. (1998). Mechanisms of central color vision. *Current Opinion in Neurobiology, 8*(4), 503–508.

Komatsu, H. (2006). The neural mechanisms of perceptual filling-in. *Nature Reviews Neuroscience, 7*(3), 220–231.

Krauskopf, J. (1963). Effect of retinal image stabilization on the appearance of heterochromatic targets. *Journal of the Optical Society of America, 53,* 741–744.

Krauskopf, J., Williams, D. R., Mandler, M. B., & Brown, A. M. (1986). Higher order color mechanisms. *Vision Research, 26,* 23–32.

Land, E. H., & McCann, J. J. (1971). Lightness and retinex theory. *Journal of the Optical Society of America, 61,* 1–11.

Lee, B. B., Pokorny, J., Smith, V. C., Martin, P. R., & Valberg, A. (1990). Luminance and chromatic modulation sensitivity of macaque ganglion cells and human observers. *Journal of the Optical Society of America A, 7,* 2223–2236.

Lennie, P., Krauskopf, J., & Sclar, G. (1990). Chromatic mechanisms in striate cortex of macaque. *Journal of Neuroscience, 10*(2), 649–669.

MacLeod, D. I. A., & Boynton, R. M. (1979). Chromaticity diagram showing cone excitation by stimuli of equal luminance. *Journal of the Optical Society of America, 69,* 1183–1185.

Martin, P. R., White, A. J., Goodchild, A. K., Wilder, H. D., & Sefton, A. E. (1997). Evidence that blue-on cells are part of the third geniculocortical pathway in primates. *European Journal of Neuroscience, 9,* 1536–1541.

Medina, J. M., & Díaz, J. A. (2006). Postreceptoral chromatic-adaptation mechanisms in the red-green and blue-yellow systems using simple reaction times. *Journal of the Optical Society of America A, 23*(5), 993–1007.

Meng, M., Remus, D. A., & Tong, F. (2005). Filling-in of visual phantoms in the human brain. *Nature Neuroscience, 8*(9), 1248–1254.

Mullen, K., & Kulikowski, J. (1990). Wavelength discrimination at detection threshold. *Journal of the Optical Society of America A, 7*(4), 733–742.

Murakami, I. (1995). Motion aftereffect after monocular adaptation to filled-in motion at the blind spot. *Vision Research, 35*(8), 1041–1045.

Newton, J. R., & Eskew, R. T. (2003). Chromatic detection and discrimination in the periphery: A postreceptoral loss of color sensitivity. *Visual Neuroscience, 20*(5), 511–521.

Paradiso, M. A., & Hahn, S. (1996). Filling-in percepts produced by luminance modulation. *Vision Research, 36*(17), 2657–2663.

Ramachandran, V. S. (1992). Blind spots. *Scientific American, 266*(5), 86–91.

Ramachandran, V. S., & Gregory, R. L. (1991). Perceptual filling in of artificially induced scotomas in human vision. *Nature, 350*(6320), 699–702.

Rudd, M. E. (2010). How attention and contrast gain control interact to regulate lightness contrast and assimilation. *Journal of Vision, 10*(14):40, 1–37, http://www.journalofvision.org/content/10/14/40, doi:10.1167/10.14.40. [PubMed] [Article]

Rudd, M. E. (2001). Lightness computation by a neural

filling-in mechanism. *Proceedings of the Society of Photo-Optical Instrumentation Engineers: Human Vision and Electronic Imaging VI, 4299,* 400–413.

Rudd, M. E., & Arrington, K. F. (2001). Darkness filling-in: A neural model of darkness induction. *Vision Research, 41*(27), 3649–3662.

Rudd, M. E., & Popa, D. (2007). Stevens' brightness law, contrast gain control, and edge integration in achromatic color perception: A unified model. *Journal of the Optical Society of America A: Optics, Image Science, and Vision, 24,* 2766–2782.

Rudd, M. E., & Zemach, I. K. (2007). Contrast polarity and edge integration in achromatic color perception. *Journal of the Optical Society of America A, 24*(8), 2134–2156.

Sakaguchi, Y. (2006). Contrast dependency in perceptual filling-in. *Vision Research, 46*(20), 3304–3312.

Sakaguchi, Y. (2001). Target/surround asymmetry in perceptual filling-in. *Vision Research, 41*(16), 2065–2077.

Sasaki, Y., & Watanabe, T. (2004). The primary visual cortex fills in color. *Proceedings of the National Academy of Sciences, USA, 101*(52), 18251–18256.

Smith, V. C., Pokorny, J., & Sun, H. (2000). Chromatic contrast discrimination: Data and prediction for stimuli varying in L and M cone excitation. *Color Research and Application, 25,* 105–115.

Spillmann, L., & Kurtenbach, A. (1992). Dynamic noise backgrounds facilitate target fading. *Vision Research, 32*(10), 1941–1946.

Stürzel, F., & Spillmann, L. (2001). Texture fading correlates with stimulus salience. *Vision research, 41*(23), 2969–2977.

Tansley, B. W., & Boynton, R. M. (1978). Chromatic border perception: The role of red- and green-sensitive cones. *Vision Research, 18,* 683–697.

Tansley, B. W., & Boynton, R. M. (1976). A line, not a space, represents visual distinctness of borders formed by different colors. *Science, 191*(4230), 954–957.

van Lier, R., Vergeer, M., & Anstis, S. (2009). Filling-in afterimage colors between the lines. *Paleobiology, 29,* 105–122.

van Tuijl, H. F., & Leeuwenberg, E. L. (1979). Neon color spreading and structural information measures. *Perception & Psychophysics, 25*(4), 269–284.

Vladusich, T., Lucassen, M. P., & Cornelissen, F. W. (2006). Edge integration and the perception of brightness and darkness. *Journal of Vision, 6*(10): 12, 1126–1147, http://www.journalofvision.org/content/6/10/12, doi:10.1167/6.10.12. [PubMed] [Article]

von der Heydt, R., Friedman, S. H., & Zhou, H. (2003). Searching for the neural mechanism of color filling-in. In L. Pessoa & P. D. Weerd (Eds.), *Filling-in: From perceptual completion to cortical reorganization* (pp. 106–127). Oxford: University Press.

Walls, G. L. (1954). The filling-in process. *American Journal of Optometry and Archives of American Academy of Optometry, 31*(7), 329–341.

Walraven, J., & Werner, J. (1991). The invariance of unique white: A possible implication for normalizing cone action spectra. *Vision Research, 31*(12), 2185–2193.

Webster, M. A., & Leonard, D. (2008). Adaptation and perceptual norms in color vision. *Journal of the Optical Society of America A, 25*(11), 2817–2825.

Webster, M. A., & Mollon, J. D. (1991). Changes in colour appearance following post-receptoral adaptation. *Nature, 349,* 235–238.

Webster, M. A., & Mollon, J. D. (1994). The influence of contrast adaptation on color appearance. *Vision Research, 34,* 1993–2020.