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# Illusory color mixing upon perceptual fading and filling-in does not result in ‘forbidden colors’

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## Abstract

A retinally stabilized object readily undergoes perceptual fading. It is commonly believed that the color of the apparently vanished object is filled in with the color of the background because the features of the filled-in area are determined by features located outside the stabilized boundary. Crane, H. D., & Piantanida, T. P. (1983) (On seeing reddish green and yellowish blue. *Science, 221*, 1078–1080) reported that the colors that are perceived upon full or partial perceptual fading can be ‘forbidden’ in the sense that they violate color opponency theory. For example, they claimed that their subjects could perceive “reddish greens” and “yellowish blues.” Here we use visual stimuli composed of spatially alternating stripes of two different colors to investigate the characteristics of color mixing during perceptual filling-in, and to determine whether ‘forbidden colors’ really occur. Our results show that (1) the filled-in color is not solely determined by the background color, but can be the mixture of the background and the foreground color; (2) apparent color mixing can occur even when the two colors are presented to different eyes, implying that color mixing during filling-in is in part a cortical phenomenon; and (3) perceived colors are not ‘forbidden colors’ at all, but rather intermediate colors.

*Keywords:* Perceptual fading; Perceptual filling-in; Color mixing

## 1. Introduction

Perceptual fading, also called the “Troxler effect” (Kanai & Kamitani, 2003; Troxler, 1804), occurs when an object, though present in the world and continually casting light upon the retina, vanishes from visual consciousness. This phenomenon is optimal when the object is located peripherally, has indistinct edges, a low luminance level equal to that of the background, and has been stabilized upon the retina, as happens under conditions of visual fixation (Livingstone & Hubel, 1987). Perceptual fading is commonly thought to arise because of bottom-up local sensory adaptation to edge information (Ramachanndran, 1992). Though previous studies have suggested that perceptual fading occurs early in the visual pathway, such as in the lateral geniculate nucleus of the thalamus (LGN) or retinal ganglion cells (Clarke & Belcher, 1962; Kotulak & Schor, 1986; Millodot, 1967), it remains an open question whether there are cortical areas involved in perceptual fading. Because perceptual fading involves both loss of signal about the presence of an object, and filling-in of the background in place of the object, it is possible that the effect has both a retinal and a cortical component arising from neuronal adaptation and filling-in, respectively. Retinal and cortical accounts are not mutually exclusive. For example, retinal adaptation could lead to a weakened edge signal sent from retinal ganglion cells, followed by a cortical filling-in process (Safran & Landis, 1998; Zur & Ullman, 2003). Such a two-stage model of the mechanism underlying perceptual filling-in has been proposed by Spillmann and DeWeerd (2003). According to their model perceptual filling-in involves a ‘slow cancellation’ of boundaries followed by a ‘fast substitution of surround features’ (i.e., an active filling-in process).

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How perceptual filling-in occurs is still unknown. There are at least two competing hypotheses. The first hypothesis (Pessoa, Thompson, & Noe, 1998) is that perceptual filling-in of a region is just a result of passive tagging by using information surround it. For example, Dennett (1991) argued that information in scotomas is simply ignored and not represented. Since information in scotomas is not represented, there is no active filling-in. The second hypothesis (De Weerd, Gattass, Desimone, & Ungerleider, 1995; Gerrits, deHaan, & Vendrik, 1966; Gerrits & Vendrik, 1970; Spillmann & DeWeerd, 2003) is that during perceptual filling-in, the void area is actively filled-in with the information of the background. Take color filling-in as an example, Krauskopf (1963) showed that the stabilized image of a green (529 nm) disk disappears and is filled in with the color of the orange (593 nm) background whose perimeter was not stabilized. It seems that the information of the filled-in area is determined by the perceptual attributes of the surrounding area located outside of the stabilized boundary. Nonetheless, Boynton, Hayhoe, and MacLeod (1977) reported a case where subjects perceived a color not presented to any patch of retina. Another example of the perception of a color not present at the retina occurs when red light is presented to one eye and green light to the other, yielding a percept of a desaturated yellow, which must take place cortically (De Weert & Wade, 1988). Thus, the color mixing induced by perceptual fading may be but one instance where colors are perceived ‘incorrectly.’

The goal of this paper was to examine the principle of color mixing upon perceptual fading and filling-in, and test the specific claim of Crane and Piantanida (1983) that ‘forbidden colors’ are perceived upon retinal stabilization of abutting red and green regions. Crane and Piantanida (1983) reported that when presenting stabilized bipartite colored fields in which no clear cues about the foreground and background exist, some observers see novel ‘forbidden’ mixtures of the two colors, and some see unstable islands of one color floating in a sea of the other. The perceived colors were deemed to be ‘forbidden’ because they seemed to violate Hering’s laws of color opponency, resulting in reddish greens and yellowish blues. Although this result was surprising and troubling because it appeared to violate Hering’s cornerstone theory of visual color processing, it has received no empirical evaluation in the literature. Because their report was just a brief phenomenological description, we reexamine their as yet untested claim of color mixing during filling-in and subject this claim to its first empirical test.

## 2. Experiment 1: The filled-in color is a mixture of perceptually faded colors

The goal of Experiment 1 was to investigate whether the perceptually filled-in color is solely determined by one of the two colors (background color or object color) or is a mixture of them. This experiment had a non-chromatic and chromatic version.

In Experiment 1a, the upper half of the screen was composed of spatially alternating stripes of dark and light grey. The borders between the two colors were blurred using a gradient of intermediate greys, creating indistinct edges between object and background. Upon fixation the borders appeared to fade, as would be expected from perceptual fading (Krauskopf, 1963) and the grey-value appeared to merge into a uniform field. Small eye movements could break this illusory color mixing and return the percept to one of the veridical stimulus. Subjects were instructed to maintain fixation and adjust the adjustable (lower) field only when they were in the perceptual state where the colors appeared to have merged into a uniform field comprised of a single color. Subjects were asked to adjust the brightness of the lower half of the screen to match the perceptually filled-in brightness that they perceived.

In Experiment 1b, the colors of the alternating stripes were replaced with red and green, and now the colors seemed to merge into a field comprised of a uniform color that was neither red nor green. Subjects were required to adjust the color of the lower half of the screen to match the perceptually filled-in color when they were in the ‘uniform field’ perceptual state.

If the perceptually filled-in color is solely determined by the background color as suggested by Krauskopf (1963) and the Troxler effect, the color adjusted by the subjects should be either dark or light grey in Experiment 1a and either red or green in Experiment 1b, depending on the currently perceived background color of the stimulus. Otherwise, if the perceptually filled-in color is determined by the mixture of the background and foreground colors, the subjectively adjusted color should be intermediate between the two colors.

### 2.1. Methods

#### 2.1.1. Observers

Four subjects (two naïve Dartmouth students and two authors, age range: 20–42) carried out Experiment 1a. The same four subjects (except one author was replaced by a naïve subject, age range: 20–42) carried out Experiment 1b. All of them had normal or corrected-to-normal vision. All of our observers in this and the following experiments were experienced observers who have been long-term subjects for vision psychophysics experiments. All of them were capable of splitting attention between the two regions (physical stimulus and adjustment area). Before each experiment, the subjects practiced several training trials until they were accustomed to the experimental procedure and were capable of fixating while conducting hand movements.

#### 2.1.2. Stimulus displays

The stimulus configurations used in Experiment 1a and 1b are shown in Figs. 1A and B. In Experiment 1a, the fixation was a white (luminance: 71.61 cd/m$^2$; CIE, $x = 0.290$, $y = 0.324$) square that subtended 0.05° of visual angle. One half (upper half or lower half) of the visual

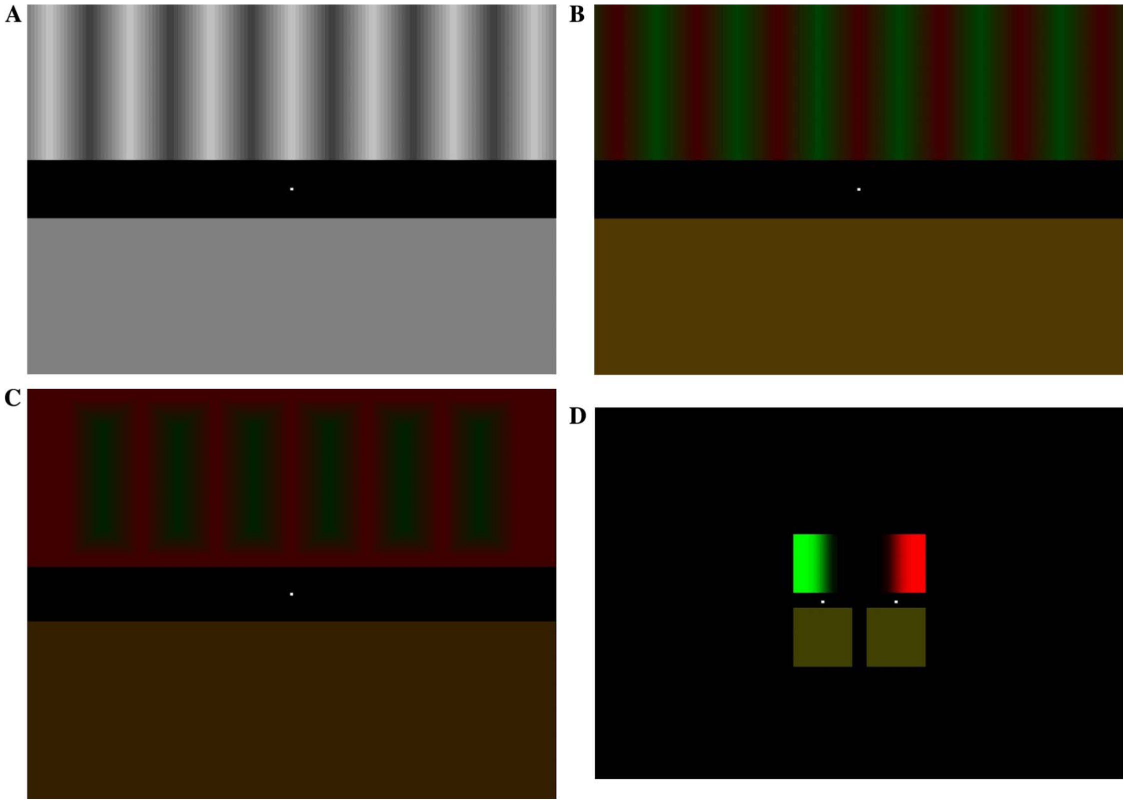

Fig. 1. Stimuli. (A) The stimulus configuration used in Experiment 1a. (B) The stimulus configuration used in Experiment 1b. (C) The stimulus configuration used in Experiment 2. (D) The stimulus configuration used in Experiment 3. (See Methods for actual sizes).

field was composed of alternating stripes (dark and light grey) in space. The distance between each stripe was 1.35° of visual angle. The borders between the two colors were blurred in order to facilitate perceptual fading. The other half of the visual field was a uniform color that could be adjusted by subjects by pressing predetermined keys on the keyboard. The two halves of the visual field were separated by a black horizontal zone (2° wide) centered at the fixation point. All the stimuli were presented binocular and monooptic. The total size of the visual field was 40 × 30 cm, viewed from a distance of 57 cm. Subjects had their chin in a chin rest. In Experiment 1b, all the stimuli were similar to those in Experiment 1a except that the alternating stripes were composed of red and green colors, and the color of the other half of the screen could be adjusted by mixing any possible combinations of red and green colors, again by manipulating set keys on the keyboard.

The visual stimulator was a 2 GHz Dell workstation running Windows 2000. The stimuli were presented on a 23-in. SONY CRT $\gamma$-corrected monitor with 1600 × 1200 pixels resolution and 85 Hz frame rate. Color was measured using a Minolta colorimeter 100LS.

### 2.1.3. Procedure

In Experiment 1a, subjects were required to adjust the brightness of one half of the screen to match the perceptually filled-in color of the other half of the screen by pressing two buttons. One button increased and the other one decreased the luminance of the lower half. In Experiment 1b, subjects were required to adjust the color of one half of the screen to match the perceptually filled-in color of the other half of the screen by pressing four buttons. Two of the buttons, respectively, increased and decreased the luminance of the red color, and two other buttons, respectively, increased and decreased the luminance of the green color. Subjects were required to rest after each trial until the afterimage disappeared.

There were three variables in Experiment 1a: (1) the color of the middle stripe of the half of the screen that induced perceptual filling-in was either dark grey (luminance: 15.86 cd/m$^2$; CIE, $x = 0.281$, $y = 0.333$) or light grey (luminance: 24.77 cd/m$^2$); (2) the half of the screen that induced perceptual filling-in was either located in the upper half or lower half; and (3) the starting brightness of the half of the screen that could be adjusted was randomly chosen from one of the three following values: (luminance: 10.55, 20.15, or 33.30 cd/m$^2$). Similarly, the same three variables were used in Experiment 1b, except that: (1) the color of the middle stripe was either red (luminance: 0.14 cd/m$^2$; CIE, $x = 0.327$, $y = 0.306$) or green (luminance: 0.21 cd/m$^2$; CIE, $x = 0.265$, $y = 0.506$); and (2) the starting luminance of the half of the screen that could be adjusted was randomly chosen from one of the three following values: (luminance: 0.21 cd/m$^2$, CIE, $x = 0.285$, $y = 0.464$; luminance: 0.38 cd/m$^2$, CIE,

$x = 0.306$, $y = 0.507$; or luminance: 1.03 cd/m$^2$, CIE, $x = 0.334$, $y = 0.543$). These variables were randomly mixed and counterbalanced in 12 trials for each experiment. The screen remained black during the period between each trial until the subjects reported that the afterimage disappeared. Eye movements were monitored using a head-mounted eyetracker (Eyelink2, SR research, Ontario, Canada; Tse, Sheinberg, & Logothetis, 2002). Trials during which the subject's monitored left eye was outside a fixation window of 1° radius were excluded from data analysis. Thus all data reported here were carried out under conditions of fixation.

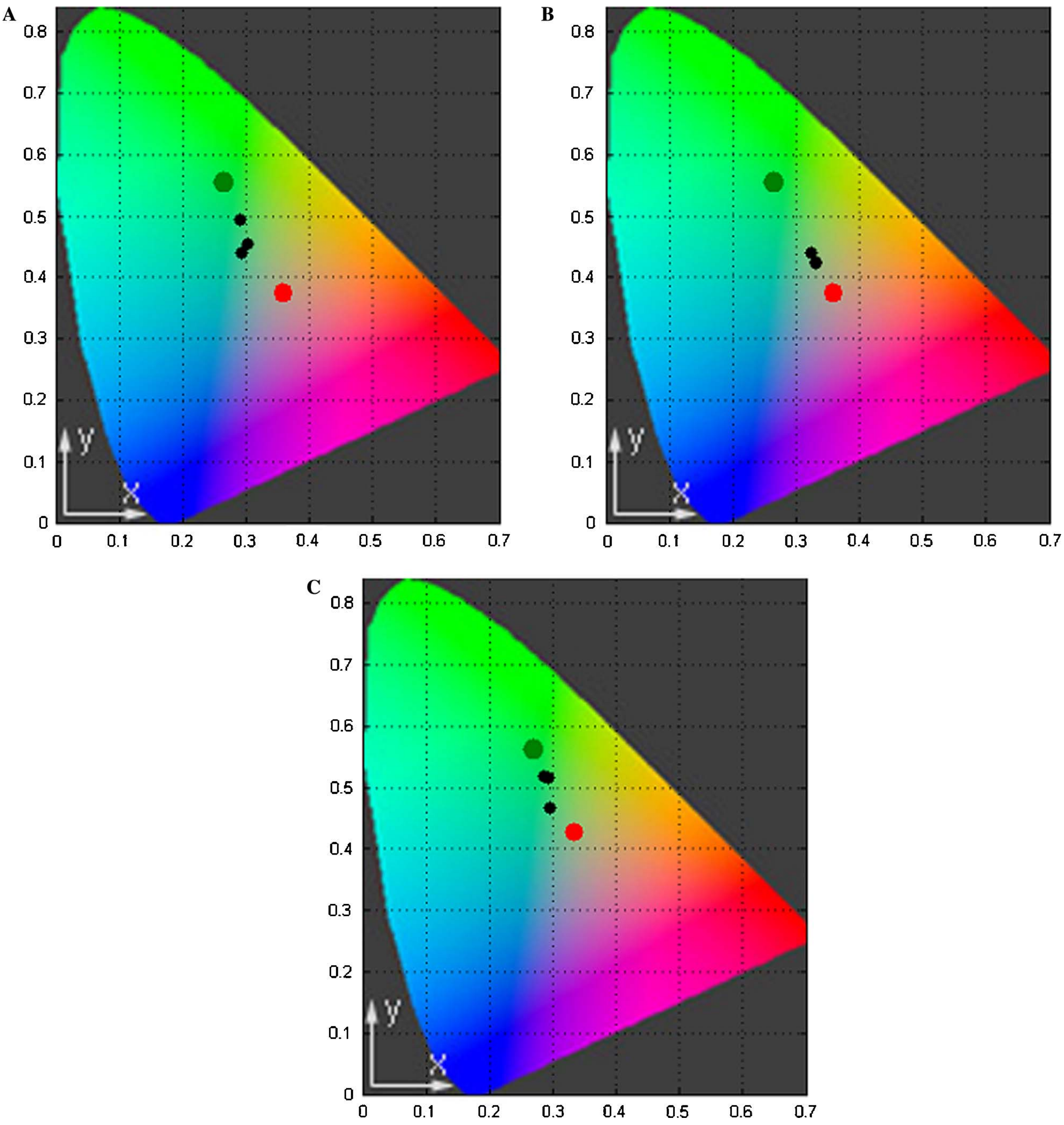

Fig. 2. Results. (A) In Experiment 1b, the mean CIE values of the subjectively adjusted color for the four subjects are plotted (black dots). The mean across subjects (CIE, $x = 0.298 \pm 0.003$, $y = 0.462 \pm 0.011$) is between red (red dot; CIE, $x = 0.327$, $y = 0.376$) and green (green dot; CIE, $x = 0.265$, $y = 0.506$) colors. (B) In Experiment 2, the mean CIE values of the subjectively adjusted color for four subjects are plotted (black dots). The mean across subjects (CIE, $x = 0.330 \pm 0.002$, $y = 0.428 \pm 0.003$) lies between red (red dot; CIE, $x = 0.327$, $y = 0.376$) and green (green dot; CIE, $x = 0.265$, $y = 0.506$) colors. (C) In Experiment 3, the mean CIE values of the subjectively adjusted color for three subjects was plotted (black dots). The mean across subjects (CIE, $x = 0.292 \pm 0.003$, $y = 0.501 \pm 0.016$) is between the red color (red dot; CIE, $x = 0.334$, $y = 0.428$) seen only by the right eye and the green color (green dot; CIE, $x = 0.269$, $y = 0.564$) seen only by the left eye. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this paper.)

### 2.2. Results and discussion

The results of Experiment 1 show that the perceptually filled-in color is a mixture of the two colors. In Experiment 1a, the mean (±SE) of the subjectively adjusted luminance across subjects ($22.02 \pm 2.49\,\text{cd/m}^2$) was between dark grey (luminance: $15.86\,\text{cd/m}^2$) and light grey (luminance: $24.77\,\text{cd/m}^2$). The results of Experiment 1b are shown in Fig. 2A. The mean CIE values (±SE) of the subjectively adjusted color for the four subjects are plotted as black dots ($x=0.304 \pm 0.003$, $y=0.458 \pm 0.010$; $x=0.294 \pm 0.006$, $y=0.439 \pm 0.037$; $x=0.303 \pm 0.007$, $y=0.455 \pm 0.016$; $x=0.290 \pm 0.005$, $y=0.495 \pm 0.015$) in Fig. 2A. The mean across subjects (CIE, $x=0.298 \pm 0.003$, $y=0.462 \pm 0.011$) is located between red (Fig. 2A; red dot; CIE, $x=0.327$, $y=0.376$) and green (Fig. 2A; green dot; CIE, $x=0.265$, $y=0.556$) colors. Together, these results suggest that the perceptually filled-in color is not solely determined by the background color. On the contrary, the perceptually filled-in color seems to be determined by mixing the background and foreground colors.

## 3. Experiment 2: The filled-in color is a mixture of the object color and the background color

One might argue that, in Experiment 1, the figure-ground assignment was ambiguous because the two colors were evenly distributed in space. In order to further rule out this ambiguity, Experiment 2 was conducted by using a more distinct stimulus in which the object and background could be better distinguished, making the stimulus more like that used in typical Troxler effect displays (Kanai & Kamitani, 2003; Krauskopf, 1963; Troxler, 1804).

### 3.1. Methods

#### 3.1.1. Observers

Four subjects (two naïve Dartmouth students and two authors, age range: 20–42) who had participated in Experiment 1a carried out the experiment.

#### 3.1.2. Stimulus displays and procedure

The stimulus configuration used in Experiment 2 is shown in Fig. 1C. In Experiment 2, all the stimuli and procedures were similar to those in Experiment 1b except that the alternating stripes were replaced by green rectangles on a red background. Each rectangle subtended 5.25° of visual angle in height and 2.4° in width. The borders of the rectangular figures were blurred as in Experiment 1. The six rectangles were centered ±1.35°, ±4.05°, and ±6.75°, to the left or right of the fixation point. There were two variables in Experiment 2: (1) the half of the screen that induced perceptual filling-in was either located in the upper half or lower half; and (2) the starting luminance of the half of the screen that could be adjusted was randomly chosen from one of the three luminance values used in Experiment 1b. These variables were randomly mixed and counterbalanced in 6 trials for each experiment.

### 3.2. Results and discussion

The results of Experiment 2 are shown in Fig. 2B. The perceptually filled-in color is indeed a mixture of the background and the foreground color. The mean CIE values (±SE) of the subjectively adjusted color for the four subjects are plotted as black dots ($x=0.332 \pm 0.003$, $y=0.426 \pm 0.004$; $x=0.325 \pm 0.007$, $y=0.439 \pm 0.006$; $x=0.334 \pm 0.008$, $y=0.423 \pm 0.011$; $x=0.330 \pm 0.004$, $y=0.423 \pm 0.002$) in Fig. 2B. The mean CIE value across subjects (CIE, $x=0.330 \pm 0.002$, $y=0.428 \pm 0.003$) is located between red (Fig. 2B; red dot; CIE, $x=0.327$, $y=0.376$) and green (Fig. 2B; green dot; CIE, $x=0.265$, $y=0.506$) colors. These results rule out the background-foreground ambiguity in Experiment 1, suggesting that the perceptually filled-in color is determined by mixing the background and foreground colors.

## 4. Experiment 3: Color mixing occurs during binocular fusion

It is not clear from Experiments 1 and 2 whether color mixing happens before or after cortical processing. In a sense, the results of Experiment 1, where the mixture of red and green is perceived to be a brownish color, suggest that filling-in may result from subtractive color mixing, since additive color mixing would have predicted that red and green combine to form yellow. Certainly no retinal account would predict subtractive color mixing. However, to more compellingly establish that color mixing occurs cortically, we presented red to one eye and green to the other by asking our subjects to observe the stimuli through a stereoscope. If color mixing occurs here, it must be due to cortical processing, since information from the two eyes is processed separately before the cortex.

### 4.1. Methods

#### 4.1.1. Observers

Three subjects (two naïve Dartmouth students and one author, age range: 28–29) with normal or corrected-to-normal vision carried out the experiment.

#### 4.1.2. Stimulus displays and procedure

The stimulus configuration used in Experiment 3 is shown in Fig. 1D. Subjects were asked to observe the stimuli through a stereoscope (KEYSTONE, No.50 Home Training Stereoscope) from a distance of 11.3 cm. The upper-left (upper-right) image was a square that subtended 10° of visual angle, centered 7.5° to the left (right) and 7.5° above center. Both images were gradient stimuli. The color/luminance of the upper-left image ranged gradually from green (luminance: $0.34\,\text{cd/m}^2$, CIE, $x=0.269$, $y=0.564$) on the left side to black (luminance: $0.10\,\text{cd/m}^2$) on the right side, and the color/luminance of the upper-right image ranged gradually from red (luminance: $0.17\,\text{cd/m}^2$, CIE, $x=0.334$, $y=0.428$) on the right side to black (luminance:

0.10 cd/m$^2$) on the left side. The two bottom images were two squares, that both subtended 10° of visual angle, centered 7.5° to the left/right and 7.5° below the center. The color/luminance of the bottom two squares was adjusted by subjects by pressing predetermined keys on the keyboard. Two white (luminance: 71.61 cd/m$^2$) squares that subtended 1° of visual angle, centered 7.5° to the left and right of the center, were presented to aid fusing of the images. The experimental procedure was otherwise the same as in Experiment 1b.

### *4.2. Results and discussion*

The results of Experiment 3 are shown in Fig. 2C. The filled-in color is a mixture of the two colors. The mean CIE values of the subjectively adjusted color for the three subjects are plotted as black dots ($x = 0.294 \pm 0.005$, $y = 0.516 \pm 0.004$; $x = 0.295 \pm 0.003$, $y = 0.468 \pm 0.020$; $x = 0.287 \pm 0.003$, $y = 0.518 \pm 0.006$) in Fig. 2C. The mean across subjects (CIE, $x = 0.292 \pm 0.003$, $y = 0.501 \pm 0.016$) is between the red color (Fig. 2C; red dot; CIE, $x = 0.334$, $y = 0.428$) seen only by the right eye and the green color (Fig. 2C; green dot; CIE, $x = 0.269$, $y = 0.564$) seen only by the left eye. This result implies that the mixing of colors during perceptual filling-in has a cortical component, because the first individual neurons in the visual processing hierarchy to respond to input from both eyes lie in striate cortex. This is consistent with past results implying a cortical locus for processing that underlies filling-in and fading. For example, binocular color mixture of a red light to one eye and green light to the other eye yields a desaturated yellow, which must take place cortically (De Weert & Wade, 1988).

## 5. General discussion

Filling-in is thought to be necessary for visual perception because retinal ganglion cell receptive fields function primarily as contour detectors. Their color-opponent center-surround organization effectively discards the ‘redundant’ information about uniform regions that lie between contours. Eliminating this redundancy amounts to data compression that may enhance the efficiency of data transfer from the retina to the cortex. However, compressed data must be decompressed by the cortex, so that information that is only implicit in the incoming signal is made explicit. A crucial part of cortical processing is therefore thought to be the “filling-in” of visual features away from contours (e.g. Grossberg & Mingolla, 1985; Pessoa et al., 1998) in order to recreate the region information that was discarded at the retina. Grossberg and Mingolla (1985) posited the existence of two complementary systems involved in filling-in. A boundary completion system defines boundaries separating regions, and a feature completion system fills in features labeled at the boundaries into the interior of regions. A key aspect of their theory is that features continue to propagate until they meet a boundary. Similarly, a two-stage model about perceptual filling-in has also been proposed by Spillmann and DeWeerd (2003), saying that perceptual filling-in is a two-stage process involving a slow cancellation of boundaries followed by a fast substitution of surround features. Empirical data suggest that this propagation takes place away from contours at a fast, though finite speed (Paradiso & Nakayama, 1991). While these models do not explicitly deal with the issue of featural mixing, they are consistent with the possibility of such mixing, because when all boundaries have faded, as occurs during perceptual fading, no boundaries exist to contain feature propagation.

Our results show that the filled-in color is not solely determined by the background color. If the filled-in color were solely determined by the background color, the color adjusted by the subjects would either be dark grey or light grey in Experiment 1a (red or green in Experiment 1b), depending on the currently perceived background color of the stimuli. Since our results show that the filled-in color is actually the mixture of the background and the foreground color, we can rule out the possibility that the filled-in color is determined solely by the background color. Illusory color mixing occurred even when the two colors (red and green) did not have the same luminance values. This makes it different from typical Troxler fading, which works best under conditions of equiluminance.

Because the color perceived at a location after perceptual filling-in can be different from any color actually present in the scene, it follows that color perception is neither entirely stimulus driven nor entirely local. Features appear to be filled-in away from a boundary, such as a closed contour, and in the absence of such “containment” freely merge with other non-local features (Grossberg & Mingolla, 1985). This raises the interesting possibility that the mixed color that we subjectively experience is indeed an averaging or merging of component colors, suggesting that filling-in itself may be a process of linear pooling of contributions within a region.

According to the qualitative report by Crane and Piantanida (1983), when presenting stabilized bipartite colored fields in which no clear cues about the foreground and background exist, some observers see novel mixtures of the two colors, such as reddish greens and bluish yellows. They argued that the mixture of two opponent colors is in violation of Hering’s laws of color opponency. Surprisingly, although these laws comprise a cornerstone of the modern understanding of color perception, this attack on that cornerstone was never met by an empirical test of their claims. They further argued that perceiving ‘forbidden’ colors under perceptual filling-in reveals a role of cortico-cortical processing because it is impossible to mix red and green by retinal connections only. However, one crucial weakness of their data is that the quality of the mixture of the two opponent colors relied only on subjects’ verbal reports. It is possible that subjects did not actually experience a new forbidden color, but just lacked the appropriate vocabulary to describe the color that they perceived. Our experiments show that interspersing two opponent colors in the real world in appropriate proportions can create a subjectively experienced color, presumably resulting from perceptual filling-in, that is subjectively equal to the mixture of the two opponent colors. Our results suggest that subjects did not experience any forbidden colors in the Crane and Piantanida (1983) experiment. For example, instead of perceiving a reddish green (or bluish yellow), observers of their phenomenological demonstrations most likely experienced a brownish (greenish) hue, as was found here empirically.

Because the original report of Crane and Piantanida (1983) is a very brief phenomenological report with no mention of luminance levels or the actual colors perceived in CIE coordinates or any other standard color space, it proved difficult to know the precise experimental setup used, and the precise perceptual states attained by observers upon color mixing in their experiment. Nonetheless, there are some differences between our stimuli and those used by Crane and Piantanida (1983). They stabilized the border between two colors on the retina using an eye tracker linked to deflector mirrors, whereas we relied on visual fixation. Perceptual fading can be induced by either technique (Martinez-Conde, Macknik, & Hubel, 2004), so we do not believe this to be a crucial difference. Crane and Piantanida (1983) used only a single pair of stripes, that is, one red line and one green line, whereas we used patterns containing more than one stripe. In preliminary testing we found the same color mixing to occur regardless of the particular number or arrangement of red and green stripes, so opted to use an arrangement that quickly led to perceptual fading and color mixing upon fixation. One might argue that we are looking at a different phenomenon than that described by Crane and Piantanida because we did not observe any of the strange subjective color effects reported by them. But this is precisely the point we wish to make. We do not believe that percepts of 'forbidden colors' that violate Hering's color opponency laws exist. Indeed the purpose of this research was to carry out the first empirical investigation of their rather radical claim. We looked for the effects reported by Crane and Piantanida and did not find them, at least in the domain of colors and luminances tested. Of course, there might be some other color or luminance domains where 'forbidden colors' are experienced by observers. However, the burden of proof lies with those who accept the existence of such colors. In particular, advocates of the existence of 'forbidden colors' must specify the precise color coordinates and stimulus parameters that lead to such phenomenal effects, so that such effects can be precisely tested and verified. It would not be acceptable for an advocate of the existence of 'forbidden colors' to assert that we failed to find them because we were looking in the wrong color or luminance domain, when there has yet to be a precise specification of the domain in which they supposedly exist. Until that occurs, we reject the existence of experienced colors that violate the fundamental laws of color opponency.

Although the results of Experiments 1 and 2 show that subjects do not experience forbidden colors, these results do not establish or rule out that the mixed color is a result of cortical processing. The results of Experiment 3, however, establish that color mixing can occur at a purely cortical stage of processing, consistent with past evidence that color mixing is a cortical effect (De Weert & Wade, 1988). In sum, our data imply that perceptual filling-in is not only a result of bottom-up local sensory adaptation to edge information, but is also a result of constructive, non-local cortical processing that generates perceived colors that are not in the stimulus by blending the colors of perceptually faded regions. Although perceived colors may not be among the colors presented to the retina, they are in no sense 'forbidden.'

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