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Feature mixing rather than feature replacement during perceptual filling-in

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A B S T R A C T

'Filling-in' occurs when a retinally stabilized object subjectively appears to vanish following perceptual fading of its boundaries. The term 'filling-in' literally means that information about the apparently vanished object is lost and replaced solely by information arising from the surrounding background. However, we find evidence that the mechanism of 'filling-in' can actually involve a process of 'feature mixing' rather than 'feature replacement,' whereby features on either side of a perceptually faded boundary merge. Here we investigate the properties of feature mixing and specify certain conditions under which such mixing occurs. Our results show that, when using visual stimuli composed of spatially alternating stripes containing different luminances or motion signals, and when using the neon-color-spreading paradigm, the filled-in luminance, motion, or color is approximately the area and magnitude weighted average of the background and the foreground luminance, motion, or color, respectively. Together, these results demonstrate that, under at least certain conditions, 'filling-in' may involve a process of feature mixing or feature averaging rather than one of feature replacement.

1. Introduction

The term 'filling-in' is commonly used to describe the phenomenon of perceptual 'fading', where information about a perceptually vanished object seems to be replaced by information arising from the surrounding background (Troxler, 1804). However, we have provided evidence (Hsieh & Tse, 2006) that the mechanism of 'filling-in' may involve a process of 'feature mixing' instead, whereby features on either side of a perceptually faded boundary merge. We used visual stimuli composed of spatially alternating stripes of two different colors to investigate the characteristics of color mixing during perceptual filling-in, and found that the filled-in color is not determined solely by either one of the two colors, but is instead the mixture of them. This result suggests that, under certain conditions, the phenomenon of perceptual 'filling-in' may instead be one of perceptual 'feature mixing'; By this we mean that information within the boundary (foreground) is not lost and replaced by information outside the boundary (background), but rather that information on either side of a perceptually faded boundary merges. In the current paper, we investigate the properties of perceptual feature mixing and examine certain conditions under which feature mixing occurs.

1.1. Perceptual filling-in/fading

Perceptual fading, also called the "Troxler effect" (Kanai & Kamitani, 2003; Krauskopf, 1963; 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 is relatively well 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 (Ramachandran, 1992), which might occur 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). Because perceptual fading involves both fading 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).

How perceptual filling-in occurs is still not well understood. There have traditionally been two competing hypotheses. The first hypothesis argues that there is no active feature replacement. According to Pessoa, Thompson, and Noe (1998), so-called perceptual filling-in of a region upon perceptual fading of its boundaries is just a result of passive tagging by using information from the region surrounding the region that appears to vanish. The second, and more widely accepted, hypothesis (Arrington, 1994; Cohen & Grossberg, 1984; De Weerd, Gattass, Desimone, & Ungerleider, 1995; Gerrits, DeHaan, & Vendrik, 1966; Gerrits & Vendrik, 1970; Pessoa et al., 1998; Spillmann & DeWeerd, 2003) is that during per-

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ceptual filling-in, the voided area is actively filled-in with the information existing in the surround region or in the background.

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). Using a color filling-in paradigm, for 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. A similar filling-in effect has been shown to occur for stimuli composed of different textures (Caputo, 1998; Ramachandran & Gregory, 1991; Stürzel & Spillmann, 2001). While featural filling-in is typically thought of in terms of static features such as color or texture, Watanabe and Cavanagh (1991) showed that filling-in up to a perceived boundary can also occur for moving features.

It is worth noting that terms such as 'filling-in', 'feature replacement', or 'feature mixing' describe events at a phenomenological level. Such terms may not correctly describe what is literally happening at the level of neuronal mechanism. Nevertheless, the term 'filling-in' is commonly used to describe the phenomenon of perceptual 'substitution' that follows the phenomenon of perceptual 'fading', and many researchers might assume that such language describes both phenomenology and mechanism. We therefore wish to investigate the properties of feature mixing, correct any ambiguous usages of the term 'filling-in,' and from this attempt to draw conclusions about how visual features are represented by neuronal activity.

1.2. Filling-in: feature replacement or feature mixing?

When the background and the foreground area cannot be easily distinguished as figure versus ground, as occurs when they occupy equal areas, the perceived uniform feature after perceptual fading appears to be a mixture between the features of the two regions, rather than solely being determined by one or the other. In Hsieh and Tse (2006), we used visual stimuli composed of spatially alternating stripes of two different colors to investigate the characteristics of color mixing during perceptual filling-in, and found that the filled-in color is not solely determined by either one of the two colors, but is the mixture of them. This feature mixing phenomenon occurs not only for color stimuli, but also for non-chromatic stimuli. For example, after fixating on the stimuli shown in Fig. 1a, the upper part of the stimuli will eventually be mixed and perceived as a uniform gray patch. The perceived brightness of the resulting percept will be similar to that shown in the lower part. Similarly, after fixating on the stimuli shown in Fig. 1b and c, the perceived color in the upper part of the stimuli will eventually be very similar to that shown in the lower part.

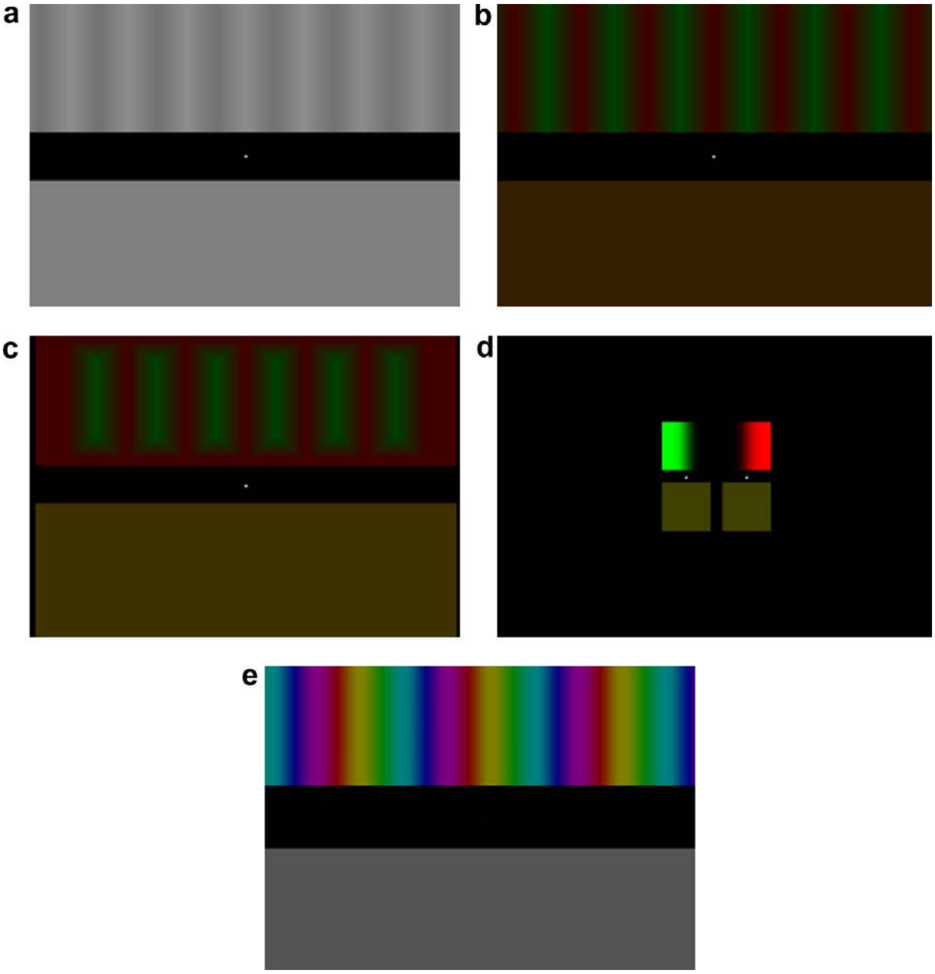

Fig. 1. Stimuli. (a), (b) and (c), After prolonged fixation, the upper part of the stimuli will appear to mix and will be perceived to be similar to the uniform color shown in the lower part. (d) After free-fusing or viewing through a stereoscope, the perceived color will be a mixture of the red and green color. (e) The stimulus configurations used in Experiment 2. (Note that the actual luminance of the stimuli was much lower than those shown in the figures, making it much easier to generate perceptual mixing. See Methods for real luminance.) (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Another example of the perception of a mixed 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. An example can be seen in Fig. 1d. After free-fusing or viewing through a stereoscope, the perceived color will be a mixture of the red and green color. This generation of colors not encoded at the level of the retina must take place cortically (De Weert & Wade, 1988), since this is the first stage in the visual pathway containing cells with direct, feedforward inputs from both eyes.

Fujita (1993) described similar phenomenological observations (though no data) that color appears to spread in both directions across a perceptually faded boundary. Our results (Hsieh & Tse, 2006), together with the subjective observations of Fujita (1993), support a view that the mechanism of perceptual filling-in does not necessarily involve ‘filling-in’ or feature replacement, but may involve a process of perceptual ‘feature mixing’ under some specific conditions.

1.3. General methods

1.3.1. Observers

Four subjects (three naïve Dartmouth students and one author, age range: 20–30) carried out the experiments. Two of the subjects (one author) participated in every experiment. All subjects had normal or corrected-to-normal vision. Before each experiment, subjects practiced several training trials until they were accustomed to the experimental procedure and were capable of fixating while conducting hand movements.

1.3.2. Stimulus displays

In Experiments 1 and 2, the fixation point was a white (luminance: 150 cd/m^2; CIE: $x = 0.341$, $y = 0.368$) square that subtended 0.05° of visual angle. The upper half of the visual field was composed of ‘adapting stimuli’, the lower half of the visual field was a uniform color (its initial color was black) 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 (6° wide) centered at the fixation point. All the stimuli were viewed with both eyes. The total size of the visual field was 40 cm × 30 cm, viewed from a distance of 57 cm. Subjects had their chin in a chin rest. The visual stimulator was a 2 GHz Dell workstation running Windows 2000. The stimuli were presented on a 20-in. Mitsubishi CRT gamma-corrected monitor with 1600 × 1200 pixels resolution and 85 Hz frame rate. Color was measured using a Minolta colorimeter 100 LS. Luminance was measured using a Pritchard 1980 A photometer.

1.3.3. Fixation

Eye movements were monitored using a head-mounted eyetracker (Eyelink2, SR research, Ontario, Canada; Tse, Sheinberg, & Logothetis, 2002). The experiment was paused whenever the subject's monitored left eye was outside a fixation window of 1° radius, and was resumed when the subject regained fixation. Thus all data reported here were carried out under conditions of fixation.

2. Experiment 1: factors affecting the feature mixing process

To examine the principles underlying the feature mixing process, we systematically varied the luminance and area of the two colors undergoing perceptual mixing.

2.1. Methods

2.1.1. Stimulus displays

The stimuli used in Experiment 1a are similar to those shown in Fig. 1b. The upper half of the visual field was composed of red and green stripes alternating in space. The distance between each stripe was 3.43° of visual angle. The borders between the two colors were linearly blurred in order to facilitate perceptual fading. The luminances of the red (CIE: $x = 0.624$, $y = 0.337$) and green (CIE: $x = 0.292$, $y = 0.607$) colors were assigned to be one of the five possible combinations: (1) green/red = 4.1 (1.26/0.31 cd/m^2); (2) green/red = 2.11 (0.65/0.31 cd/m^2); (3) red/green = 1.13 (0.31/0.27 cd/m^2); (4) red/green = 3 (0.82/0.27 cd/m^2); and (5) red/green = 4 (1.1/0.27 cd/m^2). These five conditions were counterbalanced in 15 trials.

In Experiment 1b, all the stimuli and procedures were similar to those in Experiment 1a except that the areas that contained the red and green colors were assigned to be one of the five possible combinations: (1) red area/green area = 1/8.125; (2) red area/green area = 1/1.21; (3) red area/green area = 1; (4) red area/green area = 1.21; and (5) red area/green area = 8.125. These five conditions were counterbalanced in a block (15 trials). Subjects participated in a minimum of one block and a maximum of two blocks.

2.1.2. Procedure

In the recording sessions, subjects were required to keep fixating until filling-in was perceived to have occurred in the upper half of the screen, and then started to adjust the color of the lower half of the screen to match the perceptually filled-in color of the upper half of the screen by pressing six buttons. Two of the buttons respectively increased and decreased the luminance of the red color, two other buttons respectively increased and decreased the luminance of the green color, and two other buttons respectively increased and decreased the luminance of the blue color. Subjects were required to rest after each trial until the afterimage disappeared. The screen remained black during the period between each trial until the subjects reported that the afterimage had disappeared.

2.2. Results

The results in Fig. 2a show that, given that the areas of the two colors are equal in extent, the perceived color after perceptual mixing is affected by the luminances of the two colors, such that the perceived color is biased toward the color that has a higher luminance. As can be seen in Fig. 2a, the perceived color appears to be “redder” as the luminance of the to-be-mixed red color increases. Similarly, the results in Fig. 2b show that, given that the luminances of the two colors are identical, the perceived color after perceptual mixing is determined by the areas of the two colors, such that the perceived color is biased toward the color that covers a larger area (the perceived color appears to be “redder” as the area of the to-be-mixed red color increases).

We further plotted the luminances of the stimuli and of the perceived mixed color in Experiment 1a. The results (Fig. 3) show that the luminance of the mixed color is roughly an ‘average’ of the luminances of the two to-be-mixed colors, just as the hue of the mixed color appeared to be an average of stimulus hues.

3. Experiment 2: perceptual mixing appears to be a linear process

If the feature mixing process is an additive (in the sense of additive color mixing, as occurs with light) mixing process, or one that involves averaging, one would expect that equal proportions of red, green, and blue in a stimulus should lead to a perceived color, after feature mixing, that falls along the spectrum from black to white. In Experiment 2, we further tested whether a stimulus composed of multiple colors simultaneously (Fig. 1e) can be mixed and result in a desaturated gray.

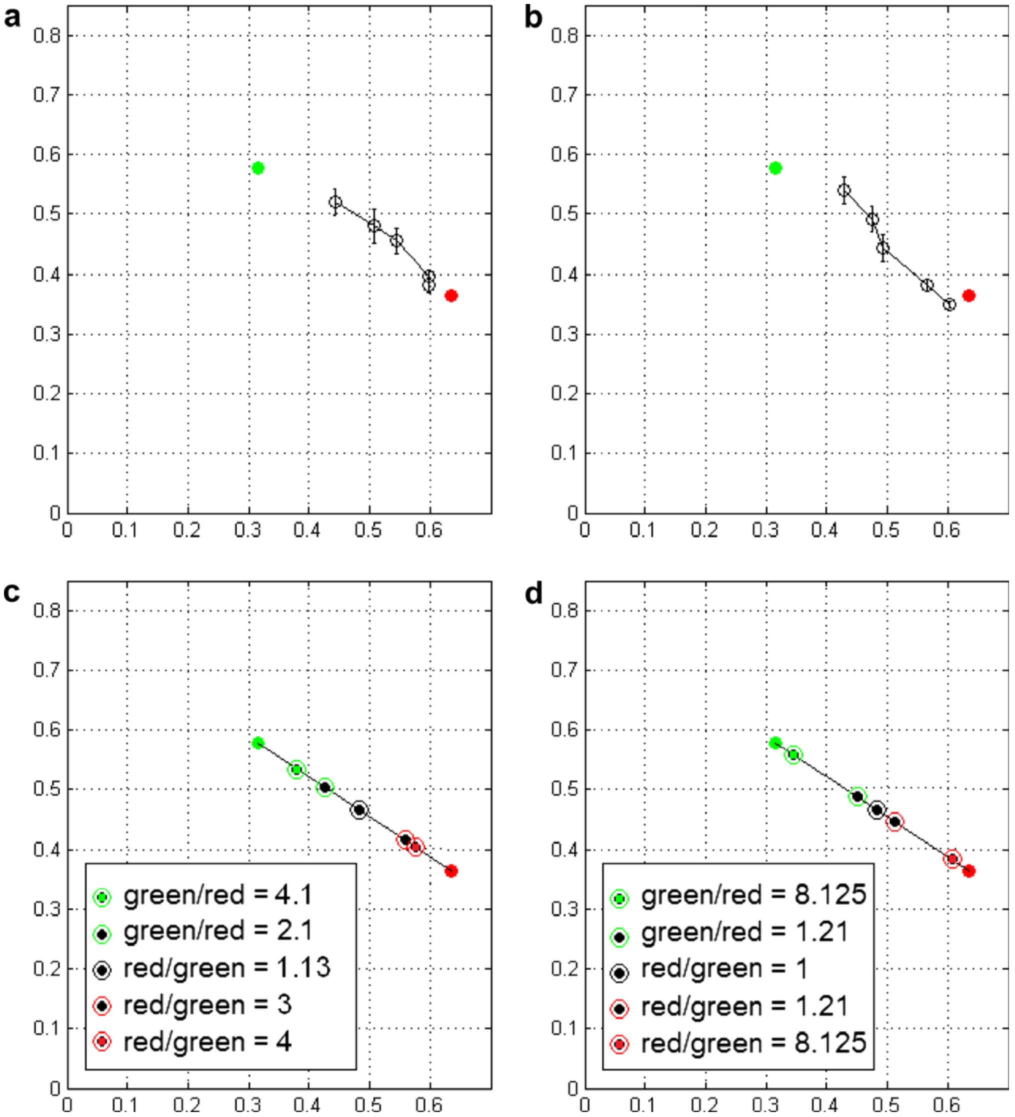

Fig. 2. (a) The results of Experiment 1a. The mean CIE values of the subjectively adjusted color for the four subjects are plotted (black hollow dots). Each black hollow dot represents the result from a different ratio of luminance (red/green), averaged across subjects (standard errors shown as bars). The results show that the perceived color appears to be "redder" as the luminance of the to-be-mixed red color increases. (b) The results of Experiment 1b. The mean CIE values of the subjectively adjusted color for the four subjects are plotted (black hollow dots). Each black hollow dot represents the result from a different ratio of areas (red/green). The results show that the perceived color after perceptual mixing is influenced by both the luminances and the areas of the two colors, that is, the perceived color is biased toward the color that has a higher luminance and/or covers a larger area (the perceived color appears to be "redder" as the luminance and/or the area of the to-be-mixed red color increases). (c) The colors predicted from linear mixing of the red and green colors (with 5 different luminance ratios). (d) The colors predicted from linear mixing of the red and green colors (with five different area ratios). See Fig. 4b for approximate colors corresponding to the CIE coordinates. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3.1. Methods

3.1.1. Stimulus displays and procedure

The stimuli used in Experiment 2 are shown in Fig. 1e. The upper half of the visual field was composed of colored stripes in space. The distance between each stripe was 2° of visual angle. The borders between stripes were linearly blurred in order to facilitate perceptual fading. For each subject, the brightness of all used colors (including red, purple, blue, bluish-green, green, and yellow) were each adjusted to become subjectively equal to a gray background by using the minimal flicker technique (Anstis & Cavanagh, 1983). For example, before the experiment, we presented a green (CIE: $x = 0.292$, $y = 0.607$) flashing (30 Hz) square that subtended 4° visual angle in the center of a gray background (CIE: $x = 0.365$, $y = 0.344$; luminance = 0.3 cd/m^2) and let the subjects adjust the green component of the square's color until minimal subjective flicker was reported. The color of the square was then fixed and applied to the green stripes for the recording sessions. The same procedure was performed for all other colors. There were 10 trials in this experiment. Other parameters were identical to Experiment 1.

3.2. Results

Results (Fig. 4) show that the perceived color is gray or very close to gray (CIE, $x = 0.3763 \pm 0.0194$, $y = 0.2899 \pm 0.0107$; luminance = 0.0825 ± 0.0225 cd/m^2), suggesting that perceptual mixing in the color domain is an approximately linear process.

4. Experiment 3: perceptual mixing of motion

While featural filling-in is typically thought of in terms of static features such as color or texture, Watanabe and Cavanagh (1991)

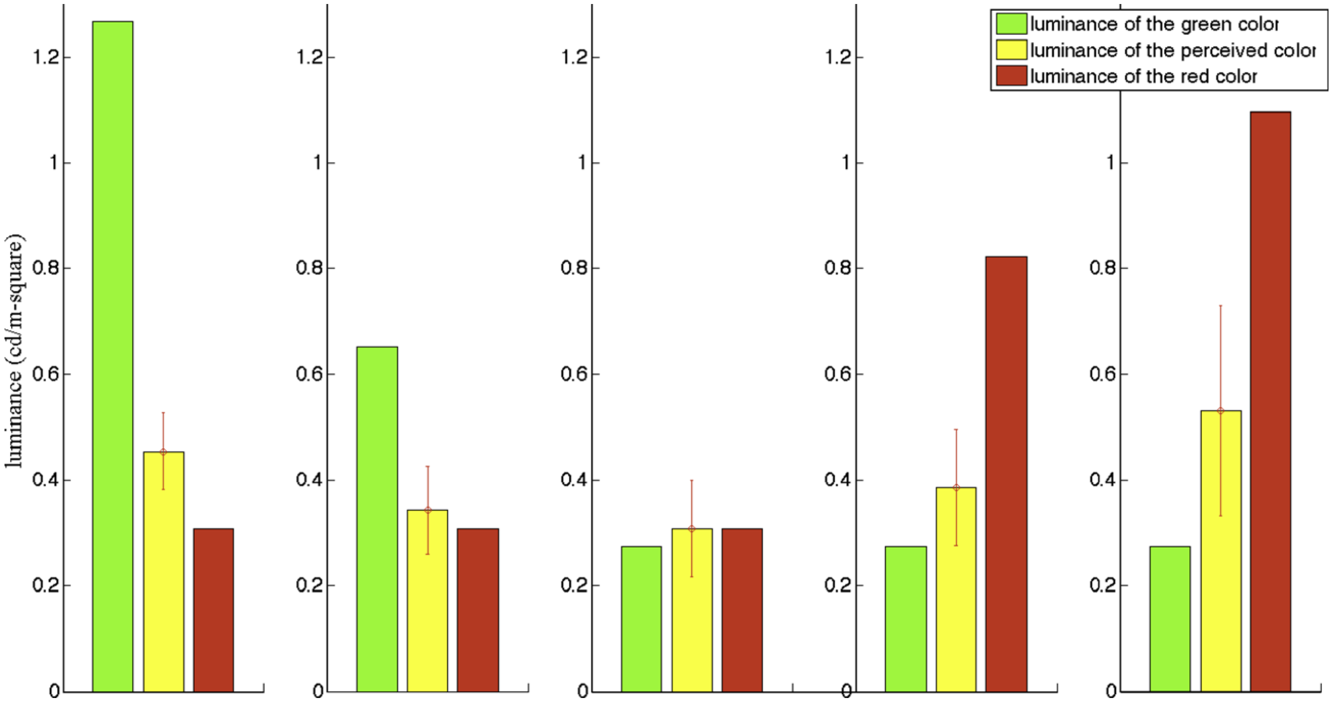

Fig. 3. (a) The luminance of the red and green stimuli and of the color matched to the perceived mixed color following perceptual fading of boudaries between red and green in Experiment 1a. Each green/red bar represents the luminance of the green/red color used in the experiment, and yellow represents the luminance of the perceived mixed color. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

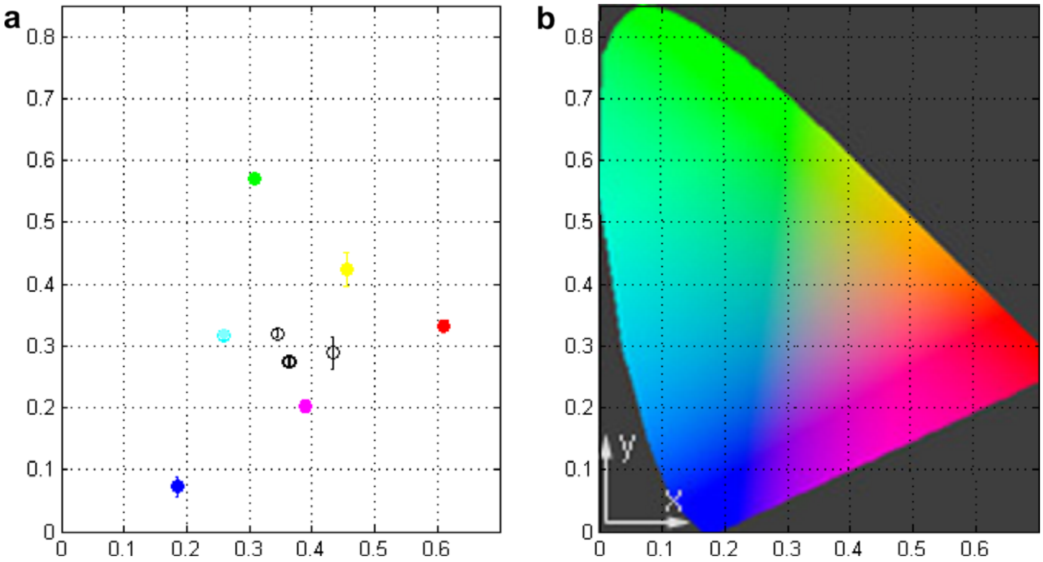

Fig. 4. (a) Results of Experiment 2. The mean CIE values of the subjectively adjusted color for the four subjects are plotted (four black hollow dots, two of which are overlapping). The dots with colors indicate the mean CIE values of the original colors presented in the stimuli. (b) The colors shown in this figure are the approximate colors corresponding to the CIE coordinates. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

showed that filling-in up to a perceived boundary can also occur for motion-defined features. In order to test whether perceptual feature mixing or feature replacement occurs between motion signals with different directions of motion, we tested whether the perceptually filled-in motion is solely determined by one of the two motion signals (background motion or foreground motion) or whether it is a mixture of the two. The stimulus is shown in Fig. 5a. The background consisted of continuous upward motion. The foreground areas were composed of spatially alternating stripes containing motion signals in a different direction. Note that we put a black disk in the middle of the stimulus because we observed during preliminary testing that motion mixing does not occur in the foveal area, presumably because the strength of boundary signals there makes it difficult for them to undergo perceptual fading. When using interleaved stripes containing different motion signals that cover the whole visual field (without putting a black disk in the middle of the stimulus), perceptual motion mixing does not occur readily. However, when putting a black disk in the middle of the stimulus, motion mixing can be observed in the areas surrounding the black disk (but the black disk itself will remain

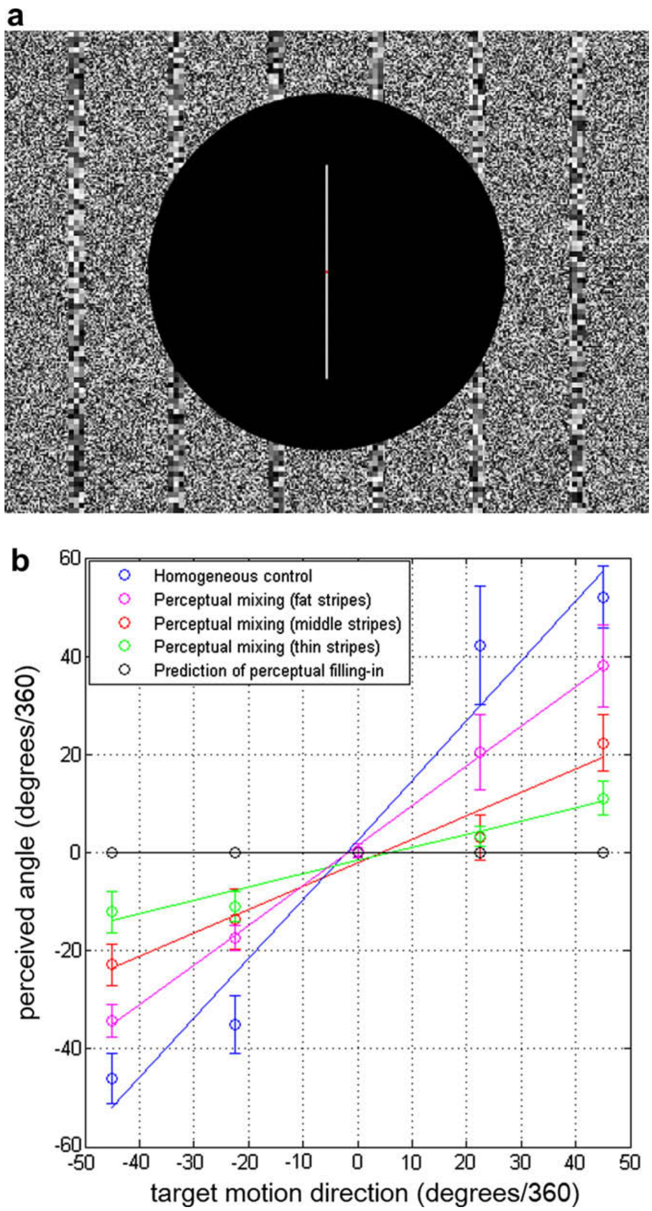

Fig. 5. (a) The stimulus configuration used in Experiment 3. The six stripes composed of random dots are moving in a different direction than that of the background. Note that the texture in the six stripes is made to be different than that of the background just for presentation purposes here, so that the stripes are visible. In the actual experiment, the foreground texture was identical to that of the background, differing only in motion direction. (b) The black curve shows the perceived directions that would be predicted if the perceptual feature replacement hypothesis of filling-in were correct. The perceptual filling-in hypothesis would predict the perceived motion direction to be always identical to the background's upward motion direction (0/360°), regardless of foreground motion directions. The blue curve shows subjects' perceived motion directions when the background and the foreground moved homogeneously in the same direction (four possible non-upward directions and one in the upward direction). The red curve shows subjects' perceived motion directions when the background and the foreground were perceptually mixed and perceived to be moving homogeneously but were in fact moving in different directions (the background always moved upward and the foreground moved in one of the four possible non-upward directions). The pink curve shows subjects' perceived motion directions when the foreground stripes were twice as wide as the case indicated in the red solid curve. The green curve shows subjects' perceived motion directions when the foreground stripes were half as thin as those corresponding to the red solid curve. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

black; no filling-in occurs in this black area). Subjects were required to report whether these different motions integrated so as to become a uniform percept of motion in a single direction upon perceptual fading of the boundary separating the two different motion direction zones.

This experimental paradigm is different than the motion integration paradigm. It is well known that local motion signals moving in different directions can be integrated into a coherent percept moving in a single direction (Adelson & Movshon, 1982; Pasternak, Albano, & Harvitt, 1990; Watamaniuk, Sekuler, & Williams, 1989; Williams & Sekuler, 1984). However, previously reported motion integration phenomena were primarily observed over dynamic random dots that consisted of many localized and spatially intermingled motion vectors (Williams & Sekuler, 1984), or spatially superimposed drifting gratings (Adelson & Movshon, 1982). Our stimulus differs in that (1) there are virtual contours dividing different motion signals so that different motion signals were not spatially intermingled or superimposed, and (2) the motion signals are not local but widely spread out across the visual field. By using our stimulus, we can, firstly, test whether motion integration can still occur or whether it is interrupted by these two factors. If motion integration can occur over widely spread motion signals in the presence of virtual contours, it might suggest that motion integration does not occur solely because of a local integration mechanism specific to the motion domain. Instead, motion integration may be a manifestation of a more general perceptual mixing phenomenon that can occur over different feature domains. Secondly, if motion integration occurs under these stimulus conditions, we can further test whether the motion signals are integrated in a filled-in or a mixed-in fashion. If the perceptually filled-in motion is solely determined by the background motion, the motion direction adjusted by subjects should be identical to that of the background motion, namely upward. Otherwise, if the perceptually filled-in motion is determined by the mixture of the background and foreground motions, the subjectively adjusted motion direction should be intermediate between the two motion directions.

4.1. Methods

4.1.1. Stimulus displays

The stimulus configurations are shown in Fig. 5a. The fixation point was a red (luminance: 37.2 cd/m^2; CIE: $x = 0.624$, $y = 0.337$) square that subtended 0.1 visual deg. The background motion was composed of random dots (288 × 216 small squares abutting each other across the 40° × 30° visual field) moving continuously upward at a speed of 0.33 visual deg/s. On average, there were 7.2 × 7.2 small squares with random brightnesses between white and black over 1 × 1 visual deg (the visual angle subtended by a single square element was 0.139 × 0.139 visual deg). Stripes composed of random dots moving in a direction different than that of the background, comprised the foreground regions. A black disk (diameter = 22 visual deg) was presented in the middle of the stimuli, and a bar (0.1 × 13.5 visual deg) was positioned in the center and its angle could be adjusted by manipulating two keys on the keyboard. All the stimuli were viewed with both eyes.

4.1.2. Procedure

Subjects were required to adjust the angle of the bar to match the direction of the perceptually filled-in motion by pressing two buttons. One button rotated the bar clockwise by 1/360° and the other rotated the bar counterclockwise by 1/360°. Subjects were required to rest after each trial until the afterimage had disappeared.

There were three variables in this experiment: (1) the motion direction in the foreground areas was randomly chosen from one of the five following values: 22.5° (0.375 visual deg/s upward and 0.1875 visual deg/s rightward), 45° (0.375 visual deg/s upward and rightward), 0° (0.375 visual deg/s upward only), −22.5° (0.375 visual deg/s upward and 0.1875 visual deg/s leftward), or −45° (0.375 visual deg/s vertically and leftward). Note that the direction corresponding to 0° was upward motion, and a positive (negative) value would indicate a non-upward direction corresponding to clockwise (counterclockwise) rotation. For example, the direction of 22.5° is 22.5° clockwise from the upward direction. (2) The background motion was either upward (0°) or identical to the foreground motion direction. (3) The width of the stripes was randomly chosen from one of the three following values: 2, 1, or 0.5 visual deg (the distance between each stripe was 6.5 visual deg). When the background and foreground motion were in the same direction, the result was a uniform field of motion. These conditions were randomly mixed and counterbalanced in 34 trials for each subject. The screen remained black during the period between each trial until subjects reported that the afterimage had disappeared. Other experimental parameters were identical to those of Experiment 1.

4.2. Results

Results show that, upon fixation, subjects reported that the borders appeared to fade and the two motion signals appeared to merge into a uniform motion field following subjective boundary disappearance. Fig. 5b shows that the perceptually filled-in motion is a mixture of the background and foreground motions. The black curve shows the motion directions that would be expected to be perceived if the feature replacement hypothesis of perceptual filling-in were correct. The feature replacement hypothesis of filling-in would predict that the perceived motion direction after perceptual fading of motion boundaries would always be identical to the background upward motion (i.e., 0°) regardless of foreground motion direction. It is obvious that the results are not consistent with the feature replacement hypothesis, but are consistent with a feature mixing hypothesis: first, the perceived motion direction after perceptual mixing varies as a function of the motion direction in the foreground stripes; second, the perceived motion direction after perceptual mixing varies as a function of the area of the foreground stripes. In particular, the pink curve shows subjects' predicted perceived motion directions when the foreground stripes are twice as wide (2 visual deg) as the case indicated by the red curve (1 visual deg). The green curve shows subjects' predicted perceived motion directions when the foreground stripes are half as wide (0.5 visual deg) as in the case indicated by the red solid curve. These results show that when the foreground stripes are wider, the perceived uniform motion field direction is closer to the motion direction in the foreground area; when the foreground stripes are thinner, the perceived motion direction is less close to the motion direction in the foreground area.

Together, our results show that motion integration can occur over widely spaced motion signals, even in the presence of virtual contours defined by the distinct motion signals themselves. Our results further show that perceived motion directions are in-between the background and the foreground motion directions. It is possible that such motion mixing may only occur over very specific stimulus conditions; nevertheless, these data suggest that the filled-in motion is not solely determined by the background motion for at

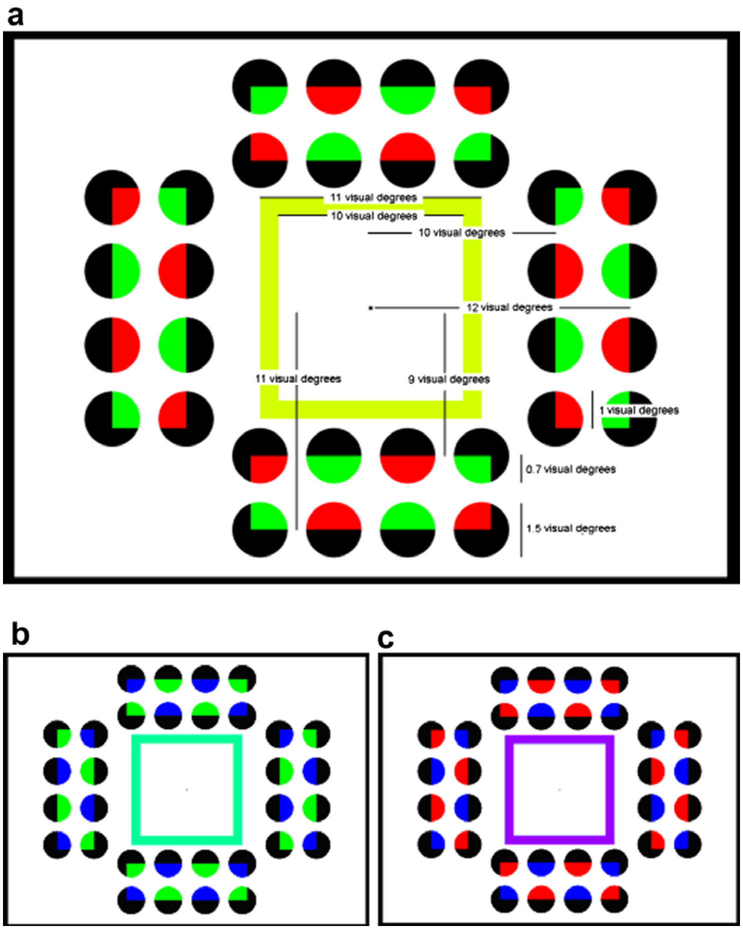

Fig. 6. (a) The stimulus configuration used in Experiment 4a. A neon-like greenish yellow color can be perceived in the four illusory rectangles. (b) The stimulus configuration used in Experiment 4b. A neon-like cyan color can be perceived in the four illusory rectangles. (c) The stimulus configuration used in Experiment 4c. A neon-like bluish purple color can be perceived in the four illusory rectangles. (Note that the luminance of the stimuli was not exactly the same as those shown in the figures. See Methods for real luminance.) (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

least some conditions, but is rather the mixture of the background and the foreground motions, which is consistent with our perceptual feature mixing hypothesis.

5. Experiment 4: perceptual mixing over neon-color spreading

In Experiment 4, we further test the perceptual mixing hypothesis in another color domain by using the neon-color-spreading paradigm. Neon color spreading (Bressan, Mingolla, Spillmann, & Watanabe, 1997; Kitaoka, Gyoba, Kawabata, & Sakurai, 2001; Redies & Spillmann, 1981; Redies, Spillmann, & Kunz, 1984; Van Tuijl, 1975; Van Tuijl & De Weert, 1979; Varin, 1971) is a visual illusion that occurs when the color or lightness of certain physical inducers spreads over an illusory shape, such as a Kanizsa triangle (Kanizsa, 1976). The mechanism of neon color spreading is still unclear. It has been hypothesized that neon color spreading may be a result of perceptual filling-in (Grossberg & Mingolla, 1985). Therefore, we take advantage of this property of neon color spreading and ask the question: how does perceptual filling-in upon neon color spreading occur if the physical inducers possess different colors and/or opponent colors such as red and green? Will the perceptually filled-in neon color during neon color spreading be the mixture of the two colors of the inducers? If the perceptually filled-in neon color is determined by the mixture of the two colors from the inducers, the subjectively adjusted color should lie at an intermediate point on the line connecting the two inducing colors in color space.

An example stimulus is shown in Fig. 6a. Subjects were required to fixate and adjust the color of the hollow square in the center to match the perceived color over neon-color spreading areas. Since any additive mixture or linear summation or averaging of two colors lies on the straight line connecting them in an additive color space (such as the CIE 1931 *xy* diagram), if the color mixing upon neon color spreading is additive, otherwise linear, or a weighted average, we would expect the CIE coordinates of the perceived, mixed color to lie on the line connecting the two CIE coordinates of the inducing colors.

5.1. Methods

5.1.1. Stimulus displays

The stimulus configurations used in Experiment 4a are shown in Fig. 6a. The fixation was a black (luminance = ~0 cd/m^2) square that subtended 0.05° of visual angle. There were 32 black disks, each containing a physical inducer. The color of the inducers was either red (luminance: 37.2 cd/m^2; CIE: $x = 0.624$, $y = 0.337$) or green (luminance: 99.4 cd/m^2; CIE: $x = 0.292$, $y = 0.607$). The stimulus configurations used in Experiment 4b (Fig. 6b) were identical to Experiment 6a except that the color of the inducers was either green or blue (luminance: 9.1 cd/m^2; CIE: $x = 0.144$, $y = 0.075$). In Experiment 4c (Fig. 6c), the color of the inducers was either red or blue. All the stimuli were viewed with both eyes. The color of the hollow square in the center could be adjusted by mixing any possible combinations of red and green and blue colors by manipulating set keys on the keyboard.

5.1.2. Procedure

In Experiment 4a, subjects were required to adjust the color of the frame to match the perceptually filled-in color induced by the four illusory rectangles by pressing six buttons. Two of the buttons respectively increased and decreased the saturation/luminance of the red color, two other buttons respectively increased and decreased the saturation/luminance of the green color, and the other two buttons respectively increased and decreased the saturation/luminance of the blue color. Subjects were required to rest after each trial until any possible afterimage had disappeared. The starting color/luminance of the frame that could be adjusted was randomly chosen from one of the three following values: (luminance: 105 cd/m^2, CIE: $x = 0.397$, $y = 0.524$; luminance: 112 cd/m^2, CIE: $x = 0.415$, $y = 0.509$; or luminance: 119 cd/m^2, CIE: $x = 0.427$, $y = 0.498$). All conditions were randomized across 10 trials. An identical procedure was used in Experiment 4b, except that the starting color/luminance of the frame that could be adjusted was randomly chosen from one of the three following values: (luminance: 88.4 cd/m^2, CIE: $x = 0.270$, $y = 0.522$; luminance: 90 cd/m^2, CIE: $x = 0.263$, $y = 0.496$; or luminance: 90.5 cd/m^2, CIE: $x = 0.253$, $y = 0.470$). In Experiment 4c, the starting color/luminance of the frame that could be adjusted was randomly chosen from one of the three following values: (luminance: 15.9 cd/m^2, CIE: $x = 0.231$, $y = 0.122$; luminance: 18.8 cd/m^2, CIE: $x = 0.257$, $y = 0.136$; or luminance: 23.1 cd/m^2, CIE: $x = 0.284$, $y = 0.151$). The screen remained black during the period between each trial until the subjects reported that the afterimage had disappeared. Other parameters were identical to Experiment 1. The CIE colors are summarized in Table 1.

5.2. Results

The results are shown in Fig. 7. The colored solid dots indicate the inducing colors. The mean CIE values (±S.E.) of the subjectively adjusted color for the four subjects are plotted as black hollow dots (Experiment 4a), blue hollow triangles (Experiment 4b), and purple hollow squares (Experiment 4c). The results show that the mean across subjects is indeed located on or very near to the line that would connect the two colors of the inducers for all three experiments. As can be seen from the figures, the perceptually filled-in colors lie on or very close to the line connecting the two inducing colors, suggesting that the perceptually filled-in color during neon color spreading is determined by mixing the two colors from the inducers.

6. General discussion

The mechanism whereby filling-in occurs is still not known. It has been argued that there is no such thing as filling-in, in the sense that perceptual filling-in of a region is just a result of passive

Table 1
CIE values of the original colors in the stimuli and the perceived colors.

	Original red	Original green	Original blue	Perceived color after mixing
Experiment 2	$x = 0.6115 \pm 0.0095$ $y = 0.3328 \pm 0.0108$	$x = 0.3078 \pm 0.0029$ $y = 0.5707 \pm 0.0032$	$x = 0.1845 \pm 0.0159$ $y = 0.0725 \pm 0.0053$	$x = 0.3763 \pm 0.0194$ $y = 0.2899 \pm 0.0107$
Experiment 4a	$x = 0.624$ $y = 0.337$	$x = 0.292$ $y = 0.607$	N/A	$x = 0.3986 \pm 0.0035$ $y = 0.5229 \pm 0.0028$
Experiment 4a	N/A	$x = 0.292$ $y = 0.607$	$x = 0.144$ $y = 0.075$	$x = 0.2560 \pm 0.0037$ $y = 0.4754 \pm 0.0136$
Experiment 4a	$x = 0.624$ $y = 0.337$	N/A	$x = 0.144$ $y = 0.075$	$x = 0.2948 \pm 0.0241$ $y = 0.1550 \pm 0.0132$

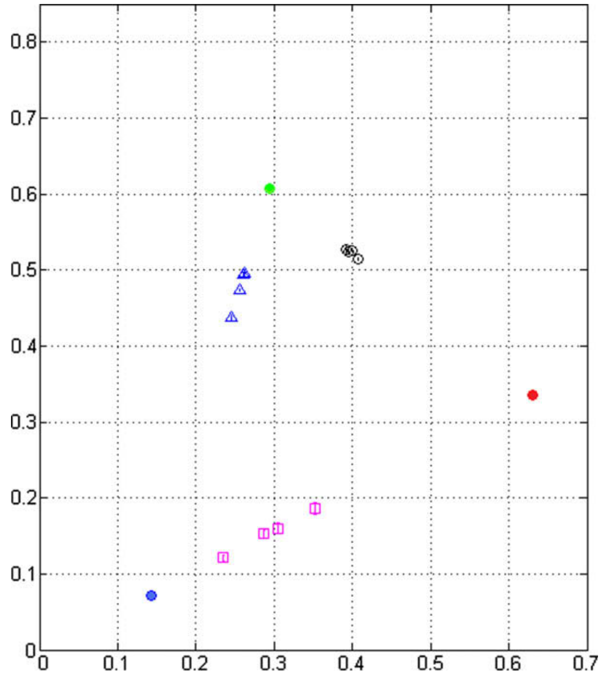

Fig. 7. Results of Experiment 4. The mean CIE values of the subjectively adjusted color for the four subjects in Experiment 4a, 4b, and 4c are plotted as black hollow dots, blue hollow triangles (two of which are overlapping), and purple hollow squares, respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

tagging by using information from the region surrounding the region that appears to vanish (For a review on competing views on filling-in, see Pessoa et al., 1998), or involves a lack of isomorphic representation in the brain for the vanished region (Dennett, 1991). Alternatively, perceptual filling-in may involve an active process of 'filling-in' of the voided area with the information existing in the surround region or in the background (Arrington, 1994; Cohen & Grossberg, 1984; De Weerd et al., 1995; Friedman, Zhou, & von der Heydt, 2003; Gerrits & Vendrik, 1970; Gerrits et al., 1966; Kinoshita & Komatsu, 2001; Neumann, Pessoa, & Hansen, 2001; Pessoa et al., 1998; Rossi, Rittenhouse, & Paradiso, 1996; Spillmann & DeWeerd, 2003).

Aside from these theoretical debates, brain-imaging data offer differing findings. Several recent fMRI studies have shown effects of filling-in in V1, including neon-color spreading (Sasaki & Watanabe, 2004), the phantom illusion (an illusory filled-in percept observed between the gap region of two moving gratings; Meng, Remus, & Tong, 2005), blind spot filling-in (Tong & Engel, 2001), and Troxler fading (Mendola, Conner, Sharma, Bahekar, & Lemieux 2006). However, when using the Craik-O'Brien-Cornsweet illusion (an illusion that the region adjacent to the lighter side of an edge looks slightly lighter than the region adjacent to the darker side of that edge, but where in fact the brightness of both regions is exactly the same; Cornsweet, 1970; Grossberg & Todorović, 1988), no correlated response was observed in early visual areas (Perna, Tosetti, Montanaro, & Morrone, 2005). Similarly, in a study using brightness/color induction (the modulation of the perceived intensity of a region by the luminance/color of surrounding regions), observed fMRI activity was considered unrelated to surface filling-in, but is a linear combination of short-range and long-range responses elicited by luminance/color edges (Cornelissen, Wade, Vladusich, Dougherty, & Wandell, 2006).

In neurophysiological data, several studies have reported effects of blind spot filling-in in V1 (Fiorani, Rosa, Gattas, & Rocha-Miranda, 1992; Komatsu, Kinoshita, & Murakami, 2000; Matsumoto & Komatsu, 2005). However, when using the Craik-O'Brien-Cornsweet illusion, neuronal activity modulated by the illusory brightness was only discovered in thin stripes of V2. Similarly, neuronal activity correlated with texture filling-in was found in V2 and V3, but not in V1 (De Weerd et al., 1995), and illusory contours evoke responses mostly in V2 cells (Peterhans & von der Heydt, 1989; von der Heydt & Peterhans, 1989; von der Heydt, Peterhans, & Baumgartner, 1984). When examining neuronal activity associated with color filling-in in the Troxler effect, von der Heydt, Friedman, and Zhou (2003) did not observe any change of neuronal activity in V1 and V2 surface cells, suggesting that surface cells respond to the retinal disc color regardless of whether filling-in occurred or not. Komatsu (2006) has pointed out that these differences might reflect (1) differences in the underlying neural mechanisms, or (2) differences in the stimuli used, or (3) differences in the recording layer (neuronal activity related to blind spot filling-in was recorded in the deep layers of V1, but those related to the Craik-O'Brien-Cornsweet illusion and Troxler fading were mostly recorded in the superficial layers of V1). Further studies are therefore required to resolve these contradictory results.

Regardless of these differing findings, our results demonstrate that a 'feature replacement' or 'feature substitution' view is not entirely accurate for the types of conditions tested. With our stimuli, we have shown that the filled-in feature can be a mixture of the foreground and background features for color, luminance, neon color, and motion. Although Fujita (1993) did not publish actual data, he describes subjective observations that colors appear to spread in both directions across a perceptually faded boundary and merge into a novel perceived color not present in the stimulus.

We believe that our results are consistent with the model of Grossberg and Mingolla (1985), which posits the existence of two complementary systems involved in filling-in: a boundary contour system (BCS) defines boundaries at multiple spatial scales separating regions, and a feature contour system (FCS) which 'fills in' features within the boundaries. Diagrams of these mechanisms are available in Grossberg and Todorović (1988), showing how the feature contour system averages signals from the concentric on-cells within boundaries generated by boundary contour signals. Fujita (1993) also describes a model involving antagonistic feature diffusion and blocking processes, analogous to the FCS and BCS of Grossberg and Mingolla (1985), which permits diffusion of feature information in both directions across a faded boundary.

Why has perceptual 'feature mixing' not been measured before? This may be due to the fact that, in previous studies, the foreground area was almost always much smaller than the background area (Anstis, 1989; De Weerd, Desimone, & Ungerleider, 1998; Hardage & Tyler, 1995; Ramachandran & Gregory, 1991; Ramachandran, Gregory, & Aiken, 1993; Spillmann & Kurtenbach, 1992; Welchman & Harris, 2001). When a foreground area is much smaller than its background area, the resulting percept after perceptual mixing is much closer to the appearance of the background, as our results here and in Hsieh and Tse (2006) show. Note that in the current study, blurred borders make these stimuli less border-like, and one could argue that this makes the adaptation and fading that goes on less likely to be representative of the kind of boundary and surface processing that goes on normally, where borders are not blurred, at least in foveal vision. Together with our choice of stimuli that use repetitive patterns, or which exploit peripheral vision (in the case of our motion stimuli), the processes we described may not be representative for surface perception in figures shown in foveal and near-peripheral vision, on which most filling-in studies concentrate. That said, the model of Grossberg and Mingolla (1985), posits boundaries and feature spreading at multiple spatial scales. For example, there are borders defined at both high and low spatial frequencies, and feature spreading itself is posited to occur at both high and low spatial frequencies. Thus, even though our borders were blurred in the color stimuli that we used (but not in the motion or neon-color stimuli used), in order to facilitate perceptual fading of boundaries, feature spreading would presumably be inhibited even by blurry boundaries. Although we at present operate under the assumption that feature mixing happens any time boundaries between features vanish, future research will have to determine how general the phenomenon of feature mixing is.

Our finding is different than a related phenomenon called 'filling-out' (De Weerd et al., 1998; Hamburger, Prior, Sarris, & Spillmann, 2006; Shimojo, Wu, & Kanai, 2003), according to which the texture/color within a boundary can spread out of a figure into the surround as if the traditional filling-in process were reversed. It has been suggested that filling-in/filling-out is a process that can go either outward or inward, depending on the relative sizes of a textured surround and figure (De Weerd et al., 1998). Our proposal is different in that we hypothesize that, during perceptual fading, the percept is a mixture of the featural information that existed on either side of the now faded boundary, rather than the replacement of one by the other. In other words, the filling-in/filling-out process is not exclusively into the figure from the surround (i.e. inward filling-in, as in Paradiso & Nakayama, 1991) or into the surround from the figure (i.e. filling-out), but occurs simultaneously as a mixing or weighted averaging of the two feature sets.

It is also worth noting that the phenomenon of perceptual mixing that we observed here might be different than the perceptual filling-in that occurs within the retinal blind spot (Murakami, 1995; Ramachandran, 1992; Sergent, 1988; Tripathy, Levi, Ogmen, & Harden, 1995) or retinal lesions (Murakami, Komatsu, & Kinoshita, 1997). In the case of the retinal blind spot and retinal lesions, there is no information sent to cortex from within the perceptually 'voided' area. Therefore no perceptual feature mixing but only perceptual feature replacement can occur in these special cases. It is therefore also not valid to use filling-in of the blind spot as evidence for a feature replacement rather than feature mixing account of filling-in.

6.1. Implications for neural encoding of visual features

At first glance, our results appear to show that perceptual feature mixing occurs in an additive manner (like the additive color mixing that occurs with light), and that it occurs in at least the four different feature domains tested (color, neon color, luminance and motion). Note, however, that additive mixing in the case of light leads not only to an intermediate hue, but also to a summation of luminances. For example, if appropriate combinations of red, green, and blue light are superimposed, the resultant color can be made to appear white, and this white will have a luminance that is higher than the red, green, or blue component lights. Here, we find evidence that is consistent with additive perceptual mixing along the dimension of hue, but not along the dimension of luminance. But hue, luminance, and motion data are all consistent with the averaging of these features following perceptual fading of boundaries. It appears that the resultant hue is closer to an (apparently weighted by luminance, area and perhaps other factors) average in hue space than an additive summation, as occurs with light. Averaging better accounts for the lack of summation along the dimension of luminance as well, although perceived brightness following perceptual fading was less consistently close to (usually lower than) the average luminance than perceived color, a fact which might arise because of the effects of adaptation (Craik, 1940; Wright, 1934, 1937; Yustova, 1958).

The results of experiment 1a suggest that luminance and wavelength (color) are not coded independently by the visual system, since perceived hue upon feature mixing is biased toward the hue of the component with greater luminance. If wavelength (color) and luminance were coded separately, by, for example, separate and independent populations of neurons, we might expect them to be averaged separately, in which case the average wavelength (color) would not be influenced by the luminance of component colors. The fact that it does so influence feature mixing suggests that the neural realization of feature representations occurs at some level in neurons or neural populations that are tuned to both color and luminance simultaneously. The fact that feature mixing was observed even when the separate features are presented to different eyes indicates that feature mixing takes place beyond input layer 4Cα in area V1. It has been shown that there is separate encoding of surface brightness and surface color in V2 thin stripes (Roe & Ts'o, 1995; Ts'o et al., 2001; Wang, Xiao, & Felleman, 2007). Thus, feature mixing might take place beyond area V2 as well.

Future work will have to determine whether a given mixed color can result from either a change in luminance, hue, or saturation of to-be-combined inputs. In other words, if this is the case, it should be possible to create 'feature mixing metamers,' where different component colors/luminances result in the same perceived mixed color. That perceived color is biased toward the more luminant to-be-mixed input color, suggests that the perceived mixed color is biased toward the 'stronger' color, where increasing luminance increases the weighting on that color. Another factor that increases the weighting of a given input color is its area (Hsieh & Tse, 2006).

Note that wavelength (color) is effectively encoded at the earliest stages in what is effectively a vector code, in terms of the relative magnitudes of input from the long, medium, and short wavelength cone responses (with the exception that cones cannot take negative values, limiting the vector space to the positive-positive-positive subspace of a normal three dimensional vector space). A vector in this 3-dimensional (rgb) space would encode a wavelength (color) in its direction given by the ratio of responses among the three cones, and its measured luminance in the magnitude of response from among sampled cones. Such a vector representation could undergo transformations into more complex types of representations, which nonetheless remain effectively vector representations. Assuming that feature mixing occurs at a level of representation that can be modeled as a vector space, feature mixing can be modeled, not as the summation of vectors, but as the averaging of vectors, such that a 'mixed' vector will be intermediate in direction and magnitude between the directions and magnitudes of the two (or more) vectors (i.e. features) present on either side of a boundary before perceptual fading.

Our data seem to rule out a vector summation code as the neural encoding of consciously experienced visual features such as motion or color, because the sum of nearby vectors is generally a longer or shorter vector, where vector magnitude corresponds to perceived brightness. Since we do not find luminance summation upon hue mixing, it seems unlikely that vector summation is the correct model of feature mixing, at least for color, motion, and luminance. Alternatively, it is possible that experienced motion and color features are still a result of vector summation, and the reason why the magnitude does not match is due to adaptation. This is consistent with the finding that, while we observe intermediate hues, the perceived brightness does not sum upon perceptual feature mixing. If anything, perceived brightness appears to decrease upon perceptual fading. Overall, however, a magnitude averaging account appears sufficient to account for most aspects of our data. Whether this involves vector averaging, rate averaging, population peak averaging, or something else, is unclear. But whatever the neuronal encoding of simple visual features is, it would appear to be an encoding that permits the operation of averaging.

A similar averaging effect has been reported: when sections of a lattice are replaced by segments of a different color, additive color mixing can be seen between the color of the segments and the color complimentary to the lattice (Da Pos & Bressan, 2003; Goda & Ejima, 1997). Together with our results, this phenomenon suggests that the visual system averages or otherwise combines color information across perceptually faded boundaries in an approximately linear manner to generate a new experienced color percept that does not exist in the stimulus. This averaging is weighted by the 'strength' of the feature signal. Strength is influenced by factors such as area, for the cases of motion and color, and luminance, for the case of color. Although we did not manipulate velocity, we would predict that the perceived direction of motion after perceptual fading would be biased toward the faster of two to-be-mixed motion inputs.

Our feature mixing theory is consistent with the findings that there are 'Luxotonic' neurons (surface neurons) in the visual system that respond to diffuse sustained light. Surface neurons responding to diffuse sustained luminance have been observed in macaques (Kayama, Riso, Bartlett, & Doty, 1979), squirrel monkeys (Bartlett & Doty, 1974) and cats (DeYoe & Bartlett, 1980). Similarly, surface neurons responding to diffuse sustained color have been observed in macaques (von der Heydt, Zhou, & Friedman, 1996; von der Heydt et al., 2003; Zhou, Friedman, & von der Heydt, 2000). These surface neurons fit well with the feature mixing theory in the sense that they may provide feature information that is located away from the contours/boundaries, and can be later used in the feature mixing process. This raises the interesting possibility that the mixed information that we subjectively experience is indeed a weighted averaging or linear merging of different components from multiple sources, suggesting that filling-in itself may be a process of linear pooling of contributions from across a wide region, in the absence of boundary signals that could inhibit such mixing. Indeed, one possibility consistent with our data, but by no means established by our data, is that the neural correlate of the conscious experience of color is realized in some averagable magnitude code of such surface neurons, or more likely, populations of such neurons, and that color feature mixing upon perceptual fading is realized in the averaging of the activity of such neurons. The neural basis of motion mixing would presumably happen in other neurons that encode motion rather than color. Much future work is needed to determine whether this idea is correct or incorrect.

Let us end with a caveat. Although our results show that perceptual mixing can occur over different feature domains, including color, neon color, luminance and motion, we have to be careful not to overgeneralize the present findings prematurely. There may be differences between the stimuli that we have used and those used in previous studies. For example, in a more traditional filling-in setting, there is usually a clear, isolated figure surrounded by a background (Anstis, 1989; De Weerd et al., 1998; Hardage & Tyler, 1995; Ramachandran & Gregory, 1991; Ramachandran et al., 1993; Spillmann & Kurtenbach, 1992; Welchman & Harris, 2001). It is possible that when a foreground area is much smaller than its background area, that the mixing of feature signals may not be an approximately linear averaging process as shown in our studies. Future work will have to determine whether this is indeed the case. Moreover, when filling-in involves several features, there may be a competition among feature types or within features, resulting in a non-linear form of feature mixing or even feature replacement. By contrast, in the stimuli used in the present study, there is no apparent figure/object and foreground/background. Under such conditions, the visual system may consider the repeated patterns to belong to the same surface. Mixing might then result from competition of neurons encoding one or the other feature within the surface. Another possibility is that attention plays a role in feature integration that our stimuli have not been able to probe because of their lack of a figure (attended) versus ground (unattended) relationship. Lastly, the processes leading to feature mixing may be different in different cases, because, for example, motion mixing and color mixing require adaptation, whereas the neon-color illusion does not. Thus, although perceptual feature mixing can occur over different stimuli types, the properties and principles of feature mixing may vary depending upon particular stimulus conditions and differences among the various feature domains.

7. Conclusion

Our results demonstrate that, at least under the conditions tested, perceptual filling-in upon perceptual fading of boundary signals may involve "perceptual feature mixing" that involves averaging in a feature space such as hue, luminance, or motion space in a manner proportional to the areas and magnitudes of the features present in the image. Furthermore, because feature information such as motion direction or color (Hsieh & Tse, 2006) perceived at a location after perceptual filling-in can be different from any motion direction or color actually present in the stimulus, it follows that the percept after perceptual mixing is neither entirely stimulus driven nor entirely local. In sum, we propose on the basis of the evidence presented here, that models of filling-in should be updated to account for feature mixing in the conditions used in the experiments reported on in the present paper.

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