Discrete color filling beyond luminance gaps along perceptual surfaces

Ryota Kanai

Psychonomics Division, Helmholtz Research Institute, Universiteit Utrecht, Utrecht, The Netherlands, & Division of Biology, California Institute of Technology, Pasadena, CA, USA

Daw-An Wu

Division of Biology, California Institute of Technology, Pasadena, CA, USA

Frans A. J. Verstraten

Psychonomics Division, Helmholtz Research Institute, Universiteit Utrecht, Utrecht, The Netherlands

Shinsuke Shimojo

Divisions of Biology & Computation and Neural Systems, California Institute of Technology, Pasadena, CA, USA & Human and Information Science Laboratory, NTT Communication Science Laboratories, Atsugi, Kanagawa, Japan

Perceived color at a point in space is not determined simply by the color directly stimulating the corresponding retinal position. Surface color is informed by flanking edge signals, which also serve to inhibit the intrusion of signals from neighboring surfaces. Spatially continuous local interactions among color and luminance signals have been implicated in a propagation process often referred to as filling-in. Here, we report a phenomenon of discrete color filling whereby color jumps over luminance gaps filling into disconnected regions of the stimulus. This color filling is found to be blocked at boundaries defined by texture. The color filling is also highly specific to the elements belonging to a common perceptual surface, even when multiple surfaces are transparently overlaid. Our results indicate that color filling can be governed by a host of visual cues outside the realm of first-order color and brightness, via their impact on perceptual surface segmentation and segregation.

Keywords: filling-in, color, surface, perceptual fading, luminance gap

Introduction

The representation of uniform color surfaces in the activity of early visual cortex is decidedly different from the intuitive assumption of isomorphic coding (such as what one might find in the array of detectors in a digital camera). When a patch of uniform color is presented, most activity is found among neurons whose receptive fields lie on the edges of the patch, rather than directly on the patch's surface (Friedman, Zhou, & von der Heydt, 2003; Hubel & Wiesel, 1968; but see Kayama, Riso, Bartlett, & Doty, 1979; Peng & Van Essen, 2005). In a corresponding set of results from psychophysical studies, the perceived color and/or brightness of a uniform surface has been found to depend on signals from the edges of the surface, rather than from its interior (Cornsweet, 1970; Kanai & Verstraten, 2006; Montag, 1997; Pinna, Brelstaff, & Spillmann, 2001; Redies & Spillmann, 1981). The mechanisms whereby the edge signals help determine the perception of the surface itself have been elucidated by the study of a broad class of visual

phenomena, which can be described as "filling-in" effects (Gerrits & Vendrik, 1970).

Color filling-in, for example, is a visual phenomenon where the perceived color of a visual region is imparted, or filled in, by the surrounding color (Pessoa, Thompson, & Noe, 1998). This process is responsible for the invisibility of the blind spot (Ramachandran, 1992) and other regions that lack bottom–up signals due to pathological scotomas (Bender & Teuber, 1946; Sergent, 1988; Zur & Ullman, 2003). Filling-in is also observed in an extensively characterized process known as Troxler fading. When a visual stimulus is fixed at a retinal position by a prolonged fixation or is stabilized optically, the visual stimulus disappears from view, its location "filled in" by the surrounding color (Cornsweet, 1970; De Weerd, Desimone, & Ungerleider, 1998; Gerrits, Dehaan, & Vendrik, 1966; Kanai & Kamitani, 2003; Pirenne, 1962; Ramachandran & Gregory, 1991; Riggs, Ratliff, Cornsweet, & Cornsweet, 1953; Troxler, 1804; Yarbus, 1967).

Two characteristics found throughout the known filling-in effects are that they are retinotopically continuous and are

disrupted by luminance gaps (Boynton, Hayhoe, & Macleod, 1977; Cole, Stromeyer, & Kronauer, 1990; Cornsweet, 1970; Eskew & Boynton, 1987; Kingdom & Moulden, 1988; Montag, 1997; Paradiso & Nakayama, 1991; Redies, Spillmann, & Kunz, 1984; Todorovic, 1987). The interposition of a luminance gap between two colored regions blocks filling-in from one side to the other. Only after prolonged adaptation, whereby the luminance gap itself fades from awareness, can filling-in proceed.

A number of extensions (Arrington, 1996; Cohen & Grossberg, 1984; Grossberg & Mingolla, 1985; Grossberg & Todorovic, 1988) and challenges to this simple model of local luminance edge-based processing exist. It has been shown that the magnitude of edge effects can be modulated by empirical considerations, such as the ecological likelihood of real surfaces and illumination conditions that would give rise to the visual input (Dakin & Bex, 2003; Purves, Shimpi, & Lotto, 1999). Furthermore, it has been proposed that the brain constructs explicit neural representations of globally defined perceptual surfaces (Nakayama & Shimojo, 1992) and that qualities such as perceived lightness are the result of explicit attributions to those surface representations (Anderson & Winawer, 2005).

These characteristics have been foundational to the classical understanding of the visual processing of surfaces and led to early mathematical and neuromorphic models of visual processing (reviewed in Grossberg & Mingolla, 1985; Pessoa et al., 1998). Under these interpretations, color and luminance information diffuses along the retinotopic map, starting and stopping at borders defined by local features such as color and luminance transitions. Through this process, information encoded at surface edges comes to fill enclosed shapes. This notion that sharp luminance transitions define surface borders and limit the spread of color information has been used to explain the illusory spread of colors across areas lacking strong edge signals (such as gradual color gradients), why dark luminance gaps enhance the contrast of colors on either side, and why they block color filling.

In this article, we investigate a color-filling effect that can skip across wide luminance gaps, filling discretely into separated regions. The artwork of Julian Stanczak (Stanczak & McCleland, 1998) is designed to induce a number of complex and interacting visual effects, and we noted that one effect involved perceptual color filling that jumped over clearly defined gaps. Unlike previously investigated demonstrations of color filling, which require adaptation to luminance gaps and perceptual fading of the gaps, this form of color filling occurred without the adaptation of the gaps and occurred over discontinuous regions of space, leaving the luminance profile perceptually intact.

To investigate this phenomenon, we constructed simplified stimuli that retained the discrete color-filling effect. The stimulus illustrated in Figure 1a is composed of a simple color gradient typical of those used in classical filling-in studies (Krauskopf, 1963, 1967) and a single set of strong, clearly presented luminance gaps. When the center of the stimulus (actual radius = 14.3° visual angle) is gazed at steadily, the foveal color red appears to fill the peripheral squares, overwriting their original color green (i.e., filling-out). Notably, the black grid pattern remains perceptually prominent. Examination of a number of stimulus configurations revealed that this effect survives a wide range of gap and patch sizes and does not require colinearity of edges (see online demonstration at http://neuro.caltech.edu/~ryota/fillingin/).

In a series of experiments manipulating the discrete color-filling effect, we examine the involvement of perceptual surface processing. We find evidence that the lateral extent of color filling is influenced by perceptual surface segmentation boundaries, rather than luminance edges per se. We also find that filling-in occurs in a highly selective fashion, traveling among regions that are segregated onto a common perceptual surface. Multiple color-filling processes can proceed on retinotopically overlaid surfaces while retaining specificity for each surface. These results indicate the importance of perceptual boundaries and surface parsing in the representation of surface color.

Experiment 1: Color jumps over gaps, filling into discrete elements

In our first experiment, we created two sets of basic stimuli using elements described in the Introduction. The first set of stimuli consisted of simple color gradients, taken from configurations known to induce classical Troxler fading (Figure 1b). The color gradient was defined as a function of the visual eccentricity from a fixation marker and had a cumulative Gaussian profile as shown in Figure 1c. These stimuli had differing values for the location parameter μ, which corresponds to the size of the central disk. The second set of stimuli was identical to the first, except for the superimposition of a dark grid pattern over each stimulus (Figure 1a).

Methods

Participants and apparatus

Four participants, including two of the authors (R.K. and D.W.), took part in this experiment. All had normal or corrected-to-normal visual acuity and normal color perception.

Stimuli were presented on a 22-in. monitor, a LaCie Electron21 with a screen image projecting 37.5×28.5 cm. Stimuli were generated in Matlab using The Psychophysics Toolbox (Brainard, 1997), running under Macintosh OS 9.
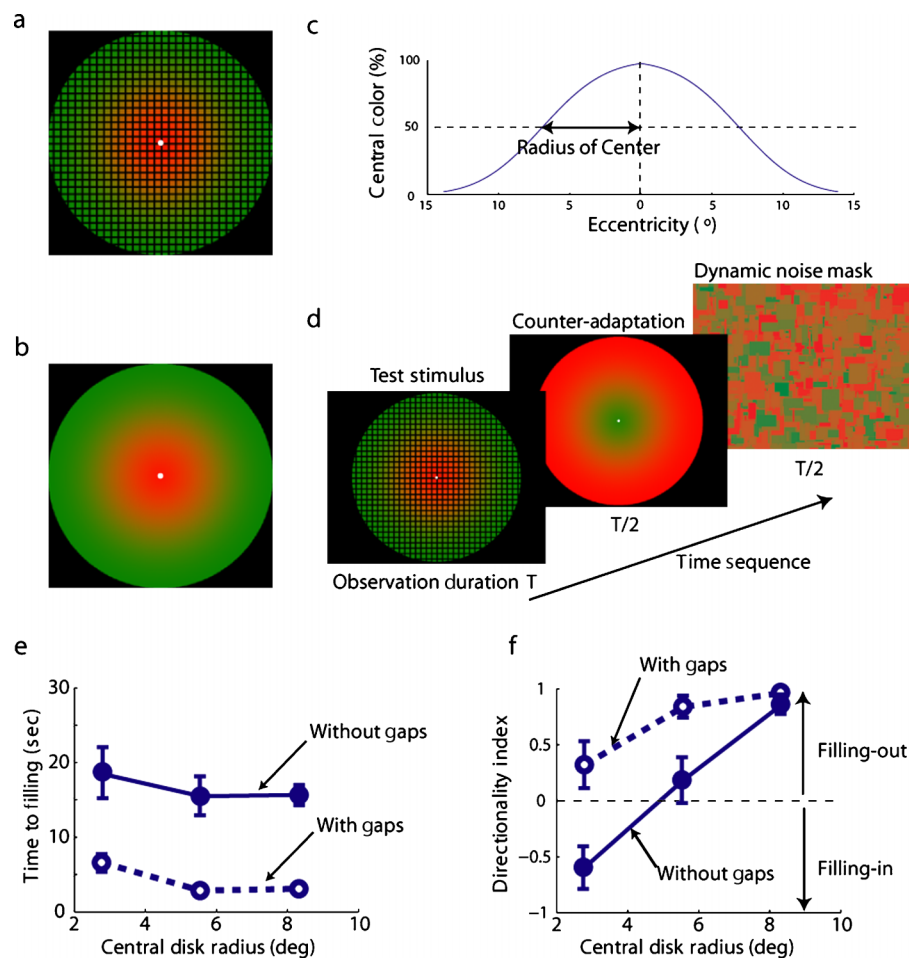
Figure 1. Stimuli and results of Experiment 1. (a) Typical color gradient stimulus with a grid pattern. (b) The corresponding control stimulus, the same gradient without the grid. This configuration is known from classical studies to cause Troxler fading. (c) Color profile of the stimuli. The percentage of a central color is defined by a cumulative Gaussian as a function of visual eccentricity. When the central color is red, 0% means 100% green. (d) Trial sequence. A trial consisted of the observation of test stimulus until response or 30-s timeout. Participants responded when the entire area of the stimulus became perceptually homogeneous. Intertrial effects were minimized by presenting a color gradient of opposite polarity and, then, a dynamic noise pattern, each for half the duration of the trial stimulus. (e) The effect of luminance gaps on the speed of color filling. Mean results of the time required for the completion of color filling are plotted as a function of central disk radius (μ). Open circles with a dotted line indicate the conditions with gaps, and solid circles with a solid line indicate the conditions without gaps. All error bars represent standard error of the mean ($n = 4 \times 40$ trials per data point). The effect of central disk radius was not significant, $F(2,18) = 0.701$, $p = .509$. The presence of luminance gaps markedly reduces the time to filling, $F(1,18) = 24.11$, $p < .001$. (f) The effects of luminance gaps on the direction of color filling. Mean results of the directionality index are plotted as a function of central disk radius (μ). A positive index indicates a tendency of the color to fill outward, whereas a negative index indicates a tendency to fill inward. An index of 1 would indicate that all observed color-filling events were in the outward direction. Color filled outward more often as disk size increased, $F(2,18) = 21.94$, $p < .001$. The presence of gaps markedly shifts the percept from filling inward to filling outward, $F(1,18) = 17.65$, $p < .001$. Discrete color filling is shown to occur systematically across a range of parameter settings. Luminance gaps, which block color filling in classical studies, do not block color filling in these stimuli.

The participants sat in front of the computer screen at a viewing distance of 57 cm; their heads were supported by a chin rest. Stimuli were binocularly viewed. Chromaticity of colors was measured at viewing distance with a Minolta Chroma Meter CS-100A, which outputs CIE 1931 *x,y* units.

Stimuli and procedure

Prior to the experiment, the green value perceptually equiluminant to the maximum intensity of the monitor's red gun was obtained for each individual participant using heterochromatic flicker photometry. The flicker frequency was 9.38 Hz.

We used radial color gradients where color gradually changes between red (CIE x,y = 0.629, 0.342) and green (0.287, 0.610), displayed at the equiluminant level for each participant (see Figure 1). Intermediate colors in the gradient were created via linear interpolation after gamma correction. The gradient was defined as a function of the visual eccentricity from a fixation marker and had a cumulative Gaussian profile (Figure 1c),

$$f(x) = \frac{1}{\sqrt{2\pi}\sigma} \int_{-\infty}^{x} \exp\left(\frac{-(t-\mu)^2}{2\sigma^2}\right) dt,$$

where x is the eccentricity, σ is the scale parameter that determines the steepness of the gradient, and μ is the location parameter for the eccentricity at which the intermediate color (yellow) occurred.

Three radii were used for the central color disk (μ = 2.8°, 5.6°, and 8.3°) with $\sigma = \mu/2$. On half the trials, we used red-center stimuli, and on the other half, green-center stimuli were used. The stimuli were displayed within a circular aperture with a radius of 14.3°. On half of the trials, a black grid (6.7 arcmin in width) was overlaid on the color gradient. Thus, the color gradient was displayed only on regularly arranged squares (26.7 × 26.7 arcmin; see Figure 1a). In the control condition, the same stimuli were presented without the black grid (Figure 1b).

On each trial, one stimulus was presented with a small fixation point at the center. When participants perceived the color-filling process to be complete, that is, when the stimulus area became perceptually homogeneous in color, they pressed one of three keys. This response indicated whether (1) the central color had filled into the peripheral squares, (2) the peripheral color had filled into the central squares, or (3) the direction of filling was ambiguous. We will call trials with Response Types 1 and 2 as "filling-out trials" and "filling-in trials," respectively. After the response, participants viewed two types of counteradaptation stimuli to minimize cross-trial effects (Figure 1d). Each trial was subject to a 30-s time limit. Trials in which participants did not perceive a homogeneous color within 30 s were aborted.

Following each stimulus presentation, intertrial effects were minimized by presenting the opposite color gradient, followed by a dynamic pattern mask consisting of all of the colors present in the stimulus. Both were presented for 15 s. Twenty trials were performed on each condition. There were thus a total of 240 trials (3 [radii] × 2 [color polarity; red center vs. green center] × 2 [with and without the grid] × 20 trials). The experiment was divided into four blocks, and each took about 30–40 min.

Analysis: The directionality index, I, was calculated as I = {(number of filling-out trials) − (number of filling-in trials)}/{(number of filling-out trials) + (number of filling-in trials)}. The value of I ranges between −1 and 1. A positive value of I indicates a tendency for the central color to fill out to the periphery, and a negative value indicates a tendency for the peripheral color to fill into the center.

Results

Two measures were made to characterize the phenomenon. First, the time at which a key press occurred (time to fill [TTF]) was used as a measure of how readily color filling occurs in a given stimulus condition. Second, the direction of the color filling was analyzed. These measures were used to characterize the effects of the size of the central color disk and the effects of superimposing the grid pattern. The comparisons would be useful to validate discrete color filling as behaving systematically across a range of conditions that are known to affect other forms of filling-in.

The TTF results are shown in Figures 1e and 1f. In the classical conditions without the grid pattern, the color filling took 15 s or longer on average. Changing the size of the disk did not significantly change the TTF (Figure 1e, dashed curve), $F(2,18) = 0.701$, $p = .509$. However, superimposing the grid significantly sped up TTFs overall (Figure 1e, solid curve vs. dashed curve), $F(1,18) = 24.11$, $p < .001$, by 3–7 s on average.

The direction of color filling had an expected relationship to the size of the central disk. With larger disk sizes, there was an increased tendency for the foveal color to fill outward (Figure 1f), $F(2,18) = 21.94$, $p < .001$. The presence of the grid overlay also drastically affected the direction of color filling. When the grid was present, the direction of color filling was biased outward (Figure 1f, solid curve vs. dashed curve), $F(1,18) = 17.65$, $p < .001$. This was particularly clear in the conditions at the smallest radius of the central color, where the presence of grid caused a complete reversal of filling direction.

The finding that color filled outward was initially surprising, as classical studies generally reported only the filling-in of objects by the background color. This experiment, however, shows that even classical configurations (such as the plain color gradient shown in Figure 1b) can cause an object's color to fill out to the background, when a color spot of sufficient size is centrally fixated. The tendency for the grid texture to change the direction of color filling might be explained by the receptive field sizes present in the fovea and in the periphery. Whereas the spatial resolution of the fovea is sufficient to separately encode the color and gap regions, this is not true for the periphery. There, receptive fields are large; thus, each field sums across larger regions of space containing both color and gap regions. The grid texture, then, reduces the strength of the color signal much more in the periphery than in the fovea. This may increase

the tendency for color of the central disk to override the color of the periphery.

More surprising was the fact that color filling across the grid of luminance gaps should occur at all. In classical color-filling experiments, it was found that the time required for filling-in increased with the strength of the edge signal surrounding the color spot. Increasing adaptation durations were required as the color gradient around the spot was made steeper, up to the point of a sharp color edge (Friedman, Zhou, & von der Heydt, 1999). Consistent with a previous study (Hamburger, Prior, Sarris, & Spillmann, 2006), an isolated luminance gap aligned with the color transition (e.g., a single dark ring around the color disk of Figure 1b) prevented filling-in from occurring. Color filling would occur only after the edge or gap itself faded from awareness due to adaptation (Paradiso & Nakayama, 1991; Spillmann & De Weerd, 2003). This was interpreted to mean that color and luminance edge signals block color filling.

An alternative interpretation, suggested by the stimulus configuration producing the discrete color-filling effect, would be that the impact of luminance gaps on color filling is dependent on how they and their flanking color regions are parsed onto perceptual surfaces. The discrete squares are perceptually grouped and processed as parts of a single continuous surface, and the luminance edges enclosing each element do not serve as a surface segmentation cue. On the other hand, an isolated black ring, coincidentally added along the color transition between the color spot and the surrounding color can be interpreted as a segregation cue and would lead to a segmentation of the inside from the outside. In other words, color filling is blocked by an isolated ring because the ring's luminance edges segment the color surface but proceed through the grid because the grid's luminance edges do not serve as a segmentation cue. This interpretation would thus explain both the classical Troxler-type filling-in and the discrete color-spreading effect that we investigate here.

Experiment 2: Texture-defined edges inhibit color filling

The first experiment showed that the color-filling process fails to be inhibited by luminance edges that do not provide segmentation cues for adjoining regions. This next experiment provides further support for the distinct role of perceptually formed boundaries and surfaces by showing the converse—that color filling *can* be inhibited by boundaries formed by cues outside the traditional realm of first-order color and luminance information.

Here, we observed color filling on texture stimuli consisting of oriented bar elements (Grossberg & Mingolla, 1985; Landy & Bergen, 1991). In texture
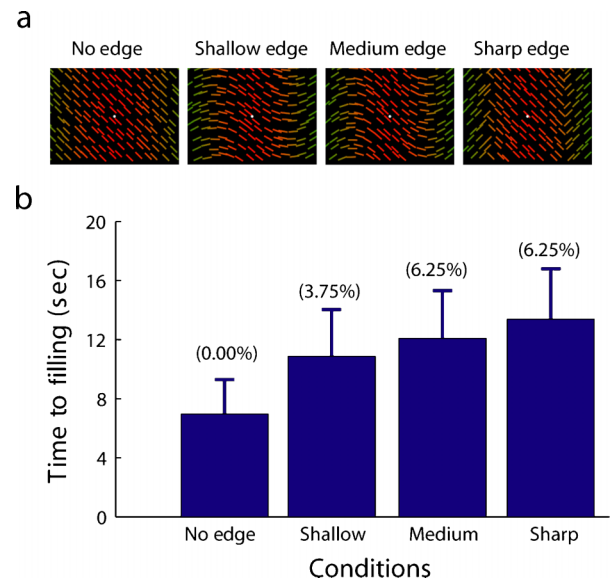

Figure 2. Color filling across a texture defined by oriented bars. (a) The four types of stimuli: no-edge condition, in which the texture was homogeneous; shallow-edge condition (σ = 5.0°); medium-edge condition (σ = 3.3°); and sharp-edge condition (σ = 0°). (b) Effects of textural borders on color filling. Mean results of time to filling for the four conditions. Error bars represent standard error of the mean ($n = 4 \times 40$ trials per category). The percentages of trials in which a participant did not respond before the 30-s time limit are shown in the parentheses and are excluded from the analysis. TTF differs significantly among conditions, repeated measures ANOVA, $F(3,9) = 6.079$, $p = .005$ (see text for post hoc pairwise comparisons).

stimuli, we can embed non-luminance-based segmentation cues, using differences in orientation to form second-order borders (Figure 2a). While keeping the color gradient constant, we varied the strength of the texture segmentation cues. We compared a condition lacking texture edges (Figure 2a, left panel) with conditions containing texture edges of three different levels of sharpness (Figure 2a, other panels), measuring the TTF for each condition. According to our hypothesis, this kind of cue might inhibit the color-filling phenomenon, especially when the texture border is sharply defined.

Methods

Participants

Four participants took part in this experiment, including two of the authors (R.K. and D.W.). All had normal or corrected-to-normal visual acuity and normal color perception.

Stimuli and procedure

Stimuli subtended the entire display. The color gradient was defined in the same manner as in the first experiment except that it was created based on horizontal, instead of

radial, eccentricity. μ and σ were fixed at $10°$ and $3.3°$, respectively. The color gradually varied from red to green or green to red as a function of horizontal eccentricity. Bar size was $3.3° \times 0.56°$. Orientation of the bar at a given horizontal eccentricity was determined in a way similar to the color gradient:

$$\phi(x) = \frac{\pi}{4} \pm \frac{\pi}{2} \cdot f(x),$$

where $\phi(x)$ is the orientation of a bar at an eccentricity x and $f(x)$ is the cumulative Gaussian function. The first term is the orientation of a bar displayed at the center. This orientation gradually changed to the orthogonal orientation through $\phi = 0$ (i.e., horizontal bars). The position of a bar, x, was based on the central point of the bar. When the stimuli were constructed, the bars were originally arranged across the display on a grid with $0.667° \times 0.667°$ separations in between. From the original grid arrangement, both horizontal and vertical positions of each bar were displaced by a random amount between $-0.556°$ and $+0.556°$. The stimulus subtended $38°$ horizontally and $28°$ vertically. The density of the bars was 2.25 bars/deg^2. For the gradient of the texture, the position of the second-order texture edge (μ) was fixed at $3.3°$, and σ, which was inversely related to the steepness of the edge, was varied between $0°$, $3.3°$, and $5.0°$. In addition, we interleave the condition in which the textural edge was absent (Figure 2a, left).

A white fixation point was provided at the center of the stimuli, and the observers were asked to fixate on the fixation point throughout the experiment. Trial types were balanced in terms of color polarity, and each trial was followed by a full-field opposing gradient and pattern mask. Each participant responded to 20 trials for each condition, for a total of 160 trials (2 [color polarity] $\times$ 4 [texture edge sharpness] $\times$ 20 [repetitions]).

Results

Participants observed that, in the condition without texture edges, the color filling occurred across the entire stimulus relatively quickly. In trials with texture edges, especially the sharpest condition, they observed that the color would fill out to the textural borders, stop there, and then require much longer before crossing over.

These subjective reports were reflected in the quantitative behavioral data (Figure 2b). A repeated measures ANOVA on the factor of the conditions showed that the TTF significantly differs among conditions, $F(3,9) = 6.079$, $p = .005$. A post hoc (Tukey) test showed that the TTFs in the "no-edge" condition were significantly smaller than those in the sharp- and medium-edge conditions ($p < .01$ and $p < .05$, respectively) but not in the shallow-edge condition ($p > .05$). Thus, as in the first experiment, color filling was not blocked by the numerous luminance gaps. Instead, it stopped at textural edges, requiring a longer duration of viewing to complete the color-filling process.

These texture stimuli contain two types of grouping and segregation cues. As before, the dark luminance gaps define a dark surface that is separate from the colored surface; in addition, color quickly passes through those gaps. This experiment adds the orientation of the bars as a cue for segmenting the elements in the central region from the elements in the peripheral regions. We find that color filling slowed down at the borders defined by the texture gradient.

It is interesting that a segmentation cue in the texture domain would affect a process in the color domain. The longer filling times associated with the steeper texture gradients are analogous to the inhibitory effects of steep color gradients in classical studies. Just as steep color gradients between color regions cause increases in the time required for filling-in to cross and proceed to completion, steep texture gradients also slowed down color filling. This shows an interaction between different visual feature maps where a border formed in one map regulates the surface appearance in another map.

We thus provide evidence for a regulatory role of perceptual segmentation boundaries, distinct from the roles played by local luminance and color edges. In our experiments, where luminance edges do not perceptually segment neighboring color regions, color filling passes through. In classical experiments, where luminance edges *do* provide cues to segment the color surface, color filling is blocked. Furthermore, segmentation borders formed by texture transitions, which lie outside the traditional realm of first-order color and luminance, are successful in inhibiting color filling.

Experiment 3: Static dual-gradient stimuli

The previous experiments explore the broad lateral spread of color filling but not the fine-scale "discreteness" of the effect. That is, color filling not only proceeds beyond the black boundaries but also seems to "jump" over them, filling into sharply delineated discrete regions. This process appears to reflect some degree of specificity for the color elements, but it is unclear whether this reflects true selectivity within the underlying mechanism.

For example, the specificity displayed in the first two experiments could be explained within the framework of a nonselective diffusion of color information plus a simple convolution with the luminance map to prevent the color from being fully expressed in the dark gaps. On the other hand, the involvement of a surface segregation process may endow a deeper level of specificity, whereby color information could flow selectively among regions segregated onto the same surface.

Insight into this possibility would be gained by examining how two color-filling processes interact when they are retinotopically overlaid. To what extent do the colors of each gradient remain restricted to their own surfaces? Do the directions and dynamics of color filling over the surfaces reflect a single, unified process or multiple, separate processes? To explore these possibilities, we created a series of stimuli in which one color gradient was presented in discrete squares as in the first experiment, but now, a second gradient was presented in the area previously occupied by the black grid (Figure 3a).

Methods

Participants

Six participants took part in this experiment, including two of the authors (D.W. and S.S.). All had normal or corrected-to-normal visual acuity and normal color perception.

Stimuli and procedure

Stimuli subtended the entire display. Squares subtended 0.37° and were spaced by 0.55°. This spacing was about three times as large as for the stimuli used in Experiment 1. The color gradient within the squares went from light blue (CIE x,y = 0.168, 0.166) to green (0.274, 0.563). The color gradient within the grid went from red (0.642, 0.346) to yellow (0.544, 0.418). We varied the size of the central disk in the grid area but held constant the gradient within the squares. Spatial parameters of the gradient were fixed for the squares, with μ = 7.32 and σ = 3.66. Spatial parameters of the gradient in the grid were varied across trials, with μ = 5.49, 7.32, or 10.98 and σ = μ/10. Color polarity was counterbalanced across trials.

Trial sequence remained the same. Participants pressed keys when they perceived the grid and/or the squares to become homogeneous in color. On each trial, participants made two key presses. With the left hand, they pressed a key when the color gradient in the squares became homogeneous. With the right hand, they did the same task for the other gradient. Key presses indicated whether the direction of the color filling was foveal-outward or peripheral-inward. Data analysis was based on responses given within a 30-s time limit for each trial. Each participant performed 10 trials per condition, for a total
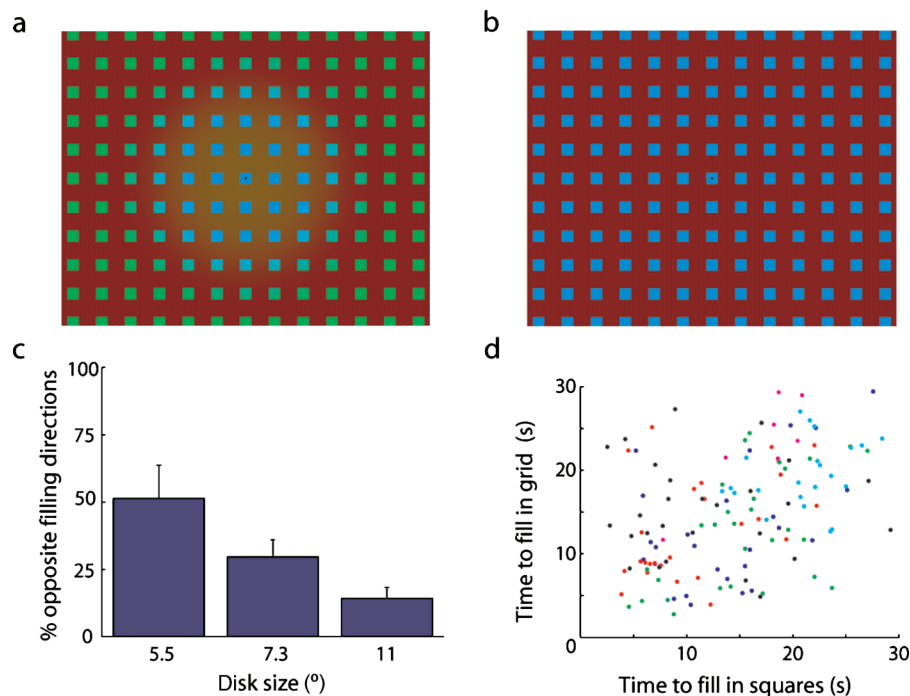

Figure 3. Color filling over two overlaid color gradients. (a) Sample stimulus. Configuration is a modified version of stimuli in Experiment 1, where the gaps between squares contain a second color gradient. (b) Illustration of an eventual percept. Participants perceived color filling to occur on both surfaces. Component colors remained confined to their own surfaces. Here, the blue color of the central squares has filled out to the peripheral squares, and the red color of the peripheral grid has filled into the central grid. (c) Participants often perceived color to spread in opposite directions in the grid and the squares. The percentage of filling events to proceed in opposite directions is plotted as a function of the grid gradient's disk size (n = 6 × 20 trials per category). (d) Color filling occurred at independent rates on the two surfaces. The TTFs for the grid and squares are plotted against each other trial by trial. Analysis includes only trials in which color filling was reported in both grid and squares. On average, responses for the grid and squares were separated by 5.7 s in either direction. Correlation between the two is poor: R^2 is .18, or .12 after correcting for intersubject contributions. This indicates that color-filling processes are occurring separately over each gradient and that they remain restricted to elements of their respective surfaces.

of 60 trials (2 [color polarity] × 3 [grid gradient] × 10 [repetitions]).

Results

Qualitatively, participants reported that color filling occurred in both the array of squares and the grid, but they remained distinct and separate. For example, given the stimulus shown in Figure 3a, a participant might see all the squares take on their foveal blue color and see the entire grid take on its peripheral red color (illustrated in Figure 3b). The colors of the squares do not fill in to areas occupied by the grid, or vice versa.

Quantitative analysis of the data also showed that two color-filling processes were acting separately. First, the directions of filling for the two gradients were reported to be opposite in many trials (an example is illustrated in Figures 3a and 3b; data are given in Figure 3c). The highest likelihood of opposite directions of filling (51%) occurred in the trials where the gradient in the grid pattern was set to the smallest disk radius.

Analyzing the TTF results trial by trial, we found that the timing of the two responses also reflected separate processes. Figure 3d is a trial-by-trial plot of the TTF for the squares versus the TTF for the grid. Participants usually reported completion of color filling at different times for the grid and the squares, which are, on average, 5.7 s apart and, often, more than 10 s apart. Overall, the correlation between completion times for the two processes is extremely weak. In the raw data plot of Figure 3d, $R^2 = .18$. Much of this is due to the contribution of systematic differences between participants. When data are scaled to each participant's mean, $R^2 = .12$.

Thus, a number of spatial and temporal results provide both qualitative and quantitative support for the notion that there are separate color-filling processes occurring along the two perceptually segregated surface groupings. First, colors remained mutually restricted to their own surfaces of origin. Second, the directions of color filling on each surface were often opposite. Finally, the color filling was completed at markedly different times for each surface.

These findings provide support for processing schemes that allow for the separate processing of overlaid perceptual surfaces. Furthermore, those separate processes selectively express themselves in regions specific to their own surface groupings.

Experiment 4: Color filling on perceptual surfaces in transparent motion

Our final experiment tests the limits of the notion that color filling is occurring across multiple perceptual surface representations. In Experiment 4, two surfaces are trans-

parently overlaid, both occupying the entire display, so that every point in retinotopic space has an equal correspondence with either surface. We tested whether two color-filling processes could still remain separate, that is, restricted to elements of their own surface.

We used a transparent motion stimulus (see Figure 4a), in which multiple surfaces coexist at the same retinal position (Snowden & Verstraten, 1999). Two surfaces consisting of random dots moved in opposite directions, each having a different color gradient from center to periphery. On one surface (say, moving upward), the color of individual dots gradually shifted from red to green as eccentricity increased, whereas on the other surface (moving downward), the color of the dots gradually shifted from green to red.

Methods

Participants

Four participants took part in this experiment, including one of the authors (R.K.). All had normal or corrected-to-normal visual acuity and normal color perception.

Stimuli and procedure

To parametrically characterize the effect, we created two sets of stimuli. The first set consisted of stimuli constructed as above, with varying steepness of the color gradient (σ). The second set consisted of single surfaces, in which only half the dots (say, the ones moving upward) were displayed. One of the extreme parameter settings in this set ($\sigma = 0$, two surfaces) replicates the steady-state misbinding effect we reported previously (Wu, Kanai, & Shimojo, 2004). Because of some similarities between stimuli that cause misbinding and the color-filling stimuli used in this experiment, this condition was included to compare and contrast the properties and dynamics of the two effects.

The transparent motion stimulus was created by superimposing two surfaces (upward and downward), each consisting of 600 random dots. Each dot has a 0.178° diameter and had a lifetime of 2 s. The velocity was 2.84°/s. The stimulus was displayed in an area subtending 14.2° vertically and 17.8° horizontally. For the color gradient for each surface, μ was fixed at 3.75° and σ varied between 0°, 2°, and 3°.

The participants viewed the stimuli for an unlimited duration of time and responded when they perceived the entire stimulus as homogeneous. Each participant performed 16 trials per condition, for a total of 192 trials (2 [color polarity] × 3 [color gradient steepness] × 2 [single or double surface] × 16 [repetitions]).

Results

In trials with two transparently overlaid surfaces, participants reported that the color filling to peripheral

dots occurred selectively for each motion-defined surface. Figure 4b illustrates the eventual percept for the stimulus diagrammed in Figure 4a. After prolonged viewing, the color of the surface moving upward appeared to become homogeneously red, whereas the color on the other surface appeared homogeneously green.

When the color gradient across the stimulus was smooth ($\sigma = 2°$, $3°$), participants took around 30 s to report the completion of color filling. No significant difference was found in the response times when dual-surface stimuli are compared with single-surface stimuli of the same σ settings (Figure 4c).

The properties of color filling across surfaces defined by transparent motion provide further support for the idea that color filling proceeds along multiple perceptual surface representations, rather than across a single retinotopic map. First, a color-filling process occurring across a surface took the same amount of time whether or not a second surface was overlaid. This indicates that color filling within a surface was relatively unaffected by the presence of another retinotopically overlaid surface. Second, in these stimuli, any given point in retinotopic space would, at times, be occupied by elements of either or both surfaces. Yet, the two color-filling processes remained separate and restricted to elements of their own perceptual surface.

Color–motion misbinding

The cases in which the color change was abrupt ($\sigma = 0$) show a different result. When only a single surface was present, filling-in took around 2 min (Figure 4c, leftmost circle). Meanwhile, when two surfaces were present, participants immediately reported the surfaces to be homogeneous (Figure 4c, leftmost square). The latter condition corresponds to our previously reported case of "steady-state misbinding" (Wu et al., 2004).

In discrete color filling, the color from one region is seen to spread and override the color of another region. If a stimulus has only one surface and/or if it has yellow transition zones, the eventual percept of homogenous surfaces requires regional color changes. Because the change is to a color that is not physically present at those regions, the eventual percept is attributable to the red and/or
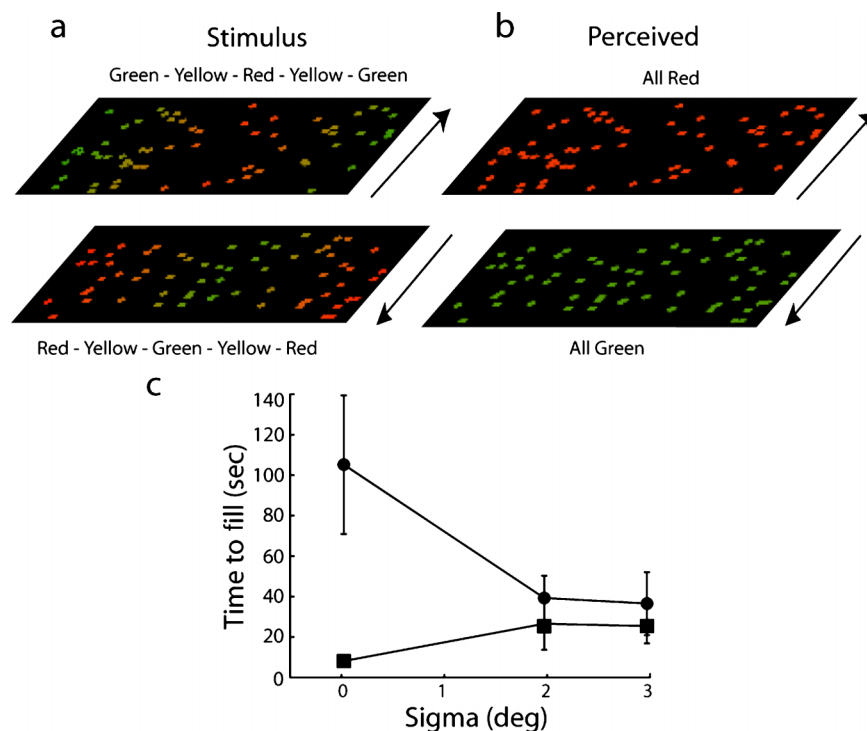

Figure 4. Selective color filling for transparently overlaid surfaces. (a) The transparent motion stimulus was created by superimposing two surfaces of random dots, each defined by common motion. On one surface, dot colors had a color gradient from red (center) to green (periphery), whereas on the other surface, the opposing color gradient was used. (b) After prolonged viewing of this stimulus, it was perceived as two homogeneously colored surfaces, the central color of each surface having filled out to the peripheral elements sharing the same motion. (c) Time required for completion of color filling for single-surface (circles) and dual-surface (squares) stimuli of varying gradient steepness ($n = 4 \times 32$ trials per data point). Error bars represent standard error of the mean. In smooth gradient conditions, no significant difference was found in terms of filling times between single- and dual-surface stimuli. Results from this experiment indicate that overlaid color-filling processes can remain segregated to elements of their respective surfaces even when every point in retinotopic space is occupied, at times, by elements from both surfaces.

green signals present in neighboring regions, that is, color filling.

In misbinding, the colors in a given region stay the same, but their associations with the motion surfaces are swapped. In the stimulus with two surfaces and no yellow transition zones, the red and green colors are already physically present throughout the stimulus. In this case, the percept of homogeneous surfaces does not require any actual color change. Instead, it requires only the misconjunction of the color and motion signals already present, that is, misbinding.

The difference in TTF between the one-surface condition and the transparent condition supports the idea that misbinding is a phenomenon distinct from color filling. As we discussed above, color filling presumably requires an adaptation period, which is longest when the transition between colors is sharply defined. This pattern was found in the first five conditions, all of which required adaptation periods. Consistent with color filling, the stimulus with the sharp color transition required the longest adaptation period. Meanwhile, the data from the last condition were inconsistent with color filling, reflecting the immediate impression of homogeneous surfaces without an adaptation period. The contrast is especially strong considering the fact that the single-surface stimulus with the same σ value took around 2 min to fill in.

The temporal dissociation between color filling and misbinding can sometimes be seen directly in the conditions with dual surfaces and smooth color gradients. From center to periphery, dots in these stimuli go from red and green in the center, transition to yellow, and then transition back to red and green in the far periphery (except with opposite color–motion pairings). Depending on the observers' confidence in their peripheral vision, color misbinding can be seen in these far peripheral regions. With varying levels of confidence, these regions were described as having the same color–motion polarity as the center. This erroneous percept occurred immediately upon stimulus presentation. Meanwhile, the yellow dots in the intermediate zones remained yellow for an extended adaptation period before color filling caused them to appear the same as the red and green dots in the flanking regions.

Although the two effects can be dissociated in terms of their timing and stimulus conditions required for induction, it seems that they may share overlapping mechanisms. For example, surface segregation based on common motion clearly plays a key role in both illusions. In the case of misbinding, the illusory misconjunction is caused by improper "sorting" of peripheral color signals to surfaces. In discrete color filling, this sorting process might also be involved in the surface assignment of red and green signals as they propagate into the yellow regions. In both cases, there is a bias toward assigning colors to motion surfaces in a manner consistent with the conjunctions present at the fovea.

Discussion

In a series of experiments, we have explored the properties of a phenomenon found in the art of Julian Stanczak, which we term discrete color filling. In this effect, conditions of fixative viewing cause participants to perceive the color of one region to spread and replace the perceived colors of other discrete regions.

We find that the spatial extent of color filling is not set by luminance edges, as in classical investigations of color filling. Instead, color is able to "jump" across wide luminance gaps, filling into distributed regions of space. Our experiments as a whole suggest that the interactions between local feature processing and perceived color are taking place in the context of an integrative computational scheme that perceptually groups elements and segregates surfaces. Our stimuli made use of multiple well-established and extensively studied methods that cause perceptual grouping and surface segmentation. In each case, it was found that the perceptually overlaid surfaces and grouped regions formed by those processes determined the spatial extent of color filling, the specific regions to which color would migrate, and, thus, the final perceived color for each element. Thus, stimulus cues in one domain could be used to regulate processes in another domain, via their impact on perceptual boundaries and surface segregation (De Weerd et al., 1998).

Psychophysics of surface perception

A number of previously studied phenomena indicate that surface segregation is a critical step for visual perception in general and for the perception of surface color in particular. For example, the filling-in of a texture (Kawabata, 1984; Ramachandran & Gregory, 1991) is constrained by the perceptual boundaries for the surface (Caputo, 1998; Spillmann & Kurtenbach, 1992), and texture can be seen to spread out of modified Ehrenstein figures, creating an illusory texture surface (Watanabe & Cavanagh, 1991).

The modulation of perceived color across spatially separated elements has also been found in a study of chromatic induction (Monnier & Shevell, 2003; Xian & Shevell, 2004). In chromatic induction, the perceived color of one region is affected by the color of neighboring regions. In the stimuli created by Shevell et al., however, chromatic induction is further enhanced when a test stimulus is placed on a patterned background as compared with simple uniform backgrounds, demonstrating an interaction of color information between spatially separated, perceptually grouped elements.

Studies on neon-color spreading (Pinna & Grossberg, 2005; Redies & Spillmann, 1981; van Tuijl, 1975) support the importance of surface interpretation as well. In neon-color spreading, color information crosses luminance edges and spreads over background regions to create the

perception of an overlying translucent surface. When grouped objects and/or aligned contours imply the existence of an overlying perceptual surface, color from the inducing elements disregards those borders, which do not segment the surface, and spreads to fill the implied surface with a translucent, neon-like color.

The primacy of surface segregation in color processing is also supported by a study of feature binding, where it has been found that surface segregation precedes the process of color binding (Moradi & Shimojo, 2004). Furthermore, the color filling found in stabilized and/or equiluminant images is more consistent with a breakdown in surface segmentation and feature binding than with an adaptive decay in bottom–up visual input (Billock & Tsou, 2004b). It has been found that optical stabilization of images on the retina causes color to be unbound from surfaces, inducing color migration or switching across borders, and, eventually, a complete visual blackout (Billock, Gleason, & Tsou, 2001). Also, an extensive history of studies shows that phenomenal progression of image fading is based on the sequential disappearance of globally organized parts, rather than on a progression along local features (reviewed in Billock & Tsou, 2004a).

Taken together, these studies and ours argue for the importance of perceptual boundaries and surfaces in regulating color filling and color perception in general. The formation of perceptual boundaries and the attribution of stimulus features to surfaces seem to be critical steps in processing surface qualities.

Ecological perspective

Speaking in broadly theoretical and ecological terms, it would seem appropriate for color computations to be surface specific. In our visual world, other surfaces of an object are often occluded by other objects. It would be advantageous to allow visual processing to deal with the visible parts of that object as if it were whole, with a minimal amount of interference from signals arising from the neighboring objects.

In this vein, it has been proposed that visual illusions of color and brightness might originate from the statistical properties of surfaces and illumination in a natural, visual environment (Dakin & Bex, 2003; Nakayama & Shimojo, 1992; Purves et al., 1999). In a series of studies, Purves et al. have proposed an empirical framework, whereby ambiguities inherent in the illumination and reflectance of real-world objects are resolved based on the statistical relationship of visual inputs obtained from perceptual learning of individuals and evolution (Purves, Williams, Nundy, & Lotto, 2004). This empirical framework has successfully explained a variety of illusions associated with surface brightness (Yang & Purves, 2004) and color (Long & Purves, 2003; Lotto & Purves, 2000, 2002).

This empirical theory of visual perception regards erroneous percepts not as a by-product of early visual processing but as a consequence of the functions subserved by the visual system. We believe that the discrete color filling we reported here may reflect the concerted and integrated processing of low-level features (e.g., luminance, texture, spatial frequency, and motion) in forming inferences on surface properties (Lotto & Purves, 2000, 2002; Purves et al., 1999).

Neurophysiology of surface color and brightness

Physiological models of perceived surface color can be categorized as isomorphic (e.g., Gerrits & Vendrik, 1970), where the distribution of activity resembles a point-by-point retinotopic map, or symbolic (e.g., Ratliff, 1978), where edge signals more or less directly encode surface qualities. There is experimental support for the relevance of both types of models to the processing of perceived surface qualities in general and to the processing of color filling-in in particular.

Although the early cortical response to uniform surfaces emphasizes edges and is, thus, not strictly isomorphic, neural activity corresponding to the interior brightness of the surfaces is still present. Luxotonic activity, which is a response to uniform illumination, is present in single neuron recordings from awake macaque (Friedman et al., 2003; Kayama et al., 1979; Peng & Van Essen, 2005) and in fMRI data from humans (Haynes, Lotto, & Rees, 2004).

Studies looking specifically at filling-in illusions show varied results with regard to the subset of surface-responsive activity that correlates with *perceived* brightness or color (but see Cornelissen, Wade, Vladusich, Dougherty, & Wandell, 2006; reviewed in Komatsu, 2006). Correlates have been found as early as V1 for certain illusions—simultaneous brightness contrast (Kinoshita & Komatsu, 2001; Rossi, Rittenhouse, & Paradiso, 1996), blind-spot filling-in (Komatsu, Kinoshita, & Murakami, 2002; Komatsu, Murakami, & Kinoshita, 1996; Tong & Engel, 2001), neon-color spreading (Sasaki & Watanabe, 2004), and the phantom effect (Meng, Remus, & Tong, 2005). Moreover, propagation of activities for neurons corresponding to a surface region following a boundary formation has been shown in electrophysiology in V1 (Lamme, Rodriguez-Rodriguez, & Spekreijse, 1999). On the other hand, correlates for other illusions—artificial scotoma (De Weerd, Gattass, Desimone, & Ungerleider, 1995) and Cornsweet effect (Perna, Tosetti, Montanaro, & Morrone, 2005; Roe, Fritsches, & Pettigrew, 2005)—were not found until V2 or even later. Finally, in a study using Troxler fading, the illusion most similar to discrete color filling, no isomorphic surface correlates were found at all (von der Heydt, Friedman, & Zhou, 2003). In this study, the neurons that were found to follow the monkey's perceptual experience were selective for the color spot's edge, not its interior surface.

Neurophysiological investigation of activity during the viewing of discrete color-filling stimuli might be informative in discerning the distinct contributions of edge and surface signals in representing perceived color surfaces. Because the illusory percept retains the high-contrast edges from the stimulus but does not reflect the color values of those edges, this presents potential situations in which strong color-edge signals are in direct conflict with surface color perception. Thus, the activity in color-edge- and color-surface-responsive neurons during discrete color filling might be informative as to the relevance of isomorphic and symbolic components of processing at various levels of cortical processing.

Neurophysiology of surface segregation

Aside from the issue of how surface color is coded, there is the question of surface segregation and the spatial specificity of filling-in. The properties of discrete color filling indicate that the influence of a local feature depends on its role in perceptual grouping and surface segregation. Well after the completion of filling-in, participants continue to perceive sharp-edged borders and fine-grained surface specificity for surface colors. This suggests that surface correspondences need to be embedded in or linked to feature detectors in early visual cortex, where receptive field sizes are small enough to resolve such details. We review evidence for such a "marking" of local edge signals in macaque V1 and V2.

In macaque V2, there is evidence for oriented edge signals, which encode border ownership relationships in figure-ground segregation. Single-cell recordings made during stimulation with solid color patches indicated that some edge-selective neurons encode not only the luminance polarity across an edge but also border ownership—which side of the edge represents figure and which side ground (Zhou, Friedman, & von der Heydt, 2000). The time course of activity suggests that feedback from higher visual areas, as opposed to lateral interactions, supplies the global surface information, as border ownership signals appeared at a timing relatively independent of figure sizes. The inclusion of border ownership components in the oriented edge signals could begin to explain why local luminance edges block color filling in some cases but not others.

In addition to the above finding with continuous surfaces, surface segregation signals have also been found in textured surfaces. In macaque V1, neurons with receptive fields in the center of a texture surface exhibit a late enhancement in their response if that surface is segregated in a figure-ground relationship (Zipser, Lamme, & Schiller, 1996). This signal is found whether the surface was defined by color, luminance, orientation, disparity, or combinations thereof. When feedback from higher visual areas is disrupted, either by anesthesia (Lamme, Zipser, & Spekreijse, 1998) or by lesion

(Lamme, Zipser, & Spekreijse, 1997), the figure-ground enhancement is eliminated, whereas the orientation-selective response pattern remains. In sum, this late enhancement of a local edge signal marks its membership in a broader segregated surface and is correlated with the behavior of the animals in detecting surface regions.

These studies of border ownership and texture surface segregation indicate that edge signals in early visual cortex are multiplexed with a map of surface correspondences that is built based on feedback from higher visual areas (Lee, Mumford, Romero, & Lamme, 1998). This may help to explain our psychophysical finding that edge signals either block or fail to block the lateral spread of color filling based on the parsing of border ownership. Furthermore, it provides a high-resolution substrate for the fine-grained surface specificity of color filling. The involvement of feedback from higher cortical areas in generating these signals provides a route for high-level perceptual processes to influence low-level processes such as color filling.

Conclusions

The experiments presented here demonstrate that discrete color filling is governed by perceptually defined borders and segregated surfaces. Color filling over a surface ignores local luminance gaps that have been attributed to another surface but is inhibited at surface-relevant borders whether they are formed by local edges or texture. Color can fill across discontinuous regions that are perceptually segregated onto the same perceptual surface. Meanwhile, color will avoid filling into intervening regions that have been segregated as belonging to different surfaces. Underlying this specificity is the ability of visual processing to support multiple processes of color filling when multiple surfaces are present. The color interactions occurring on each surface remain separate even when the surfaces are defined by transparent motion, such that each point in retinotopic space can be occupied at different times by either or both surfaces. We believe that these properties of discrete color filling reflect the concerted and integrated processing of low-level features such as luminance, texture, spatial frequency, motion, and so forth, in the context of forming correspondences to perceptual surfaces. Cues from all of these visual modalities were found to regulate color filling via their impact on perceptual surface segmentation and segregation.

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Corresponding author: Ryota Kanai
Email: kanair@gmail.com.
Address: Psychonomics Division, Helmholtz Research Institute, Universiteit Utrecht, Heidelberglaan 2, 3584 CS, Utrecht, The Netherlands.

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