Color selection, color capture, and afterimage filling-in

Jihyun Kim
Department of Psychological Sciences, Purdue University, West Lafayette, IN, USA

Gregory Francis
Department of Psychological Sciences, Purdue University, West Lafayette, IN, USA

R. van Lier, M. Vergeer, and S. Anstis (2009) reported an afterimage that produced different percepts from an inducing stimulus depending on the shape of a subsequent contour. G. Francis (2010) explained this phenomenon with a model where the contour forms a boundary that traps the afterimage color as it spreads across a surface. We conducted a series of additional model simulations and experiments to test the explanation. We first tested the hypothesis that the contour traps the afterimage color by adding additional contours. Model simulations suggest that additional contours could block color from spreading to the middle of the surface. In two experiments, additional contours blocked color spreading when they were at the inducer edges but not when they were drawn away from the inducer edges. In a second set of experiments, we investigated the model prediction that the drawn contour defines the perceived shape of the afterimage. New model simulations predict that variations in the size of the drawn contour force the perceived afterimage to vary accordingly. However, an experimental study revealed that the perceived afterimage size remains the same as the inducing stimulus. The simulation and experimental results both highlight and challenge important characteristics of the model.

Keywords: color appearance/constancy, color vision, computational modeling, shape and contour, temporal vision


Introduction

A negative afterimage is a visual phenomenon in which adaptation to a chromatic stimulus induces color perception of the opposite chromaticity after the removal of the stimulus. In some situations, the complementary color experienced in the afterimage is known to be produced by the adaptation of photoreceptors to the color stimulation and, thus, to rely on the visual representation on the retina (Virsu, 1978). However, not all afterimage phenomena can be explained by adaptation of photoreceptors. For example, Shimojo, Kamitani, and Nishida (2001) suggested that a negative afterimage could result from adaptation to a cortical representation of visual information. They reported that illusory color perceived in a filled-in surface by neon color spreading could produce a negative afterimage. Recently, van Lier, Vergeer, and Anstis (2009) also reported an afterimage that seems to involve cortical filling-in. Interestingly, while Shimojo et al. (2001) showed the induction of an afterimage by cortical filling-in, van Lier et al. (2009) further suggested that an induced afterimage undergoes a cortical filling-in process.

The afterimage described by van Lier et al. (2009) matched neither the retinotopic nor the cortical visual information in the inducing stimulus. Instead, the afterimage percept differed according to the properties of a contour drawn on the adapted visual field at the offset of the inducing stimulus. To induce the afterimage, the authors used an eight-pointed star-like stimulus with opposite-chromatic colors (e.g., red and cyan) neighboring one another at each point (i.e., tips of the star). The shape of the inducing stimulus could be seen as 2 four-pointed overlapping stars (Figure 1). The common region for both of the four-pointed stars (middle area) was colored with gray. After the inducing stimulus was removed, an outline contour with a shape matching one of the four-pointed stars was presented. A different complementary afterimage color was perceived according to the shape of the drawn outline contour. When the outline matched the red-pointed star of the inducer, a cyan afterimage was visible, but when the outline matched the cyan-pointed star of the inducer, a reddish afterimage was visible. Importantly, this afterimage color was seen across the entire surface within the outline, including the region corresponding to the gray area of the inducing stimulus. The two key properties of the afterimage percept are given as follows: (1) the drawn contour seems to select one part of the inducing stimulus to form the basis of the afterimage and (2) the selected afterimage color spreads across the middle achromatic region where color adaptation did not occur.

van Lier et al. (2009) proposed that the effect of the contour on afterimage perception involves color–contour interactions in a cortical filling-in process (Pessoa & DeWeerd, 2003). Specifically, they argued that the outline contour of the four-pointed star following the inducing stimulus might have triggered and constrained spreading
of afterimage color signals during a filling-in process. The authors consequently suggested that the van Lier afterimage involves the same filling-in mechanism that is involved in various real color visual phenomena, such as the neon color effect and the watercolor illusion (Komatsu, 2006; Pinna, Brelstaff, & Spillmann, 2001).

Francis (2010) showed a model simulation supporting the involvement of a contour-based filling-in process in the van Lier afterimage. The model is based on a perceptual filling-in theory that hypothesizes two complementary systems in the visual processing stream: a Feature Contour System (FCS) and a Boundary Contour System (BCS; Grossberg, 1997; Grossberg & Mingolla, 1985a, 1985b). Surface feature information (e.g., color and brightness) and boundary and edge information of the surface are processed separately in each system and then bound together at a filling-in stage to produce the perceptual experience. At the filling-in stage, FCS networks diffuse signals containing feature information about color and brightness across a surface, while boundaries in the BCS block this spreading to trap the signals within a set of boundaries. An object with color and brightness is perceived only when feature signals are trapped within a closed boundary since otherwise the signals dissipate across the entire field.

Model after-responses are generated by a gated dipole circuit, which creates a neural after-response as a result of synaptic habituation and competition (Francis, 2010; Grossberg, 1972; Francis, Grossberg, & Mingolla, 1994). Information at each model pixel is processed through pairs of color channels: red–green, blue–yellow, and black–white (Figure 2a). Each pair of channels behaves antagonistically such that activity in one channel inhibits the other through cross-channel competition. When seeing a red stimulus, for example, the red channel activity inhibits the green channel activity through this competition. However, when a channel is stimulated, the synaptic connection within the channel is weakened by decreasing amounts of available neurotransmitter, which leads to a slow decrease in the activity of the stimulated channel (Figure 2b). Importantly, the effect of synaptic habituation is prolonged after the stimulus offset, consequently reversing the relative inhibition strength between the channels when they both receive a baseline stimulation. As a result, a color after-response is produced upon stimulus removal because the non-stimulated channel receives less inhibition than the previously stimulated channel.

The afterimage percept is created at the filling-in stage of the model, which involves the interaction between color and boundary processing. In this stage, any color after-response generated through the color-opponent process diffuses across a surface until a boundary blocks it. A closed set of contours can contain colors to create a percept. In the van Lier afterimage, the color after-responses are too weak by themselves to form boundaries that will support a visible afterimage percept. However, a drawn contour of a four-pointed star that overlaps with the location of the color after-responses produces strong

Figure 1. Illustration of the van Lier afterimage (van Lier et al., 2009). The first row depicts the stimulus, the second row schematizes how color after-responses would overlap with the drawn contour at each time, and the third row represents the resulting visual percept.
boundary signals that trap the spread of the color after-response. As a result, the after-response color fills in the entire surface within the drawn contour, including the gray inducer regions. In addition, the afterimage percept corresponds to the shape of the drawn contour, while color after-responses from color points without a subsequently drawn outline star are too weak to create their own boundaries and thereby blend into the background. Thus, the filling-in stage determines both the selection of the parts of the inducing stimulus that contribute to the afterimage percept and the spread of the afterimage color across the selected surface. The same model properties have previously been used to explain a related type of afterimage (Francis & Rothmayer, 2003; Francis & Schoonveld, 2005; van Horn & Francis, 2007).

In this study, we investigated whether the model simulations used by Francis (2010) could predict afterimage percepts for new stimulus conditions. The selected conditions were chosen to highlight fundamental properties of the model’s explanation of the van Lier afterimage. We first look at the effect of adding a closed contour to the inside of the drawn contour. Model simulations suggest that this new contour should block the spread of color into the gray region. This prediction is tested in two experiments. We then explore what happens as the size of the drawn contour varies from the size of the color inducing stimuli. Two empirical studies test the model prediction that the afterimage percept should become the size of the drawn contour. To anticipate the main findings, although the data do match the model prediction in a few cases, in general, the empirical data suggest that the model is missing some fundamental aspects of how the van Lier afterimage is generated in the visual system.

Adding an inner contour boundary

We first explored whether a contour drawn at the offset of the inducing stimulus can block the spreading of the afterimage color signal by adding an inner contour to the drawn contour used in the original study of van Lier et al. (2009). An inner contour corresponding to the outline of the gray middle region of the inducing stimulus was drawn inside of the four-pointed star (now called the outer contour). See the bottom row of Figure 3 for a sample image. Here, we report the model simulation results and then subsequently describe the psychophysical experiment that tests the model predictions.

Model simulations

Details of the model equations, parameters, and calculations can be found in Appendix A. The simulation results for one condition are demonstrated in Figure 3. Each row of the leftmost column represents the stimulus given at the time indicated. The second column shows the activity of cells that output from the networks of the
opponent-color stage. These cells retinotopically code color information. When the inducing stimulus is present, the network represents the colors of the inducing stimulus. When the inducing stimulus is turned off, the gated dipole circuit at each pixel produces a neural after-response that represents the complementary color signal. The black drawn contours are also represented as color signals at this stage of the model.

The third column of Figure 3 illustrates the boundary representation in the boundary signal stage. During the onset of the inducing stimulus, boundaries are formed by the color and luminance contrasts between the different surfaces, as they are represented at the opponent-color stage of the model. During the presentation of the inducing stimulus, these boundaries outline the stimulus. At the offset of the inducing stimulus, the after-response signals at the opponent-color stage are too weak to form strong boundaries. On the other hand, the drawn contours are strong enough to produce strong boundaries, but these boundaries only outline parts of the color after-responses.

The rightmost column of Figure 3 shows the filling-in stage of the model. Here, percepts are derived from the interactions between color and boundary signals. The color signal in the opponent-color stage feeds into and spreads across a surface until it is blocked by a boundary formed in the boundary signal stage. Thus, during the presence of the inducing stimulus, the percept matches the stimulus because the boundaries correctly outline each surface and the opponent-color signals spread across just those surfaces. After the offset of the inducing stimulus and the appearance of the drawn four-pointed star (1900-ms row in Figure 3), the opponent-color signals at the tips that match the shape of the four-pointed star spread within their tip and across what had previously been the gray middle region. Any edges at the gray middle region are too weak to support boundaries that would prevent such color spreading. In a similar way, the opponent-color signals at the tips that are not surrounded by the drawn contour spread out and merge into the background to become essentially invisible. Therefore, only the color signal falling inside of the drawn outer contour is trapped and perceived. This is the explanation of the van Lier afterimage that was proposed by Francis (2010).

The predicted percept for the bottom row of Figure 3 is a variation of a model simulation presented by Francis (2010). The additional inner contour generates boundaries along what was previously the edge of the gray center. These additional boundaries trap the after-response colors in the tips of the star and keep the central region a solid gray. In many respects, this condition is similar to the filling-in investigations carried out by Paradiso and Nakayama (1991) with flickering stimuli. They found that a contour drawn inside a larger filled circle could apparently block the spread of brightness from edges to the middle of the circle.

In addition to testing whether the inner contour could trap the afterimage colors in the tips and prevent them from spreading across the middle gray region, we were also interested in the timing of color spreading. In particular, we were curious whether different sequences...
of two drawn contours might produce different afterimage percepts.

Thus, we ran a variety of conditions that varied the order of drawn contours that either had or did not have an inner contour. Figure 4 shows the predicted percepts from the filling-in stage of the model for these different conditions. The labels above each column indicate the absence or presence of the inner contour boundary (NB: no boundary, B: boundary, see Design and procedure section in Experiment 1). When the contour is absent throughout the sequence (the first column), which is identical to the stimulus configurations used for the simulation by Francis (2010), the afterimage color is seen on the entire surface within the contour. On the contrary, if the inner contour is present throughout (the last column), the model predicts that the inner contour blocks the spreading of the afterimage signal, and color is perceived only at the points of the four-pointed star while the inside of the inner contour is gray. The simulation results further show that the inner contour can modulate the afterimage percepts dynamically over time by trapping and spreading afterimage colors according to the contour drawn at the moment (the two middle columns). One side effect of the color habituation is that the colors in Figure 4 tend to get darker as time passes. This model property is not central to the model predictions, but it does reflect some behavior studies on color fading (e.g., Gur, 1989; Hamburger, Prior, Sarris, & Spillmann, 2006). These kinds of effect might also be mitigated if the model included anchoring mechanisms (Grossberg & Hong, 2006).

A key property of the model is that the source of the color signals is projected as a feedforward signal from the color-opponent circuits to the filling-in stage. The simulation results in Figure 3 (and the second column of Figure 4) reflect this model property by showing that the subsequent inner contour does not trap previously filled-in afterimage colors. Instead, the perceived afterimage is based on the spreading of the current inputs from the opponent-color stage as they spread around the current boundaries. These model predictions were tested in the following experiment.

### Experiment 1

**Methods**

**Participants**

Twenty students from Purdue University participated in Experiment 1 for course credit. They reported normal or corrected-to-normal visual acuity and color perception. For every experiment, an Ishihara color perception test was performed prior to the main experiment to confirm the correctness of color vision. All participants in Experiment 1 passed the color vision test.

**Stimuli**

Stimuli were shown on 24" iMac Monitor (1920 × 1200 pixels) calibrated by an Eye-One Color Management device and run with the Mac OS X v10.5 Leopard operating system. Matlab in conjunction with the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) was used to create the stimuli. Participants were seated in a lighted room and rested their heads on a chin rest fixed at a distance of 70 cm from the monitor.

The eight-pointed star-shaped figure comprised of alternating red ($R = 185, G = 96, B = 85$; $L = 92, a = 52, b = 33$) and cyan ($R = 69, G = 124, B = 106$; $L = 85, a = −45, b = −3$) points and a gray ($R = 133, G = 114, B = 106$; $L = 89, a = 4, b = 3$) middle was drawn on a lighter...
gray background \((R = 162, G = 141, B = 122; L = 106, a = 2, b = 12)\) to induce the afterimage as in the study by van Lier et al. (2009). The inducing stimuli extended 13.03° in maximum size.

The two different shapes of the four-pointed outer drawn contours were defined by their orientation alignments, each encompassing the same-colored points (cross-shaped or x-shaped, see Figure 1). They were the same size as the inducing stimuli and were drawn in black lines with a thickness of 0.07 mm. These contours were further varied according to the absence or presence of the inner contour in the middle area that corresponded to the gray area of the inducing stimulus. One type of contour included only the outer boundary (the four-pointed star) and the other type included both the outer boundary and the inner boundary (see Figure 4). A square mask stimulus was made of random pixel noise containing the full range of luminance values from white to black.

**Design and procedure**

Figure 5 describes the inducing phase, afterimage phase, mask phase, and response phase of each trial. The eight-pointed star inducer was presented for 1200 ms in the inducing phase. The afterimage phase was comprised of a series of two successive contours each of which lasted for 700 ms. Within a trial, the shape of the outer contour (either cross- or x-shaped) was consistent throughout, while the presence and absence of the inner contour varied across time. The contour sequence for a given trial was one of the following four conditions: a No Boundary to No Boundary condition (NB–NB), a No Boundary to Boundary condition (NB–B), a Boundary to No Boundary condition (B–NB), and a Boundary to Boundary condition (B–B). The terms Boundary and No Boundary refer to the presence and absence of the inner contour, respectively.

In every case, a mask followed the afterimage phase for 1200 ms. In the response phase, the participants were asked to report the most recently perceived color (just before the mask appeared) either at the points (inside the outer contour but outside of the inner contour) or in the middle (inside the inner contour, two-thirds of the trials, 16 trials per participant for each condition) according to the question on the screen. They were forced to choose a color among red, green, or gray by pressing a designated button. Responses for the points reflected the afterimage color perceived in the outer contour and were compared with the responses for the middle to measure the relative effect of the inner contour. The assignment of the red and cyan colors at the points and the shape of the contour (cross-shaped or x-shaped) was counterbalanced and presented in a random order (24 trials \(\times\) 4 conditions of contour sequences = 96 trials in total per participant).

At the beginning of each trial, a fixation cross appeared together with a “hit space bar” message. When participants pressed the space bar, the four successive experimental phases described above (inducer, afterimage, mask, response) proceeded after a 1000-ms fixation delay. A 3000-ms Inter-Trial Interval followed the response phase. Ten practice trials preceded the main experimental session in all the experiments.

**Results**

Figure 6 plots the percentage of responses where the reported afterimage color matched what was expected...
The main conclusion is that the inner contour does block the afterimage color from the points, as predicted by the model simulations. This is most easily demonstrated by comparing the percentages for the points and the middle for each condition. The percentage of the expected color responses was significantly lower in the middle as compared to at the points in the B–B condition ($t(19) = 12.196, p < 0.001$). Thus, the presence of the inner contour prevented the perception of the afterimage color in the middle. The points vs. middle differences were significant in the NB–B ($t(19) = 9.525, p < 0.001$) and the B–NB ($t(19) = 5.255, p < 0.001$) conditions as well, thereby showing that the afterimage color in the middle differed from that at the points whenever the inner contour was present.

Cross-condition comparisons largely support the model prediction that afterimage perception changes with a contour given at the moment, and the perceived color of a surface was not based on previously perceived colors. There was no difference in color reports for the middle under the NB–B condition compared to the B–B condition ($t(19) = −0.860, p = 0.4$), indicating that later presence of the inner boundary ceased the color percept in the middle irrespective of whether it was previously filled-in or not.

On the other hand, having the inner contour present and then removing it (B–NB condition) reduces the likelihood that the afterimage color spreads from the points to the middle, as compared to the NB–NB condition ($t(19) = 4.348, p < 0.001$). This difference may indicate that color spreading weakens as the color after-response fades. If this were true, then in the B–NB condition, the afterimage color may not fully spread to the middle with the disappearance of the inner boundary because the color after-responses in the tips have faded. In contrast, the stronger after-responses for the first contour of the NB–NB condition quickly spread to the middle and are maintained during the second contour.

Another possible interpretation of the data is that in the B–NB condition, the disappearance of the inner contour produces its own after-responses that interfere with the spreading of the color after-responses.

We also cannot rule out that the participants’ responses were biased by the first drawn contour in the B–NB condition. Overall, the presence of the inner contour led participants to dominantly report perceiving gray in the middle (constituting 79 of the 89% points that were not the expected color in the NB–B condition and 75 of the 87% points in the B–B condition). Similarly in the B–NB condition, participants mostly reported gray when they did not see the expected color (46 of the 58% points) and these reports could be influenced by the inner contour in the first drawn contour. However, this explanation is less convincing when considering that the first drawn contour seems not to affect the reports in the NB–B condition. Overall, Experiment 1 results support the model prediction that boundary information from the contour drawn at the offset of the stimulus blocks the afterimage color.

---

**Figure 6.** The results of Experiment 1. Each solid blue and checkered red bar represents the percentage of expected color responses at the points and in the middle, respectively. The $x$-axis depicts the contour sequence conditions used (NB: No Boundary, the contour without inner boundary; B: Boundary, the contour with inner boundary). When the inner boundary was present later, the newest afterimage in the middle did not contain afterimage color (NB–B, B–B) regardless of the shape of the first contour. In the opposite conditions, when the inner boundary was not present, the afterimage color was perceived in the middle (NB–NB, B–NB). These results suggest a robust interaction between the inner contour and afterimage. The error bars correspond to one standard error of the mean.

from the results of van Lier et al. (2009). That is, the expected color response counted the reports of the color complementary to the color of inducer points that were aligned in the same orientation as the given contour (expected color responses = total responses − gray responses − unexpected color responses). An average of 83% of the reported afterimage color at the points matched the expected color. This result shows that the afterimage colors perceived in the points of the drawn star were essentially the same as those reported by van Lier et al. (2009). There were no significant differences among the contour sequence conditions at the points ($F(3, 57) = 2.115, p = 0.108$).

The NB–NB condition also shows that, without an inner contour, the afterimage color perceived in the middle of the image is the same as at the points of the star ($t(19) = 0.543, p = 0.594$). This is a replication of the afterimage reported by van Lier et al. (2009). However, the contour sequence had a significant effect on the responses for the middle. The expected color responses were less common when the contour with the inner boundary was present ($F(3, 57) = 38.977, p < 0.001$), especially when it was the second presented contour that determined the final afterimage percept and formed the basis of the participant’s report.
Varying the size of the inner contour

The results in Experiment 1 showed that presenting an inner contour at the gray area boundary blocked the inward color spreading in the afterimage. In Experiment 2, we further investigated the contour–afterimage interaction by drawing the inner contour in five different sizes. The inner contour was scaled to be smaller than, match to, or bigger than the size of the gray area of the inducing stimulus.

Model simulations

The inner contours were scaled in various sizes ranging from 85% to 115% relative to the size of the gray area of the inducing stimulus. The size of the outer contour was fixed to be the same as the inducing stimulus. Contrary to the simulations for Experiment 1, the inner contour was always presented simultaneously with the outer contour of either one of the four-pointed stars.

Figure 7 shows the responses from the opponent color, the boundary signal, and the filling-in stages of the model for the five different sizes of the inner contour. When the inner contour is 100% or smaller than the size of the gray area, the model behavior is very similar to what was described in Figure 3. The inner contour is predicted to block the spread of afterimage color from the points into the region inside the inner contour. The model prediction is slightly more complicated when the inner contour is larger than the middle gray area. Now, the inner contour still blocks most parts of the color from spreading but not entirely. Some parts of the after-response signal produced by the colored points are able to spread across the inner contour since it overlaps with the parts of the region carrying chromatic after-response signals. For the current model parameters, this overlap is predicted to produce only a very small effect, and in all conditions, the middle region should look gray.

Experiment 2

Methods

Participants

Another twenty-two students from Purdue University participated in Experiment 2 in return for course credit. All the participants reported normal or corrected-to-normal visual acuity. One participant scored 81% in the color vision test and reported not perceiving any afterimage during the practice session. Another participant could not finish the Ishihara test due to what appeared to be red–green color blindness. These two participants did not participate in the main experiments. All the other
participants had normal color vision (20 participants for the main experiment).

**Stimuli**

The apparatus was the same as in Experiment 1.

All the aspects of stimuli (the inducer, the outer contour, and the mask) were the same as in Experiment 1 except that the inner contour was always present with the outer contour and its size varied. The sizes of the inner contours were scaled relative to the size of the gray area of the inducer such that these contours were smaller than the size of the gray area (93%, 6.55° in size, diff = −0.49° off from the gray area boundary; 85%, 5.99°, diff = −1.06°) in some conditions. In another condition, they matched to the size of the gray area (100%, 7.04°, diff = 0°). In the other conditions, the inner boundary contours extended outside of the gray area (115%, 8.08°, diff = 1.06°; 107%, 7.53°, diff = 0.49°).

**Design and procedure**

We changed the presentation time for the stimuli since only one contour was shown in the afterimage phase in Experiment 2 (Figure 8). In the inducing phase, an inducing stimulus appeared for 1000 ms. In the afterimage phase, a drawn outer contour containing an inner contour with one of the five sizes was presented for 800 ms. After 1000 ms of the mask presentation, a question appeared on the screen asking the perceived color either at the points or in the middle. The next trial began after 3000 ms of ITI.

The procedure of Experiment 2 starts with the inducing stimulus being presented for 1000 ms. The contour with one of the varying sizes of the inner contour followed for 800 ms. After 1000 ms of the mask presentation, a question appeared on the screen asking the perceived color either at the points or in the middle. The next trial began after 3000 ms of ITI.

The percentage of the expected color response is calculated as in Experiment 1 and plotted in Figure 9. For reports at the points, the response percentages did not significantly differ by the size of the inner contour ($F(4, 76) = 0.4, p = 0.808$), with an average of 84% of the responses corresponding to the expected color at the points. The result is in agreement with Experiment 1 and the reports by van Lier et al. (2009).

On the other hand, and contrary to the model prediction, the size of the inner contour affected the expected color responses in the middle area ($F(4, 76) = 17.479, p < 0.001$). These color reports are smaller than the reported color at the points, but their variability suggest that the inner contour is only partly blocking the spreading of color from the points into the middle. When the color in the middle did not correspond to the expected color, participants mostly reported the inside of the inner contour to be gray (percentage of gray/unexpected + gray responses: 38/45%, 52/70%, 54/76%, 42/57%, 24/26%, respectively, from the 85% to the 115% contour size scales).

The reduction of afterimage color in the middle relative to the points is generally consistent with Experiment 1 and the model predictions. However, contrary to the model...
prediction, making the inner contour size different than 100% also led to higher reports of the afterimage color being perceived in the middle. The model had predicted that color reports should be low for all inner contour sizes because the inner contour would block the spread of color from the points into the region defined by the inner contour. It is difficult to reconcile the model with this experimental finding. A key part of the model's explanation of the van Lier afterimage is that boundaries block colors from spreading, but this explanation implies that the inner contour should always block colors from spreading to the interior of the inner contour. It may be that the distance between the source of color and the boundary influences the ability of the boundary to block the spreading. With increasing separation, the boundary may be less effective. We explore this issue further with an investigation of the outer contour.

The outer contour boundary

One way of summarizing Experiment 2 is that, contrary to the model prediction, the shape of the surfaces in the afterimage were not determined solely by the shapes of the drawn contours, which is in conflict with a key prediction of the model. In Experiments 3a and 3b, we tested whether the outer contour (four-pointed star in the original stimulus configuration by van Lier et al., 2009) really formed the boundary for the afterimage by varying the size of the outer contour boundary. The sizes of the outer contour were scaled relative to the size of the inducing stimulus. We measured the perceived location of the afterimage boundary relatively to the location of the contour to test whether the afterimage boundary coincided with the drawn contour.

Model simulations

Figure 10 shows simulation results when the outer contour sizes were scaled in 85, 100, and 115% relative to the size of the inducing stimulus (additional simulations were run with 90, 95, 105, and 110% sizes, but the model behavior is the same). No inner contour was drawn. Figure 10 shows the signals from the opponent color, the boundary signal, and the filling-in model stages for various sizes of the drawn contour. The key model prediction is that any color after-responses located within the interior of the drawn contour are trapped by the contour. The strength of the perceived color varies slightly across the sizes because different amounts of color signals are trapped for the different sizes of the perceived surface, but these effects are small in the current simulation. As for the previous model simulations, color after-responses outside of the drawn contour spread into the background and effectively disappear. Most importantly, the model predicts both inward and outward spreading of the color in all the contour size conditions. That is, the perceived afterimage always appears to fill entirely and exclusively the shape of the drawn contour. We tested this prediction with two related experiments.

Experiment 3a

Methods

Participants

Another twenty-one students received course credit for participating in Experiment 3a. They all reported normal or corrected-to-normal visual acuity and passed the color vision test. However, one participant reported not perceiving any afterimages during the practice session and therefore did not participate in the main experiment (20 participants for the main experiment).

Stimuli

We used the same apparatus as in the previous experiments. While maintaining the general aspects of the stimuli as in the previous experiments, we used only the outer contour in varying the sizes in Experiment 3a. Seven different sizes of the outer contours were scaled relative to the size of the inducing stimulus such that the contours
were 85, 90, 95, 100, 105, 110, or 115% of the size of the inducing stimulus.

**Design and procedure**

Figure 11 schematizes the phases of a single trial. An inducing stimulus lasted for 1000 ms, followed by the contour phase in which an outer contour in one of the seven sizes was presented for 800 ms. A mask was then presented for 1000 ms and the participant’s task was to answer questions about any afterimage that was seen just before the mask appeared. In the response phase, participants were asked two successive questions. The first question concerned the location of any seen afterimage boundary relative to the drawn contour boundary. Participants reported whether they saw the afterimage

Figure 10. The model simulation for Experiments 3a and 3b (The outer contour boundary section) depicts the model responses just before the offset of the drawn contour (1800 ms). The three contour size scales (85, 100, 115%) shown here illustrate the model’s behavior with variations to the outer contour size. (a) The opponent-color stage shows color after-responses from the inducing stimulus and the drawn contour. (b) The boundary signal stage shows activity corresponding to drawn contour. The color after-responses are too weak to produce strong boundaries. (c) The filling-in stage shows that the afterimage color spreads all across the surface within the boundary.
removing the perception of an afterimage color) and this figure plots the proportion of no color responses for each contour size condition (16 trials per participant). We counterbalanced and randomized the assignment of the red and cyan colors at the outer boundary contour (presented only if the answer to the first question indicated an afterimage was seen), they reported the afterimage color by choosing either red or green. There were 16 trials for each contour size condition (16 × 7 = 112 trials in total per participant). We counterbalanced and randomized the assignment of the red and cyan colors at the points of the inducing stimuli and the shapes of the contour.

Results

First, we calculated the proportion of the expected color response (i.e., the total responses minus the no color responses and unexpected color responses), as defined relative to the perceived colors reported by van Lier et al. (2009). Consistent with the previous experiments in this study, an average of 85% of responses corresponded to the expected color, showing that the afterimage color is predominately derived from the color complement of the inducer shape that is subsequently outlined by the drawn contour.

Figure 12 shows that the proportion of the expected color response was significantly affected by the size of the outer boundary contour ($F(6, 114) = 6.207, p < 0.001$). This figure plots the proportion of no color responses (reporting no perception of an afterimage color) and unexpected color responses (e.g., reporting green when the contour shape was expected to trigger a red afterimage). Participants were less likely to perceive the expected afterimage color as the size difference between the inducer and the contour increased (up to 17% of the responses in the 85 and 115% scale conditions). These results imply that close proximity between the inducer and the contour enhanced the afterimage perception. It is also noteworthy that the pattern for unexpected color responses is different from that of the no color responses. The unexpected color responses increased only with the bigger contours but not with the smaller contours.

The model simulations do not necessarily predict either of these findings, but the findings are not inconsistent with the model’s general behavior. Increasing or decreasing the size of the outer contour means that different amounts of color after-responses from the points are captured within the interior of the contour. With smaller contours, the proportion of the interior that receives color after-response signals is smaller compared to the 100% case. Likewise, a larger contour has an interior that covers a larger area without color after-response signals (or with complimentary color signals), and this increase in area may dilute the afterimage. These effects suggest that the model should produce weaker color signals at the filling-in stage when the contour is different from 100%. The unbalanced effect of size on the unexpected color reports might reflect the regions of color after-responses that fall within the surface defined by the drawn contour. The after-responses for the unexpected color were excluded from the surface for the sizes of 100% or less, but they partially fall inside the surface when the drawn contour is bigger than 100%. Therefore, although most of the percepts followed the color expected by the contour, there were opportunities for the unexpected color to affect the percept when the contour was bigger than 100%.

The second analysis focused on the in/out judgment. The model predicts that the size of the drawn contour should not influence these judgments because the afterimage color should always spread up to the contour boundary. We calculated the percentage of “out” responses among the trials where participants reported the expected color response. Figure 13 shows that there was a decrease of “out” responses as the size of the contour increased ($F(6, 114) = 65.018, p < 0.001$). In other words, when the contour was smaller than the inducing stimulus, participants were more likely to observe the afterimage color extending outside of the contour. As the contour size increased, the afterimage color was more often perceived inside of the drawn contour and was hardly ever seen to extend outside in the 115% scale condition. These results show that, contrary to the model prediction, the afterimage boundary was not defined by the contour boundary. Rather, given that the “out” responses showed a proportional decrease with the increasing relative size of the contour to the inducing stimulus, the in/out judgment seems to have relied on the...
relative location between the inducer and the contour boundaries. These results suggest that the afterimage boundary was seen at the location where the boundary from the inducing stimulus had been formed rather than where the contour was drawn.

**Experiment 3b**

In Experiment 3a, we varied the outer contour size relative to one fixed size of the inducing stimulus. One shortcoming of this stimulus configuration was that the size of the contour was consistently related to a global coordinate such that the absolute contour sizes could be measured relative to the size of the monitor screen. Therefore, the participants could potentially use the size difference between the contours and the monitor in judging the location of the afterimage boundary, thereby biasing the responses to be “out” when the contour appeared small, for example. Although we think this kind of bias is unlikely to be related to our findings, in Experiment 3b, we varied the size of the inducing stimulus together with the size of the contour to rule out the possible use of the absolute size of the contour for the in/out judgment.

**Methods**

**Participants**

Another twenty students with normal or corrected-to-normal visual acuity and normal color vision participated in Experiment 3b in return for course credit.

**Stimuli**

The apparatus and stimuli were the same as in Experiment 3a except for the sizes of the inducing stimulus and the contour. The inducing stimulus was scaled in three different sizes, to have a visual angle of 11.77°, 13.03°, and 14.28° at its widest. Based on the results in Experiment 3a, we chose five size scales for the outer contour that effectively covered the response proportion range (90%, 95%, 100%, 105%, and 110%) and varied the contour sizes accordingly relative to each inducer size (Table 1). This stimulus set allowed us to use the same absolute size of a contour to be bigger than the inducer in one condition and smaller in other condition (compare the (1,5) vs. (3,1) cells in Table 1) and, therefore, reduced the potential use of the absolute size of the contour for judging the location of the afterimage boundary.

**Design and procedure**

The experimental procedure was the same as in Experiment 3a. There were 24 trials for each contour size condition (24 × 5 = 120 trials in total per participant). The size of the inducing stimulus was counterbalanced together with the assignment of colors at the points of the inducing stimulus and the contour shapes.

**Results**

All the results in Experiment 3b were consistent with the results in Experiment 3a. An average of 94% of the reported afterimage colors matched the expected color suggested by the contour shape. We again found a significant effect of the size of the contour that showed a bidirectional decrease of the expected color response with an increasing size difference between the inducing stimulus and the
contour \((F(4, 76) = 2.741, p < 0.05)\). In addition, as shown in Figure 13, the “out” responses among the expected color responses proportionally decreased as the contour scale changed from smaller to bigger than the inducing stimulus \((F(4, 76) = 78.786, p < 0.001)\).

The results of Experiments 3a and 3b are in direct conflict with the predictions of the model, which hypothesized that the contour drawn at the offset of the inducing stimulus forms the boundary for the afterimage. By spatially separating the contour from the location of the inducing stimulus boundary, the experimental data suggest that the afterimage edge was perceived at the location of the inducing stimulus boundary, thereby implying that the inducing stimulus formed the boundary for the afterimage rather than the drawn contour. These results generally agree with the results in Experiment 2 in that the contour did not interact with the afterimage when drawn far from the location of the inducing stimulus boundary. We further found an effect of the spatial proximity between the locations of the inducing stimulus and outer contour boundaries in enhancing the perception of the afterimage in Experiments 3a and 3b.

Confusing the issue even further, one might think that if the inducing stimulus boundary forms the afterimage boundary, then the edge between the gray area and the colored points should also have generated a boundary and thereby prevented a color percept in the middle. However, the inward color spreading was robust except for when the inner contour was drawn close to the location of the gray area boundary (in Experiments 1 and 2). Likewise, if the color after-responses from the inducing stimulus were strong enough to contain the color filling-in process, then one would expect the afterimage to include the color points that were not surrounded by a drawn contour. We did not specifically ask the observers about these points, but the absence of an afterimage at this location is a key part of the observations in the van Lier afterimage. These results suggest that more complicated processing is involved in the van Lier afterimage than the simple contour–afterimage interactions that were described by Francis (2010).

General discussion

We conducted new model simulations and psychophysical experiments to investigate hypothesized mechanisms involved in the van Lier afterimage (van Lier et al., 2009). Francis (2010) showed that his model explained how a new contour appearing at the location of the inducing stimulus forms a boundary that traps afterimage color spreading. To further test the model hypotheses, the effects of inner and outer contours were explored. The findings suggest that the model predictions hold when the contour spatially coincides with the boundary location of the inducing stimulus. However, the hypothesized mechanisms appear to be invalid when the drawn contour and the inducing stimulus edges are separated in space.

The experimental data are a challenge to the model’s explanation in that they go against key components of the model. Diffusive filling-in and the role of boundaries to block such spreading are central components of the BCS/FCS theory. It is difficult to imagine how a change in parameters that retained these key properties might somehow be able to match the empirical data.

One possibility is that the lack of correspondence between the reported model simulations and the empirical data is due to shortcomings in the simulations rather than fundamental shortcomings of the model. It is true that the current simulations do not include many features and calculations that play an important role in other investigations of the theory. Indeed, the current simulations are most like those used in the study of Grossberg and Todorovic (1988) to investigate properties of brightness perception. The current simulations do not include model mechanisms important for perceptual grouping, figure–ground distinctions, texture segmentation, and 3-D perception (e.g., Grossberg & Hong, 2006, Grossberg & Howe, 2003; Grossberg & Yazdanbakhsh, 2005). It may be that including these other mechanisms would allow the model to explain the new empirical findings. Indeed, the van Lier inducing stimulus and the drawn contours used here can generate several different percepts that vary in perceived depth order and figure–ground relationships of different stimulus parts. At the moment, however, we have not been able to identify how these additional model properties would offer an account of the empirical findings.

Of course, it is possible that the model is fundamentally wrong. Perhaps, the visual system does not perform a spreading of color signals and/or boundaries do not block such spreading. In a similar way, maybe the model hypothesis that colored surfaces are represented with an isomorphic representation in the visual system is invalid (e.g., Blakeslee, Pasieka, & McCourt, 2005). Our experimental findings can be used as ammunition for opponents to this kind of model, but we are reluctant to switch sides so quickly. The arguments for an isomorphic representation of surfaces and for the role of boundaries in defining such surfaces are, in our view, quite convincing (Grossberg, 1983; Todorovic, 1987).

An in-between stance might be that the basic ideas of filling-in and boundary blocking are correct, but that the mechanistic details in the simulations/model are wrong. For example, the current simulations of the filling-in process assume that color and brightness signals spread through isotropic diffusion in all directions. Our empirical work suggests that afterimage color signals do not fill up regions defined by larger outline contours, which suggests that there may be anisotropic rules that govern how the color signals spread. Indeed, some variations of diffusive filling-in have suggested anisotropic mechanisms (e.g.,
Arrington, 1996), although it is not clear whether these mechanisms will be able to provide an account of our empirical findings. The direction of the diffusion process seems to be an important topic that filling-in theories need to elaborate on. Other studies have found that spreading of surface information dominantly occurs in an inward direction for a prompt filling-in of brightness of an object (Paradiso & Nakayama, 1991) and for a steady-state filling-in of color on stabilized images (Hamburger et al., 2006). The data in all of these studies are complex, but they suggest that color spreading may not be an isomorphic process.

One of the computational benefits of the interaction between boundaries and diffusive filling-in is that it performs two key activities at once. The filling-in process simultaneously identifies different surfaces (distinct sets of closed contours) and computes the color and brightness percept for each surface. One possible interpretation of our finding is that these two processes are separate. That is, there may be a “selection” stage where different surfaces are identified according to the closed boundaries, but that this selection stage is different from the computed color and brightness percept.

At the moment, our data raise more challenges than guidance. We do not have a clear indication of how to best modify existing models or to develop alternative models that might explain the properties of the van Lier afterimages. We do find it very promising that this type of afterimage is able to rigorously test a complex model of images. We do not have a clear indication of how to best elaborate on. Other studies have found that spreading of color and brightness percept.

**Appendix A**

**Simulations**

The simulations were similar to previous simulations of the model (Francis, 2010; Francis & Ericson, 2004; Francis & Rothmayer, 2003).

**Stimuli**

All stimuli were generated as RGB pixel images that were based on the colors used by van Lier et al. (2009). For the inducing stimulus, red was RGB = (186, 129, 131), cyan was RGB = (107, 186, 180), and gray was (188, 188, 188). The outline stimulus was a dark gray line, RGB = (53, 53, 53), two-pixel thick on a white background, RGB = (255, 255, 255). All images were drawn on an image plane of 200 by 200 pixels. The basic shapes were identical to those used by van Lier et al. (2009), with differences as described in the text.

**Model input**

At each pixel of the model, the RGB values were converted into opponent-color channels with the following formula for a white–black channel:

\[
WB_{ij} = \frac{R(i,j) + G(i,j) + B(i,j)}{3(127)} - 1, \tag{A1}
\]

where the value 127 corresponds to neutral gray. Positive values of \(WB_{ij}\) indicate bright signals (white) and negative values indicate dark signals (black). Similar equations converted the RGB values into a red–green opponent-color channel:

\[
RG_{ij} = \frac{R(i,j) - G(i,j)}{2(127)}, \tag{A2}
\]

and a blue–yellow opponent-color channel:

\[
BY_{ij} = \frac{B(i,j) - (R(i,j) + G(i,j))}{2(127)}. \tag{A3}
\]

**Opponent colors**

Each color-opponent signal feeds into a habituating gate of a color gated dipole. The equations were the same for each pair of opponent colors. The equation for the white habituating gate, \(g_{ij}\), of the white color pathway at pixel \((i, j)\) was

\[
\frac{dg_{ij}}{dt} = [A - B g_{ij} - C g_{ij}(\lfloor WB_{ij}\rfloor + J)] D. \tag{A4}
\]

The term \(A - B g_{ij}\) allows the gate to increase to the value \(A/B\). The last term describes how the habituating gate is depleted by a tonic signal \(J\) and by the white input signal \([WB_{ij}]^+\). The notation \([\ ]^+\) indicates that any values below zero are set to zero, so black signals will not contribute to the white pathway at this stage of the gated dipole. Parameter \(D\) controls the overall rate of change. The black opponent pathway was identical except that \([WB_{ij}]^+\) was changed to \([-WB_{ij}]^+\) so that only black signals would pass through the gate. The initial values of the gate that correspond to an equilibrium value of the gates with no outside input are

\[
g_{ij}(0) = G_{ij}(0) = \frac{A}{B + CJ}, \tag{A5}
\]

where \(g_{ij}\) denotes the white gate and \(G_{ij}\) denotes the black gate. The parameters were set as \(A = 100, B = 0.9, C = 1, D = 0.05, \) and \(J = 5\).
The opponent output of the white color gated dipole was calculated by multiplying the total input into the white channel by the habituating gate and subtracting the same value computed for the black input. This difference was thresholded and the white output, \( w_{ij} \), was computed as

\[
w_{ij} = \left[ (\text{WB}_{ij}^+ + J) g_{ij} - (\text{-WB}_{ij}^+ + J) G_{ij}^+ \right], \tag{A6}
\]

where \( \text{WB}_{ij} \) is the response from a horizontal edge detector, \( \text{RB}_{ij} \) is the response from a vertical edge detector, and \( G_{ij} \) is the response from a horizontal edge detector. The output for a vertically tuned orientation gated dipole followed the equation:

\[
w_{ij} = E[(y_{ij} + J) g_{ij} - (Y_{ij} + J) G_{ij}], \tag{A10}
\]

with \( E = 4 \) scaling the overall output response. Here, \( xi \) refers to the output of the orientation gated dipole for a vertically tuned cell, \( y_{ij} \) is the response from a vertical edge detector, and \( Y_{ij} \) is the response from a horizontal edge detector. The differential equations for the color and orientation habituating gate were solved simultaneously since the outputs from the color gated dipoles feed into the orientation detectors and the output from the orientation detectors feed into the habituative gates for the orientation gated dipole. The equations were solved with Euler’s method with a step size of 0.01 time units.

### Boundary grouping

Signals in the BCS were grouped by bipoles that receive excitation from cells with the same orientation and inhibition from cells with the orthogonal orientation. Once again, these mechanisms play almost no role in the current simulations (because the drawn contours form closed contours on their own). These responses were then summed:

\[
y_{ij} = v_{ij}^\text{WB} + v_{ij}^\text{RG} + v_{ij}^\text{BY}. \tag{A8}
\]

A similar value, \( Y_{ij} \), was computed for the horizontally tuned edges.

### Opponent edges

For consistency with other simulations (e.g., Francis & Rothmayer, 2003), the orientation signals also feed into a gated dipole circuit, although the dynamics of this circuit play almost no role in the current simulations. The equations for a BCS oriented gated dipole had the same form as those used for the color gated dipoles. The parameter values for the oriented gated dipoles are \( A = 10, B = 5, C = 1, D = 0.0075, \) and \( J = 25 \). The equation for the habituating gate for the vertically tuned cell is

\[
\frac{dg_{ij}}{dt} = [A - B g_{ij} - C g_{ij} (y_{ij} + J)] D. \tag{A9}
\]
where \( x_{ij} \) and \( X_{ij} \) refer to the output of the orientation gated dipole for vertically and horizontally tuned cells, respectively. The number of cells a bipole cell combines in each direction is \( M = 16 \). A bipole cell has positive activity as long as the two intermediate terms are greater than zero or if the bottom-up edge detection information at the bipole location and one of the intermediate terms are non-zero. If two of the three inputs have a positive value, then the activity of the vertical bipole cell at pixel \((i, j)\) is

\[
B_{ij} = \left[ \frac{\text{Up}_{ij} + \text{Down}_{ij}}{M} - H \right]^+ , \tag{A13}
\]

where \( H = 0.05 \) is a threshold. If at least two of the three inputs are not positive, the value \( B_{ij} \) is set equal to zero.

The equations for the horizontally tuned bipole cell are defined similarly. The horizontal bipole cell receives excitation from other horizontally tuned cells within its reach and inhibition from vertically tuned cells within its reach. Raizada and Grossberg (2001, 2003) describe how these sorts of calculations can be computed among laminar circuits of the visual cortex. The bipole cell activities, \( B_{ij} \), are plotted as the boundary signals in Figures 3, 7, and 10.

### Filling-in

Filling-in of color information used the method described by Francis and Rothmayer (2003) but now included separate stages for white–black, red–green, and blue–yellow. The regions that are fully connected by bipole boundary signals spread color signals across the entire region to compute an opponent-color average. For example, in the white–black filling-in stage, each pixel in the region \( S_{ij}^{WB} \) was set to be the average of the difference of opponent-color inputs \( w_{ij} - b_{ij} \) across the region. A similar calculation was made separately for the red–green and blue–yellow filling-in stages.

### Displaying model color representations

The simulated percept of color is the pattern of activity across the color filling-in stages. To display these patterns in Figures 3, 4, 7, and 10, the opponent-color activities were converted to RGB values using the following equations:

\[
G(i, j) = \frac{127(3S_{ij}^{WB} - 3S_{ij}^{RG} - 2S_{ij}^{BY})}{3S_{\text{max}}} , \tag{A14}
\]

where \( S_{\text{max}} \) is the maximum value across all filling-in colors for the entire simulation, and 127 corresponds to neutral gray. Likewise,

\[
R(i, j) = \frac{127(2S_{ij}^{RG})}{S_{\text{max}}} + G(i, j) , \tag{A15}
\]

and

\[
B(i, j) = \frac{127(2S_{ij}^{BY})}{S_{\text{max}}} + \frac{R(i, j) - G(i, j)}{2}. \tag{A16}
\]

Finally, a value of 127 was added to each RGB value. These calculations invert the transformation from RGB to opponent colors in Equations A1–A3, with a rescaling of the opponent-color signals relative to the maximum activity at the filling-in stages.

The same kind of transformation was used for displaying the activities of the opponent-color stages in Figures 3, 4, 7, and 10.

### Acknowledgments

Commercial relationships: none.

Corresponding author: Jihyun Kim.

Email: kim510@purdue.edu.

Address: Department of Psychological Sciences, Purdue University, 703 Third Street, West Lafayette, IN 47906, USA.

### References


