BRIEF REPORTS

Modeling filling-in of afterimages

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Van Lier, Vergeer, and Anstis (2009) reported that color information in a visual afterimage could spread across regions that were not colored in the inducing stimulus. The perceived color and shape of the afterimage could be manipulated by drawn contours that apparently trap the spread of afterimage color signals. They further hypothesized that the observed effects indicated a common mechanism for afterimage color filling-in and real-color filling-in phenomena. New simulations of the existing boundary contour system/feature contour system model of visual perception (Grossberg & Mingolla, 1985a, 1985b) demonstrate the connection between these phenomena.

Van Lier and Vergeer (2008) took first prize in the 2008 Best Visual Illusion of the Year contest by demonstrating an effect in which afterimage colors spread across regions that were not colored in the inducing image. An experiment measuring the effect was recently published by van Lier, Vergeer, and Anstis (2009). The effect is extremely robust and can be experienced with the images in the stimulus column of Figures 1A and 1B. The inducing stimulus is the eight-pointed star whose points alternate spatially between red and cyan. The middle of the star is an achromatic gray color.

Fixation of the inducing stimulus for about 1 sec can lead to an interesting afterimage that depends on the properties of the viewing surface. An eye movement from the inducing image to the middle of the first four-pointed outline star produces an afterimage percept of a faintly cyanish star. Significantly, the cyan color is not restricted to the star's points, but spreads across the region that was an achromatic gray in the inducing stimulus. The afterimage percept changes dramatically with an eye movement to the second four-pointed outline star. Now, a reddish afterimage color spreads within the confines of the drawn contour.

Van Lier et al. (2009) concluded that cortical color filling-in processes were responsible for the spread of afterimage colors and that the drawn contours of the four-pointed stars triggered and constrained the filling-in process. These ideas have long been an integral part of a theory of visual perception proposed by Grossberg and Mingolla (1985a, 1985b), and new simulations described here demonstrate that this theory is able to explain the findings of van Lier et al.

Model Description and Simulations

Grossberg and Mingolla (1985a, 1985b) proposed that the visual system includes two complementary processing

streams of visual information, as is schematized in Figure 2. A boundary contour system (BCS) processes boundary or edge information, whereas a feature contour system (FCS) uses information from the BCS to control spreading of surface properties such as color and brightness. The distribution of activity across a filling-in stage corresponds to the visual percept. Filling-in effects such as neon-color spreading (Redies & Spillmann, 1981) were integral in the development of the theory, and the theory has subsequently been used to explain other filling-in effects, such as the watercolor illusion (Pinna & Grossberg, 2005).

Over the years, the model has become extremely complex, primarily through development of perceptual grouping effects in the BCS (e.g., Bhatt, Carpenter, & Grossberg, 2007) and interactions between BCS and FCS representations that are involved in depth perception (e.g., Cao & Grossberg, 2005). Fortunately, this complexity is not necessary to explain the findings of van Lier et al. (2009). A core idea of the model is that representations of colors spread in all directions at the filling-in stage until blocked by boundary signals. Boundary signals that form closed connected contours can trap the spreading colors to create a surface of relatively uniform color. A side effect of this process is that color contrasts that are too weak to form boundaries may spread beyond their physical location and that boundaries created by illusory contours can sometimes trap spreading color signals.

These spreading and trapping effects play a significant role in some types of afterimages. Francis and Rothmayer (2003) analyzed the model's dynamic behavior to explain and predict properties of afterimages where achromatic color signals from one stimulus were influenced by boundary signals from another stimulus. The spreading of colors throughout the filling-in process played an integral role in explaining why an afterimage percept was seen in some

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Figure 1. A model simulation of the van Lier, Vergeer, and Anstis (2009) afterimage effects. (A) The model responses for the sequence of stimuli used in the original study. Color filling-in for the model matches reported human percepts. (B) A model prediction when the second four-pointed star includes an interior box. The model predicts that the box should block the filling-in of red color signals and should not trap the cyan color that had spread over the region during the presentation of the first four-pointed star. See the text for details of the model stages.

conditions but not in others (Francis & Rothmayer, 2003), why the perceived shape of the afterimage percept was determined by the boundary signals (Francis & Schoonveld, 2005), and how color could spread across a gap (Francis & Ericson, 2004). As is shown below, these very same mechanisms can account for the percepts reported by van Lier et al. (2009).

Model simulations create neural after-responses with a gated dipole circuit that uses synaptic habituation and competition (Grossberg, 1972). A gated dipole contains two pathways that compete as signals pass from lower to

higher levels. A signal passing through one pathway inhibits a signal passing through the competing pathway, and the signals undergo a relatively slow synaptic habituation prior to the competition. At the offset of stimulation, the stimulated channel remains habituated, and this produces a reduction in cross-channel inhibition from the stimulated channel to the unstimulated channel. This reduction in inhibition leads to a rebound of activity in the unstimulated pathway. After-responses in the FCS stream are similar to common explanations of color after-responses, where, for example, the offset of a red stimulus produces

Figure 2. A schematic of the main components of the boundary contour system (BCS)/feature contour system (FCS) theory. The input image feeds into a retinotopic representation of red/green, blue/yellow, and black/white opponent circuits. These opponent circuits can produce complementary after-responses. The color information then feeds into edge detection in the BCS, which detects oriented boundaries and includes an opponent circuit that creates orthogonal after-responses. The oriented signals are grouped together, and these groupings of boundaries contain the spread of color information in the filling-in stage of the FCS.

greenish after-responses. However, it is important to note that these neural after-responses do not always give rise to a perceptual experience. Perceptual awareness occurs only when these after-responses induce a pattern of activity across the filling-in stage. The influence of the color after-responses on the filling-in stage depends on the spatial layout of the boundary signals.

As is schematized in Figure 2, the model also includes a gated dipole circuit for orthogonal boundary contours. The boundary after-responses play an integral role in explaining a variety of afterimage percepts (Francis & Rothmayer, 2003), the role of attention on afterimages (Suzuki & Grabowecy, 2003; Wede & Francis, 2007), regulation of visual persistence (Francis, Grossberg, & Mingolla, 1994), and perceptual switches in binocular rivalry (Grossberg, Yazdanbakhsh, Cao, & Swaminathan, 2008). However, these after-responses play only a minor role in the present simulations. Likewise, the boundary grouping stage schematized in Figure 2 does not play a major role in the present simulations, because all of the physical contours form connected boundaries.

Figure 1A shows simulation results that demonstrate how the model produces afterimage percepts in agreement with the findings of van Lier et al. (2009). In the simulations, we used the images from van Lier and Vergeer (2008). The first column shows the stimulus presented at each indicated time. As in van Lier et al., the inducing stimulus was presented for 1 sec, and then the two viewing patterns were shown in succession for 0.5 sec each, so each row shows the model's behavior just before the current stimulus disappears. Details of the simulations can be found in Francis and Rothmayer (2003) and Francis and Asem (2009).

The opponent colors stage of the model represents retinotopic coding of color information and produces color after-responses. During the presentation of the inducing star image, this stage codes a pattern of information very similar to the inducing stimulus. The colors are slightly muted, because of the habituation that occurs in the gated dipole circuit. At 1.5 sec, the opponent color stage represents color after-responses because of the offset of the inducing star. The black outline of the four-pointed star is also represented at this stage. A similar pattern is produced at the presentation of the second four-pointed star, although there is also a weak color after-response generated by the previous four-pointed star. The slight offset of the four-pointed stars relative to the location of the colored points is due to a mistake in cropping the images by hand, whereby the stimuli were not precisely centered. The mistake was retained, because it demonstrates that the model's explanation is robust enough to deal with a small eye movement from a human observer.

The opponent boundaries stage of the model detects spatial edges across the opponent colors stage. For the inducing image, the boundaries outline each color against the background and the gray interior. During the presentation of the four-pointed stars, the boundaries correspond to the black lines of the four-pointed stars. At the offset of the inducing stimulus, the color after-responses produce only very weak boundaries that are below a threshold value. Most notably, the changes in after-response color signals between the gray interior and the colored points of the inducer are too weak to produce boundaries.

Finally, the filling-in column shows the model's predicted perceptual experience. The signals from the opponent boundaries stage define separate regions within which the opponent colors spread. When the inducing stimulus is present, this results in a veridical percept of the eight-pointed star, because every color is kept separate from the other colors by the strong boundaries. At the offset of the inducing stimulus and the onset of the first four-pointed star, the model percept is of a uniformly colored cyanish four-pointed star. The cyan colors at the opponent colors stage spread across the surface until blocked by the boundaries generated by the four-pointed star. In contrast, the reddish colors at the opponent stage are blocked by the same contours from spreading into the interior of the star and instead blend into the background. The same phenomenon occurs for the second four-pointed star, but now it is

the reddish colors that spread within the boundaries of the four-pointed star.

Conclusions

The model simulations provide a good explanation of the afterimage properties reported by van Lier et al. (2009). Significantly, the explanation requires no additional model mechanisms (there are some minor changes in parameters relative to other simulations). All of the new observations can be explained with mechanisms that were previously used to account for entirely different data sets.

In a second experiment, van Lier et al. (2009) found evidence that spatial color contrast mechanisms also influenced the color filling-in process. Although the BCS/FCS theory includes spatial color contrast mechanisms (Grossberg & Mingolla, 1985a, 1985b), in order to speed up the computations, the present simulations do not include these processes. Accounting for these effects would be a natural direction for further analysis.

Van Lier et al. (2009) suggested that modifications of their stimuli can be used to explore the underlying mechanisms of filling-in. This is certainly true of the model simulations. Figure 1B shows a model prediction in which the second four-pointed star includes a closed contour in the center. The model predicts that this additional contour should block the flow of red color from the points and keep the interior of the square an achromatic gray. Van Lier and Vergeer (2008) reported a somewhat similar experience with very different stimuli.

Perhaps more significant, at time = 1.5 sec in this simulation, the region corresponding to the middle of the box was filled in with a cyan color (as in Figure 1A, second row). The model simulation suggests that this cyan color does not get trapped by the new boundary contours of the box but is instead replaced by new color signals. A failure to find this prediction in experimental data would require modification of the model mechanisms and thereby push the model toward a better representation of human perception.

AUTHOR NOTE

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