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# The watercolor effect: Quantitative evidence for luminance-dependent mechanisms of long-range color assimilation 

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#### Abstract

When a dark chromatic contour delineating a figure is flanked on the inside by a brighter chromatic contour, the brighter color will spread into the entire enclosed area. This is known as the watercolor effect (WCE). Here we quantified the effect of color spreading using both color-matching and hue-cancellation tasks. Over a wide range of stimulus chromaticities, there was a reliable shift in color appearance that closely followed the direction of the inducing contour. When the contours were equated in luminance, the WCE was still present, but weak. The magnitude of the color spreading increased with increases in luminance contrast between the two contours. Additionally, as the luminance contrast between the contours increased, the chromaticity of the induced color more closely resembled that of the inside contour. The results support the hypothesis that the WCE is mediated by luminance-dependent mechanisms of long-range color assimilation.


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Keywords: Watercolor effect; Assimilation; Color spreading; Long-range interactions

## 1. Introduction

The watercolor effect (WCE) is a phenomenon of long-range color assimilation arising from thin chromatic contours. For example, when a dark purple, closed contour flanks a light-orange, closed contour on the inside, the orange color will spread evenly across the entire enclosed surface area resembling the faint coloration of a watercolor painting (Pinna, Brelstaff, \& Spillmann, 2001; Pinna, Werner, \& Spillmann, 2003). This is an example of color filling-in and is illustrated by Fig. 1. Pinna et al. (2003) studied the figural strength of the WCE by pitting it against the classical Gestalt fac-

[^0]tors such as proximity, good continuation, closure, and parallelism. The results clearly demonstrate that the WCE overrules each of the predicted figure-ground organizations thus suggesting that it is a dominant factor.

It is not yet clear whether a purely chromatic WCE can be obtained or whether it is dependent on luminance contrast. Pinna et al. (2001) reported a weak WCE at nominal isoluminance with color leaching out to either side; thus high luminance contrast was deemed essential for a strong spreading effect. With a dark outer contour, the WCE is stronger and is limited to only one side. This may be related to a more general characteristic of chromatic processing and the influence of luminance contrast borders. Previous work has demonstrated that a luminance edge enhances color discrimination (Boynton, Hayhoe, \& MacLeod, 1977; Cole, Stromeyer, \&


Fig. 1. Stimulus patterns. Stimulus 1 (top panel): The left square is the test side, and the right side is the standard. Stimulus 2 (bottom panel): Observers adjusted the middle and outermost lateral columns simultaneously to cancel the WCE.

Kronauer, 1990), whereas without it, there is a tendency for colors to "bleed" together (Eskew \& Boynton, 1987). These results suggest a threshold mechanism by which a luminance edge enclosing a chromatic patch should enhance sensitivity to color on the inside while containing color spreading to the outside (Gowdy, Stromeyer, \& Kronauer, 1999; Montag, 1997). A possible neurophysiological correlate of this effect was reported by Zhou, Friedman, and von der Heydt (2000) who demonstrated that approximately half of the neurons in early cortical areas are selective in coding the polarity of color contrast (e.g., a neuron may respond to a red-gray border, but not a gray-red border).

To evaluate the possible role of luminance-dependent color mechanisms, it was necessary to develop methods using individually-determined isoluminant stimuli with results quantified in chromaticity space. To that end, Experiment 1 evaluates color-matching and hue-cancellation methods using two different spatial configurations. In Experiment 2, we measured the WCE over a range of stimulus chromaticities with a hue-cancellation
method. Then, we tested the hypothesis that long-range color spreading is dependent on luminance differences between the inner and outer contours (Experiment 3). The results of this experiment show that the WCE occurs, but only weakly, with pure chromatic contrast. These results are consistent with the idea that the WCE is mediated by luminance-dependent color mechanisms.

## 2. General methods

### 2.1. Observers

All observers were normal trichromats based upon testing with the Neitz anomaloscope, the HRR pseudoisochromatic plates and the Farnsworth F-2 plate. Consent forms were obtained following the Tenets of Helsinki, and with the approval of the Office of Human Research Protection of the University of California, Davis.

### 2.2. Apparatus

Stimuli were presented on a 33 cm CRT video monitor (Sony Multiscan G220) driven by a Macintosh G4 computer ( 733 MHz using a 10-bit video card, ATI Radeon 7500). Experiments were performed in a dark room. The experimental software was written in MATLAB (http://www.mathworks.com/) using the Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997). The monitor was calibrated using a Minolta colorimeter (CS 100 Chroma Meter) and procedures set out in Brainard, Pelli, and Robson (2002). Observer position was stabilized by a chin rest so that the screen was viewed binocularly at a distance of 217 cm .

### 2.3. Stimuli

Two stimulus patterns were used to produce a WCE. Stimulus 1 (Fig. 1, top) was composed of two $3.4^{\circ}$ outer squares surrounding small inner squares of $1.7^{\circ}$. The squares were defined by sinusoidally shaped contours ( 2.35 cycles per degree, peak-to-trough amplitude $=$ $0.13^{\circ}$ ). A central vertical black bar extending from the top to the bottom of the monitor $\left(6.79 \times 0.51^{\circ}\right)$ served to separate the two squares. Stimulus 2 (Fig. 1, bottom) consisted of 5 vertical columns that were each $5.35 \times 1.12^{\circ}$ and connected by a contour on the top and bottom. The contours were sinusoidally shaped at 1.5 cycles per degree $\left(\right.$ amplitude $\left.=0.13^{\circ}\right)$.

### 2.4. Procedure

Observers adapted to the screen for 2 min before starting the experiment. They were asked to adjust the

Table 1
CIE $a^{*} b^{*}, x y$, and $u^{\prime} v^{\prime}$ chromaticity coordinates for the stimuli used in all of the experiments

| Color | $a^{*}$ | $b^{*}$ | $x$ | $y$ | $u^{\prime}$ | $v^{\prime}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Background "White" | 0 | 0 | 0.3 | 0.33 | 0.1887 | 0.4670 |
| Blue | 27.5602 | -37.3207 | 0.2659 | 0.2425 | 0.1978 | 0.4058 |
| Green | -39.8219 | -0.1781 | 0.2419 | 0.3568 | 0.1423 | 0.4724 |
| Orange | 24.3662 | 66.3867 | 0.447 | 0.423 | 0.2490 | 0.5301 |
| Purple | 55.3343 | -61.1416 | 0.261 | 0.206 | 0.2109 | 0.3745 |
| Red | 33.6096 | 0.1307 | 0.35 | 0.3068 | 0.2341 | 0.4616 |
| Yellow | -31.3569 | 70.9118 | 0.3713 | 0.5133 | 0.1765 | 0.5489 |

chromaticity of the test patch to the specific criterion (matching or cancellation as described below) using a game-pad that was programmed to permit variation of the stimulus along $a^{*}$ and $b^{*}$ chromaticity coordinates in CIE $L^{*} a^{*} b^{*}$ space. The chromaticity coordinates for these and other stimuli used in subsequent experiments are presented in Table 1. Three step sizes were provided ( $0.5,0.1$ and 0.02 ) in CIE $a^{*} b^{*}$ color space to optimize the match, and observers could toggle between these step sizes as required. To reduce adaptation to the stimulus patterns, the stimuli were presented for 2 s intervals, with an inter-stimulus interval of 2 s consisting of a large blank field identical to the white background. This sequence was repeated continuously until the observer made a satisfactory setting and clicked a mouse to end the trial and start the next one. Each observer made 10 settings in each condition tested. Two methods were used to measure the WCE, matching and huecancellation.

### 2.5. Matching task

Observers adjusted the chromaticity of the test area until it perceptually matched the WCE reference stimulus. For Stimulus 1, the adjustable area was the inner square with the inner 'inducing' contour removed (see Fig. 1 top panel, left side). The position of the adjustable and WCE squares was reversed after each trial. For Stimulus 2, the adjustable areas were the two outermost columns. The chromaticity of the test areas was adjusted simultaneously. When the matching task was used with Stimulus 2, the inner 'inducing' color contours in the two outermost columns were removed to effectively eliminate the WCE in these regions. These areas were adjusted to match the WCE in the central column (see Fig. 1 bottom panel).

Note that in the matching task observers did not adjust the luminance of the matching color (it was fixed at the same luminance as the background). In a control experiment, we allowed observers to adjust luminance as well as chromaticity and the results showed that effectively no luminance adjustment was required to make a perceptual match (there was less than $0.1 \%$ difference between the mean matching luminance for three observers and the luminance of the background). Therefore in the
matching tasks used here, only the chromaticity of the adjustable square was changed by the observer.

### 2.6. Hue-cancellation

Observers adjusted the chromaticity of the test areas until they appeared achromatic. Both stimulus arrangements were tested with the hue-cancellation technique. For Stimulus 1 (Fig. 1, upper panel), the test areas were the inner squares. The inner squares were presented with both the orange and purple contours (as in Fig. 1, upper panel, right stimulus) and the chromaticity was adjusted in the two squares simultaneously. For Stimulus 2, the test areas were the inside of the middle and outermost columns (Fig. 1, bottom panel) and the chromaticity of these three areas was adjusted simultaneously.

## 3. Experiment 1: Quantifying the WCE

This experiment served to quantify the WCE in CIE $u^{\prime} v^{\prime}$ color space using two stimulus patterns with a purple outer and an orange inner contour as used by Pinna et al. (2001).

Two different procedures were used to measure the effect. In Experiment 1A, we used a color-matching task; in Experiment 1B we used a hue-cancellation task.

### 3.1. Experiment 1A: Color matching

Three experienced psychophysical observers (2 male, 1 female, age range 20-40) perceptually matched the WCE perceived in both Stimulus 1 and 2. In addition, a naïve observer (female, age 20) made matches in the Stimulus 1 condition. The stimulus patterns were composed of orange $\left(55 \mathrm{~cd} / \mathrm{m}^{2}\right)$ and purple ( $20 \mathrm{~cd} / \mathrm{m}^{2}$ ) contours on a white ( $80 \mathrm{~cd} / \mathrm{m}^{2}$ ) background, which was identical to the center of the stimuli.

Fig. 2 shows each observer's mean setting plotted in CIE $u^{\prime} v^{\prime}$ coordinates. If the induced color (WCE) were in the same color direction as the inner orange contour, it would follow the black solid line so-labeled. The chromaticity of the induced color was similar in direction to the inner contour but not quite the same. We calculated the difference angle by subtracting the angle for the
induced-color vector from that of the orange contour vector. Appendix A lists the difference angle for each observer. The matching color deviates from the orangecontour vector by a mean difference of $11.2^{\circ}$ for Stimulus 1, and $13.66^{\circ}$ for Stimulus 2. This result shows that the color induced by the WCE is shifted slightly toward yellow rather than following exactly the color of the inducing contour itself. The chromaticity of the induced color is much less saturated than the inner inducing


Fig. 2. The mean vector for all observers required for matching the WCE is shown by the arrow originating at the white background in CIE $u^{\prime} v^{\prime}$ color space. Symbols denote color shifts for different observers: subject $1(\diamond)$, subject $2(\bigcirc)$, subject $3(\square)$ and subject 4 $(\Delta)$. Solid lines show the direction of the orange (inner) and purple (outer) contour chromaticities. Dotted lines represent cone-opponent axes, $S /(L+M)$ and $L /(L+M)$. Values from the cone excitation space are displayed near the ends of the dotted lines and at the intersection. Error bars are $\pm 1$ SEM. The top panel shows the results using Stimulus 1 , and the bottom panel shows the results using Stimulus 2 .
color, with a mean shift of $5.61 \%$ (Stimulus 1) and $0.92 \%$ (Stimulus 2) of the inducing contour color vector length measured in CIE $u^{\prime} v^{\prime}$ color space. Data presented in Appendix A show the variability across observers.

### 3.2. Experiment 1B: Hue-cancellation

Three of the observers who participated in Experiment 1 A also served in this experiment. The hue-cancellation method was used to cancel the WCE in the test areas of both Stimulus 1 and 2. The results are shown in Fig. 3. Each observer's mean setting is shown in CIE $u^{\prime} v^{\prime}$ coordinates. The mean color direction of the settings is effectively in the opposite direction to the


Fig. 3. Results of the cancellation experiment for Stimulus 1 (top panel) and Stimulus 2 (bottom panel). Details as in Fig. 2.
inducing orange contour as was to be expected if one assumes that the subject must add an approximately complementary color to cancel the induction. The mean perceptual shift was $4.12 \%$ (Stimulus 1) and $3.21 \%$ (Stimulus 2). The data followed the opposite color direction of the inducing contour with a mean difference of $9.06^{\circ}$ for Stimulus 1 and $8.58^{\circ}$ for Stimulus 2.

### 3.3. Experiment 1: Discussion

We used both matching and hue-cancellation techniques to measure the WCE produced by two different stimulus patterns. When viewing the stimuli initially, the observers described the WCE as salient and strong. However, the measured shift in appearance is surprisingly small, albeit reliable. We will discuss this point further in Section 6.

The settings followed the direction of the orange contour in the matching experiments, and opposite this direction for the hue-cancellation task. The shift in color appearance therefore, depends mainly on the chromaticity of the brighter inner contour. The data were not, however, perfectly aligned with the vector of the inducing contour. The possible reasons for this deviation from perfect assimilation are discussed in relation to Experiment 3.

The mean effect sizes were different for the two patterns, with a larger effect size produced by Stimulus 1 for color-matching. One possible reason is that to perform the color-matching task, we modified the second pattern by removing the inner contours from the two outermost columns to use them as the test areas. Although this did not appear to change the inner region noticeably, it may have produced small shifts in color appearance confounding the results with a purplish appearance. This might explain the difference found with the second pattern in color-matching. The hue-cancellation stimuli did not require removal of any contours so this problem was not encountered. We are therefore more confident that we are measuring the WCE directly using hue-cancellation. In addition, observers generally found the hue-cancellation task to be easier than matching and were able to perform this task relatively quickly. For this reason, all subsequent experiments in this paper used the hue-cancellation method.

## 4. Experiment 2: Variation of contour chromaticity

The orange/purple contour combination has been used because these chromaticities are similar to those considered optimal for producing the effect, based on previous experiments (Pinna et al., 2001; Pinna et al., 2003). In this experiment we compare the strength of the effect using a variety of colors to determine if the strength of the WCE is dependent on color direction.

The same observers from Experiment 1B participated in this experiment. Three different contour color pairs were used, the original orange/purple combination, and two color pairs that were on cardinal axes of an MBDKL color space (Derrington, Krauskopf, \& Lennie, 1984; MacLeod \& Boynton, 1979), the $S$-varying and $(L-M)$-varying axes. (Note that because the color contours had different luminance values, the stimuli did not isolate mechanisms tuned to those axes.) We refer to these color pairs as blue/yellow and red/green. Each color pair was tested with the contours in original and reversed positions, so that each color within a pair acted as an inducing color for one condition. Three color pairs were used with each chromaticity serving as the inside (inducing) contour in one stimulus and the outside contour in another, producing six stimulus conditions.

The luminance of the inner and outer contours was the same as before. The background had a luminance of $80 \mathrm{~cd} / \mathrm{m}^{2}$. The chromaticities of the contours are presented in Table 1. The order of the presentation was randomized for each observer.

Fig. 4 shows the results for the 6 conditions, with each observer's mean setting plotted in CIE $u^{\prime} v^{\prime}$ color space. In each case, the color vector specifying the change in the stimulus required to cancel the WCE is effectively opposite the direction of the vector representing the coordinates of the inducing contour. Note that the coordinates of the inducing color were not equidistant from the white point and therefore the size of the effects across inducing contours are more easily compared using the shift size (see Fig. 5). For color spreading in five of the six color directions (orange, purple, green, red and blue), the results were similar; the mean shift ranged from $3.21 \%$ to $4.38 \%$. For all observers, the yellow spreading was the weakest effect with a mean shift of $1.81 \%$. Moreover, the angle difference diverged slightly from $3.18^{\circ}$ to $9.11^{\circ}$, and the yellow spreading deviated more from the inducing contour with an angle difference of $9.11^{\circ}$.

## 5. Experiment 3: Contour luminance contrast

In this experiment, our aim was to determine the role of luminance contrast on the strength of watercolor spreading. Bressan (1995) found for neon color spreading that the effect increased with increasing luminance contrast. Based on the previous experiments we predicted that increasing the luminance contrast between the two contours would also enhance the WCE. In addition, we asked whether the watercolor always spreads from the smaller decrement (relative to the background) to the enclosed surface or whether there is also spreading if the luminance of the orange contour falls below that of the luminance of the purple contour.


Fig. 4. Watercolor effect quantified by color-cancellation. Each panel shows a different inner/outer contour chromaticity. Solid lines indicate the direction of the inducing contour. Details as in Fig. 2. Values for $L /(L+M)$ and $S /(L+M)$ are the same as in Fig. 3.

For each observer, we first determined the luminance match for the two contours to be tested using a variation of the minimally-distinct border technique of Wagner and Boynton (1972). Orange and purple contours, with the same width and luminance as in Experiment 1A, were presented on a white background of $80 \mathrm{~cd} / \mathrm{m}^{2}$
(see Table 1 for coordinates). The luminance of the purple contour was fixed at $20 \mathrm{~cd} / \mathrm{m}^{2}$ and observers adjusted the luminance of the orange contour until the border between the contours was minimally distinct. Each observer completed 10 trials. The contours had the same spatial characteristics as Stimulus 2. Then the same


Fig. 5. Mean shift sizes (top panel) and angle difference (bottom panel) obtained for each of the inducing contour colors used in Experiment 2. Errors bars show $\pm 1$ SEM.
observers participated in the main experiment and the luminance values of the orange contours were: 21.6, 17.6, and $16.9 \mathrm{~cd} / \mathrm{m}^{2}$ for observer 1,2 and 3 respectively. Two out of the three observers had participated in the previous experiments. The additional observer was a 40 -year old color-normal male who was an experienced observer.

In the main experiment, Stimulus 2 was used together with the hue-cancellation task to determine the strength of the WCE as a function of the luminance contrast. The contours were orange and purple with the same white background (see Table 1 for coordinates). Five luminance conditions were used for the orange contour, two above and two below the individual isoluminant level. The highest and lowest luminances were 57 and $5 \mathrm{~cd} / \mathrm{m}^{2}$, respectively; they were the same for all three observers. The other two conditions were chosen according to the mean between the isoluminance level and each of the two extremes.

The results are presented in Fig. 6. The main result is that the color coordinates of the WCE are similar to the color vector of the orange contour when the luminance ratio between the orange and purple contours is high (as in Experiment 1B). With a decreasing ratio (luminance contrast) the color coordinates become increasingly dis-
similar, especially after the luminance of the orange contour falls below the luminance of the purple contour (except for one observer). Figs. 6 and 7 also show that there was a difference in vector shift for the different luminance ratios: when the luminance ratio increased between the two contours, the vector shift increased also (see Appendix A and Fig. 7 top panel for the vector shift).

We conclude that the WCE is most salient when the luminance of the inner contour is higher than that of the outer contour. When the two contours are isoluminant or the contrast between them is reversed, the WCE continues to be seen, but is weak. This is shown in Fig. 7 (bottom panel) which plots the difference angle between the orange contour and the color coordinates of the WCE for each observer. As the luminance of the orange contour decreases, the curve rises steeply reflecting the increase in difference angle.

## 6. General discussion

We have quantified the WCE using classical psychophysical methods based upon color-matching and huecancellation. These results demonstrate that the color


Fig. 6. Watercolor effect quantified by color-cancellation for five luminance contrasts between the inner (orange) and outer (purple, $20 \mathrm{~cd} / \mathrm{m}^{2}$ ) contours. Details as in Fig. 2. Values for $L /(L+M)$ and $S /(L+M)$ are the same as in Fig. 3.
spreading in the WCE is much less saturated than and slightly shifted in chromaticity from the inner inducing contour. This was observed across six chromatic combinations of stimuli. When observers were allowed to vary both luminance and chromaticity to make a perceptual match to the WCE, no adjustments in luminance were required. We therefore conclude that the WCE is predominantly a chromatic effect. Yet, the strength of the

WCE depends strongly on the luminance relations between the borders. It is possible that this is because at isoluminance, both contours interact and contribute to color spreading, but when there is a luminance border, the spread of color is more confined to that produced by the brighter inner contour. The rotation in color space of the induced color relative to the inner contour may be related to the relative excitation of $S$ vs. $L-M$


Fig. 7. Watercolor effect quantified by color-cancellation and expressed by vector length (top panel) and difference angle (bottom panel) between the color coordinates plotted as a function of the ratio (contrast) between the luminances of the inner (orange) and outer (purple) contours. Individual observers as in Fig. 2; mean shown by bold line. Values on the right of the axis of abscissas represent results using the same stimulus as in Experiment 1B. Values toward the left are associated with lower luminance of the orange contour.
excitation. Notice from Figs. 6 and 7 that the rotation of the WCE is directly related to the intensity of the orange and hence the excitation of an $L /(L+M)$ mechanism.

These experiments demonstrated that a strong WCE is obtained only when the luminance contrast between orange and purple contours is high. These results are consistent with those found by DeWeert and Spillmann (1995) showing that a stimulus decrement relative to the background is required to obtain color assimilation.

When the contrast in our experiment was decreased, the WCE was weak.

### 6.1. Perceptually salient, but small measured chromaticity shifts

When first viewing the WCE, the color spreading usually appears perceptually strong and compelling. However, the measured shift in chromaticity is surprisingly small (range of $0.92-5.61 \%$ of the inducing contour). The WCE is often described as a color "veil" that appears separate from the background surface. It is possible that when performing the matching or cancellation task, this veil is partially discounted because it appears to be like fog (Hagedorn \& D'Zmura, 2000) or transparency (Khang \& Zaidi, 2002) resulting in the appearance of the 'underlying' surface becoming more salient. This is in agreement with informal discussions with observers after completing the tasks.

In color appearance experiments, the measured effect size can depend on the instructions to the observer (Arend \& Reeves, 1986; Bauml, 1999; Bloj \& Hurbert, 2002; Delahunt \& Brainard, 2004). For example, a distinction can be made between (i) appearance matches, for which the observer is instructed to judge the appearance of the light reaching the eye, and (ii) surface matches, where the observer is instructed to judge the appearance of a surface. In the current experiments, we used neutral instructions that did not emphasize any judgment strategy. It is conceivable that larger color shifts would have been observed for the matching results if subjects had been instructed to judge the surface appearance.

Recent experiments on color induction using thin contours have shown that the shift in color appearance for a pattern composed of concentric circles alternating between two chromaticities is larger than with a uniform background (Monnier \& Shevell, 2003, 2004). Large shifts in color appearance were obtained from patterned chromatic stimuli. This difference in strength compared to the WCE could be explained by the size of the induced color area. In our experiment, color spreading occurs over a large uniform background. In comparison, the chromatic induction area used by Monnier and Shevell $(2003,2004)$ was only 9 arc min. Further experiments are necessary to clarify whether mechanisms involved are the same or not.

### 6.2. Luminance-dependent color processing and higher-order mechanisms

The experiments presented here clearly demonstrated that the WCE depends critically on luminance contrast information, even though the perceptual effect is largely chromatic. It is well known that color and luminance information is multiplexed early in the visual system (De

Valois \& De Valois, 1975). The consequences of this early multiplexing are not thoroughly understood. However, many perceptual phenomena involve mechanisms that are selectively tuned for luminance-chromatic conjunctions (e.g., Hardy \& De Valois, 2002; McCollough, 1965; Takeuchi, DeValois, \& Hardy, 2003). The WCE appears to be yet another phenomenon that depends upon the operation of mechanisms tuned selectively to particular luminance-chromatic conjunctions.

### 6.3. Neural mechanisms that may contribute to the WCE

The WCE is characterized by a spread of color from the inner contour onto the enclosed surface area, suggesting a global effect from sparse (local) stimulation. The question is how the color diffuses out of the boundary to fill the adjacent area.

A classical explanation for filling-in is that this process requires a neuronal mechanism that detects the contour and generalizes it beyond the confines of the immediate stimulus. Long-range interaction via horizontal cortical axons have been assumed to provide for the large-scale convergence necessary to perceive the WCE in extended areas (Gilbert, 1996; Gilbert, Das, Ito, Kapadia, \& Westheimer, 1996; Spillmann \& Werner, 1996). In addition, Roe and Ts'o (1999) reported that the activity of color and orientation-specific neurons in V1 was correlated with the activity of nonoriented V2-cells whose receptive fields did not overlap. This correlation might play a role in the explanation of color filling-in from inducing contours as it would provide a neurophysiological basis for the transformation of local signals to global signals.

An analogy exists between the WCE and stabilized images (or the Troxler effect). In both effects, we perceive something different than the physical background depending on the surrounding area. Using the stimulus pattern described by Krauskopf (1963) with a red disk and a green ring, von der Heydt, Friedman, and Zhou (2003) found that while recording from neurons in V1 of the trained monkey, the neuronal response did not change although the behavioral response signaled a perceptual change from red to green (filling-in). This result is consistent with a "symbolic" color representation, assuming that the signals from the edge-detectors are integrated at a higher level to produce a response that represents the color of the surface.

An analogy may exist between the WCE and the spreading of neural activity in the Craik-O'Brien-Cornsweet effect (COCE). Both illusory effects are obtained with the change of the contour luminance profiles. Because the double contour of the WCE could be blurred by the visual system and processed like a sawtooth to yield long-range color spreading, it is unclear whether
the WCE is a variant of the COCE or not. Further experiments are necessary to delineate a distinction between the two effects.

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## Appendix A. Individual WCE effect sizes for all observers and all experiments

| Condition | Observers | $\begin{array}{l}\text { Angle } \\ \text { difference }\end{array}$ | $\begin{array}{l}\text { Shift size } \\ \text { vector/ } \\ \text { inducing } \\ \text { contour }\end{array}$ |
| :--- | :--- | ---: | :--- |
|  |  |  |  |
| vector |  |  |  |$]$

## Appendix A (coninued)

| Condition | Observers | Angle difference ${ }^{\circ}$ ) | Shift size vector/ inducing contour vector |
| :---: | :---: | :---: | :---: |
| Blue spreading | Observer 1 | 24.66 | 0.0258 |
|  | Observer 2 | 4.43 | 0.0420 |
|  | Observer 3 | 6.24 | 0.0323 |
|  | Mean | 4.66 | 0.0339 |
| Yellow spreading | Observer 1 | 18.33 | 0.0181 |
|  | Observer 2 | 2.92 | 0.0109 |
|  | Observer 3 | 6.09 | 0.0266 |
|  | Mean | 9.11 | 0.0181 |
| Green spreading | Observer 1 | 6.18 | 0.0534 |
|  | Observer 2 | 1.79 | 0.0214 |
|  | Observer 3 | 17.51 | 0.0363 |
|  | Mean | 3.18 | 0.0321 |
| Red spreading | Observer 1 | 6.05 | 0.0328 |
|  | Observer 2 | 4.37 | 0.0503 |
|  | Observer 3 | 12.43 | 0.0481 |
|  | Mean | 7.61 | 0.0438 |
|  |  |  |  |
| Luminance ratio 0.25:1 (orange/purple) | Observer 1 | 45.02 | 0.0137 |
|  | Observer 2 | 29.09 | 0.0010 |
|  | Observer 3 | 41.05 | 0.0241 |
|  | Mean | 38.39 | 0.0126 |
| Luminance ratio 0.615-0.645:1 | Observer 1 | 37.72 | 0.0137 |
|  | Observer 2 | 20.86 | 0.0092 |
|  | Observer 3 | 38.10 | 0.0298 |
|  | Mean | 32.23 | 0.0172 |
| Luminance ratio 1:1 | Observer 1 | 22.43 | 0.0172 |
|  | Observer 2 | 21.09 | 0.0126 |
|  | Observer 3 | $29.51$ | 0.0344 |
|  | Mean | 24.34 | 0.0218 |
| Luminance ratio 1.81-2.18:1 | Observer 1 | 0.73 | 0.0195 |
|  | Observer 2 | 21.39 | 0.0263 |
|  | Observer 3 | 24.21 | 0.0378 |
|  | Mean | 15.44 | 0.0275 |
| Luminance ratio 2.85:1 | Observer 1 | 0.07 | 0.0229 |
|  | Observer 2 | 21.46 | 0.0332 |
|  | Observer 3 | 19.07 | 0.0470 |
|  | Mean | 13.53 | 0.0344 |

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