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# Illusory spreading of watercolor 

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#### Abstract

The watercolor effect（WCE）is a phenomenon of long－range color assimilation occurring when a dark chromatic contour delineating a figure is flanked on the inside by a brighter chromatic contour；the brighter color spreads into the entire enclosed area．Here，we determined the optimal chromatic parameters and the cone signals supporting the WCE．To that end，we quantified the effect of color assimilation using hue cancellation as a function of hue，colorimetric purity，and cone modulation of inducing contours．When the inner and outer contours had chromaticities that were in opposite directions in color space，a stronger WCE was obtained as compared with other color directions．Additionally，equal colorimetric purity between the outer and inner contours was necessary to obtain a large effect compared with conditions in which the contours differed in colorimetric purity．However， there was no further increase in the magnitude of the effect when the colorimetric purity increased beyond a value corresponding to an equal vector length between the inner and outer contours．Finally，L－M－cone－modulated WCE was perceptually stronger than S－cone－modulated WCE for our conditions．This last result demonstrates that both L－M－cone and S－cone pathways are important for watercolor spreading．Our data suggest that the WCE depends critically upon the particular spatiochromatic arrangement in the display，with the relative chromatic contrast between the inducing contours being particularly important．


Keywords：watercolor effect，color assimilation，hue，colorimetric purity，cone－modulated pattern

## Introduction

Color appearance is determined not only by the local light signals from each object but also by the relative light signals across the visual scene（Knoblauch \＆Shevell，2004）．The change in color appearance caused by the nearby light is called chromatic induction．There are two different types of induction：chromatic contrast and chromatic assimilation． Chromatic contrast is the shift in appearance of the test field away from the chromaticity of the inducing color．Chromatic assimilation is the opposite phenomenon，in which color appearance of the test field shifts toward the chromaticity of the inducing color．Chromatic contrast has been studied extensively，whereas assimilation has received less atten－ tion．Assimilation may，however，be the more common phe－ nomenon in natural scenes（De Valois \＆De Valois，1988）．

This study concerns long－range color assimilation in the phenomenon known as the watercolor effect（WCE），dem－ onstrated first by Pinna（1987；see also Pinna，Brelstaff，\＆ Spillmann，2001）．An example is shown in Figure 1．In this pattern，when a dark chromatic contour（e．g．，purple）sur－
rounds a lighter chromatic contour（e．g．，orange），the enclosed area appears tinted with the color of the inner contour（the orange color），resembling the faint coloration of a water－ color painting（aquarelle）．

Assimilation effects are most often observed in displays con－ taining high spatial frequency patterns（Helson，1963；Smith， Jin，\＆Pokorny，2001）；however，other factors such as the width of the inducing contour（Fach \＆Sharpe，1986）or the luminance relationships within the stimulus can also influ－ ence whether assimilation is observed（Cao \＆Shevell，2005； De Weert \＆Spillmann，1995；Hamburger，2005；Helson， 1963；Wook Hong \＆Shevell，2004）．As with other assimila－ tion patterns，the strength of the WCE decreases with increas－ ing edge width（Pinna et al．，2001）and induced area（Devinck， Delahunt，Hardy，Spillmann，\＆Werner，2006）or increases with the luminance contrast between the two double contours （Devinck，Delahunt，Hardy，Spillmann，\＆Werner，2005）． These variables are also known to influence the strength of color contrast tested under a wide range of conditions （Krauskopf，Zaidi，\＆Mandler，1986；Ware \＆Cowan，1982； Zaidi，Yoshimi，Flanigan，\＆Canova，1992）．Factors such as the chromatic composition of the inducing field have been


Figure 1. Example of WCE pattern used in this study.
systematically explored in color contrast (Barnes, Wei, \& Shevell, 1999; Jameson \& Hurvich, 1959; Kinney, 1962; Tiplitz-Blackwell \& Buchsbaum, 1988; Valberg, 1974) but not in color assimilation.

The WCE can be induced using double-contour patterns such as the one shown in Figure 1. The extent to which the strength of the effect depends on the choice of contour chromaticity is not, however, clear. To that end, we performed three experiments. The goal of the first experiment was to test directly the strength of the WCE as a function of the hue contrast between the inner and outer contours. In the second experiment, we estimated the strength of the WCE as a function of the colorimetric purity of the inner and outer contours. Finally, in the third experiment, we determined how the strength of the WCE differs using S-cone- and L-M-cone-modulated patterns.

## General methods

## Observers

Three observers participated in the study. Their ages ranged from 26 to 35 years, and they had normal or corrected-tonormal visual acuity. All had normal color vision as evaluated by a Neitz anomaloscope, the HRR pseudoisochromatic plates, and the Farnsworth F-2 plates. Two observers were naive regarding the purpose of the experiment, and the third observer was one of the authors. Each observer signed a consent form prior to participating in the study. The experimental procedure was approved by the Office of Human Research Protection of the University of California, Davis.

## Apparatus

Stimuli were presented on a $33-\mathrm{cm}$ CRT video monitor (Sony Multiscan G220) controlled by a Macintosh G4 computer with an ATI Radeon 7500 video card. The video board provided a 10 -bit resolution for each of the $\mathrm{R}, \mathrm{G}$, and B guns. The experimental design was written in Matlab 5.2.1 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). The screen was viewed with both eyes at a distance of 217 cm . A chin rest maintained the observer's head position. All experiments were performed in a dark room.

## Stimuli

Stimuli consisted of five vertical columns arranged in rectangular patterns that were each $5.35 \times 1.12 \mathrm{deg}$ and connected by a contour on the top and bottom. These rectangular patterns were surrounded by double contours to produce the WCE, as illustrated in Figure 1. The contours were sinusoidally shaped (along the contour) or undulating at 1.5 cycles/deg (amplitude $=$ 0.13 deg ) with a width of 1.7 deg . The test areas were the inside of the middle and outermost columns, and the chromaticity of these three areas was adjusted simultaneously. The outer contour luminance should be lower than the inner contour to obtain orange color spreading, and the luminance contrast between the two contours needs to be high to obtain the WCE (Devinck et al., 2005). Thus, the inner contour had a luminance of $60 \mathrm{~cd} / \mathrm{m}^{2}$, and the outer contour had a luminance of $20 \mathrm{~cd} / \mathrm{m}^{2}$; these contours were presented on a white background (CIE $u^{\prime}=0.189 ; v^{\prime}=0.467$ ) of $80 \mathrm{~cd} / \mathrm{m}^{2}$.

## Procedure

Observers were first dark adapted for 3 min and were then asked to null the chromaticity of the test areas until they appeared achromatic (hue-cancellation technique). To this end, observers used a game pad to vary the enclosed area along $a^{*}$ and $b^{*}$ chromaticity coordinates in CIE $L^{*} a^{*} b^{*}$ space. 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 the step sizes as required by pressing a separate button. To reduce adaptation to the stimulus patterns, we presented the stimuli for 2-s intervals, with an interstimulus 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. A training session preceded the experiments; thereafter, each observer made 10 settings in each condition tested.

## Experiment 1: Influence of contour hue on the WCE

## Additional methods

In the first experiment, 16 different contour color pairs were used. The inner contour had fixed chromaticity coordinates


Figure 2. Chromaticity coordinates used in the first experiment are plotted in a CIE $u^{\prime} v^{\prime}$ diagram. Coordinates of the outer contour are represented by open symbols. The arrow shows the coordinates of the orange (inner) contour chromaticity. Dotted lines represent cone-opponent axes, $S /(L+M)$ and $L /(L+M)$. The intersection of these two lines coincides with the chromaticity coordinates of the white background.
$\left(u^{\prime}=0.224 ; v^{\prime}=0.502\right)$ and appeared orange, whereas 16 different colors were used for the outer contour. The chromaticity coordinates of the outer contour were equated in vector length in a CIE $u^{\prime} v^{\prime}$ color space relative to the background (0.05), and all points were separated by an angle difference of 22.5 deg. The chromaticity coordinates of the outer contour are represented in Figure 2. Note that for one condition, the inner and outer coordinates were identical (angle difference $=0 \mathrm{deg}$ ).

## Results

Hue-cancellation results from Experiment 1 were plotted in CIE $u^{\prime} v^{\prime}$ color space, and two indices were used to evaluate the chromaticity shift for each observer in both experiments. We calculated the difference angle by subtracting the angle for the induced color vector (mean of the huecancellation settings) from that of the orange contour vector in the opposite direction. If induced color has the same apparent hue as the inducing contour, then the chromaticity necessary to cancel it will be in the opposite direction in chromaticity space, and the difference angle will be zero. However, if the induced color has a hue that is different from that of the inducing contour, the difference angle will be greater than or less than zero. We also determined the magnitude of the assimilation effect by dividing the magnitude of the chromaticity shift vector (the difference between the background chromaticity and the hue-cancellation setting chromaticity) by the inducing contour vector magnitude.


Figure 3. Chromaticity shift of the WCE plotted as a function of the color direction between the chromaticity coordinates of the inner and outer contours. Symbols denote color shifts for different observers: Subject $1(\diamond)$, Subject $2(\square)$, and Subject $3(\Delta)$. The mean is shown by the bold line and the symbol $\bullet$. Error bars show $\pm 1$ SEM. Note that the results for the color direction at 0 and 360 deg are the same because the outer contour has the same chromaticity coordinates as the inner contour.

In the first experiment, mean chromaticity settings were close to the opposite color direction from the orange inducing contour with a mean difference angle ranging from 0.68 to 22.2 deg. Although the direction of the WCE was consistent across different chromaticities of the outer inducing contour, the magnitude of the effect varied systematically with the color direction of this contour (Figure 3), where color direction is the relative direction in $u^{\prime} v^{\prime}$ chromaticity space between the inner inducing contour and the outer contour. A color direction of 0 deg indicates no chromatic contrast, and a color direction of 180 deg indicates a chromaticity in the opposite direction in color space. The relation between color direction of the inducing contour and magnitude of the WCE was similar across observers. The chromaticity shift increased when the color direction increased between the two contours until the color direction was equal to 180 deg; thereafter, the shift in chromaticity decreased. Chromaticity shifts were maximum (4.47-5.09\%) for hue cancellation when the two color contours were in opposite direction (180 deg); shifts of
only $0.56-1.08 \%$ were required when the two contours had the same color ( 0 deg ). Results were relatively symmetric on both sides of the 180 deg color direction. For example, when the color of the outer contour differs by 90 deg from that of the inner contour, the shift in chromaticity was around $2.62 \%$ of the inducing contour; when the color direction differed by 270 deg, the mean of the chromaticity shift was $2.81 \%$. We conclude that the WCE is most salient when the chromatic contrast between the two contours is maximal.

## Experiment 2: Influence of colorimetric purity on the WCE

## Additional methods

In this experiment, the chromaticity of the inner contour was held constant $\left(u^{\prime}=0.224 ; v^{\prime}=0.502\right)$, whereas the outer contour varied in colorimetric purity. We used eight chromaticity coordinates corresponding to eight colorimetric purity levels. The method was as follows: we calculated a line connecting the chromaticity coordinates of the outer contour, the background, and the inner contour $(y=1.003 x+0.278)$. The chromaticity coordinates of the outer contour were chosen along the line with colorimetric purity vector lengths from 0 to 0.07 separated by equal steps of 0.01 . Note that a vector length of 0 corresponded to the chromaticity coordinates of the background and that a vector length of 0.05 was used in the first experiment. The coordinates of the outer contour are presented in Figure 4 (top panel). In a separate condition, we varied the colorimetric purity of the inner contour. In this case, the outer contour did not change $\left(u^{\prime}=0.153 ; v^{\prime}=0.432\right.$; corresponding to the chromaticity used in the first experiment and a colorimetric purity vector length of 0.05 ), and the chromaticity coordinates of the inner contour were chosen in the same fashion as in the previous condition for the outer contour. The coordinates are shown in Figure 4 (bottom panel).

## Results

Hue-cancellation results demonstrated color assimilation from the inner contour, with difference angles ranging from 8.75 to 21.51 deg. Figure 5 (top panel) shows that there was a difference in the magnitude of the chromaticity shift as a function of colorimetric purity. The chromaticity shift increased when the colorimetric purity of the outer contour increased up to a vector length of 0.05 . Thus, the chromaticity of the induced color increased with a mean ranging from 1.43-2.24\% $($ vector length $=0)$ to $3.46-4.69 \%$ (vector length $=0.05$ ). For colorimetric purities greater than a vector length of 0.05 , there was no further increase in the magnitude of the effect. A similar result is obtained when the inner contour varied in colorimetric purity and the chromaticity coordinates of the outer contour were kept constant. Figure 5 (bottom panel) indicates


Figure 4. Chromaticity coordinates used in the second experiment are displayed in CIE $u^{\prime} v^{\prime}$ color space. Top panel: Square symbols represent the seven points used to display the outer contour, and the circle indicates the chromaticity coordinates of the inner contour. Bottom panel: Square symbols represent the seven points used for the inner contour, and the circle indicates the chromatic coordinates of the outer contour.
that the chromaticity shift increased when the colorimetric purity of the inner contour increased up to a vector length of 0.05. In this case, the mean range increased from $0.27-0.90 \%$ (vector length $=0$ ) to $2.44-3.59 \%$ (vector length $=0.05$ ); thereafter, the chromaticity shift leveled off at the following ranges: $2.10-3.59 \%$ (vector length $=0.06$ ) and $2.41-3.42 \%$ (vector length $=0.07$ ). Note that the chromaticity shift is less pronounced when the colorimetric purity of the inner contour varied in comparison with the outer contour.


Figure 5. WCE quantified by color cancellation and expressed by vector length between the color coordinates plotted as a function of the colorimetric purity of the outer contour (top panel) and inner contour (bottom panel). Details are the same as in Figure 3.

## Experiment 3: Dependence of WCE on modulation of <br> cone pathways

## Additional methods

In the third experiment, the WCE was modulated along S-varying and $\mathrm{L}-\mathrm{M}$-varying cone axes. Comparing the effects of modulation along the different cardinal axes in
color space is complicated in that the scaling of the axes relative to one another will greatly affect how the results of a given color experiment are interpreted. One method that can be used to scale magnitudes in different directions in color space is to equate for chromatic discrimination thresholds along those directions. This is the method we have employed in this experiment. We scaled the coordinates of the double contour in CIE $u^{\prime} v^{\prime}$ color space using classic color discrimination data (LeGrand, 1949, 1994; MacAdam, 1942). We chose one MacAdam ellipse with a chromatic center close to the coordinates of our white background $(x, y=$ $0.305,0.323$ ) as tabulated by Wyszecki and Stiles (1982, pp. 306-310). The MacAdam ellipse was defined with the following equation:

$$
\begin{equation*}
(\mathrm{d} s)^{2}=g_{11}(\mathrm{~d} x)^{2}+2 g_{12}(\mathrm{~d} x \times \mathrm{d} y)+g_{22}(\mathrm{~d} y)^{2} \tag{1}
\end{equation*}
$$

where $\mathrm{d} x$ and $\mathrm{d} y$ are the difference of the $x$ and $y$ coordinates between the center of the ellipse and any points along the ellipse; $g_{11}, g_{12}$, and $g_{22}$ are constants for each ellipse. In the present experiment, we chose a MacAdam unit of color difference (ds) equal to 7. The relations of each constant are the following:

$$
\begin{align*}
& g_{11}=\frac{1}{a^{2}} \cos ^{2} \theta+\frac{1}{b^{2}} \sin ^{2} \theta  \tag{2a}\\
& g_{12}=\left(\frac{1}{a^{2}}-\frac{1}{b^{2}}\right) \sin \theta \cos \theta  \tag{2b}\\
& g_{22}=\frac{1}{a^{2}} \sin ^{2} \theta+\frac{1}{b^{2}} \cos ^{2} \theta \tag{2c}
\end{align*}
$$

For this constant, the values are calculated from the length of the major (a) and minor (b) semiaxes of the ellipse, and the angle $\theta$ defined the inclination of the major axis along the $x$-axis. The values $a, b$, and $\theta$ are specific to each MacAdam ellipse and may be found in Wyszecki and Stiles (1982, p. 309).
The MacAdam ellipse was defined by 30 points in CIE $x y$ color space, and these were transformed to CIE $u^{\prime} v^{\prime}$ color space. We then fitted an ellipse function to these new chromatic coordinates with the equation described above. We chose the chromatic coordinates for the inner and outer contours of the WCE along the S- and L-M-cone axes intersecting the MacAdam ellipse. We also defined two control conditions along the MacAdam ellipse. These chromatic coordinates were chosen by dividing the angle difference between the $\mathrm{S} /(\mathrm{L}+\mathrm{M})$ and $\mathrm{L} /(\mathrm{L}+\mathrm{M})$ axes by 2 . All chromaticity coordinates are displayed in Figure 6. Note that all chromaticity coordinates for inner and outer contours are in opposite directions in chromaticity space. To obtain a conemodulated pattern, we displayed the WCE with an equiluminance condition. For each observer, we determined the luminance match for the two contours with the luminance


Figure 6. Chromaticity coordinates used in the third experiment are plotted in a CIE $u^{\prime} v^{\prime}$ diagram. Here, the chromaticity coordinates used are displayed on the MacAdam ellipse. The points used to display the S-cone WCE are on the $S /(L+M)$ axis; the points used to display the $\mathrm{L}-\mathrm{M}$-cone WCE are on the $\mathrm{L} /(\mathrm{L}+\mathrm{M})$ axis. Chromaticity coordinates of the two control conditions are represented by the two solid lines. Details are the same as in Figure 2.
background to be tested using a variation of the minimally distinct border technique of Boynton and Kaiser (1968). Moreover, the luminance of the background was reduced to $55 \mathrm{~cd} / \mathrm{m}^{2}$ because the CRT video monitor did not permit the chromatic contour to be displayed at a high luminance level.

## Results

Figure 7 shows the mean chromaticity shifts due to watercolor spreading measured via hue cancellation. The mean range of difference angles for the effect was 7.92 to 30.33 deg ; the difference angle varied among observers and for each chromatic condition used. In this case, the shift size differed for different directions in color space. Thus, the chromaticity shift was higher for an L-M-cone WCE than an S-cone WCE or WCE modulated along intermediate directions in color space, even when the chromaticity coordinates of the contours were adjusted along these axes for constant chromatic discriminability. An ANOVA verified that the difference in magnitude of the WCE obtained for the L-M-modulated contours differed significantly from the S-modulated contours, $F(1,4)=12.90, p<.0229$. Moreover, the L-M-cone pattern was significantly different from the first control condition, $F(1,4)=16.27, p=.0157$, but not from the second control condition; in comparison, the S -cone pattern


Figure 7. Mean shift sizes obtained for each condition used in Experiment 3. Details are the same as in Figure 3.
did not differ significantly from the two control conditions. In this way, the S-cone-modulated pattern seems to have a similar influence on the WCE in comparison with the two intermediate directions in color space. These results suggest that the L-M-cone pathway mediates the WCE to a greater extent than the S -cone pathway under our conditions.

## Discussion

We characterized the effects of chromatic modulation along the dimensions of relative hue, colorimetric purity, and axis of modulation of the double contour on the strength and direction of chromatic assimilation in the WCE using classical psychophysical methods based on hue cancellation. The first experiment showed that the strength of the WCE depends on the relative hue differences between the borders. This experiment demonstrated that the strongest WCE is obtained when the chromaticity coordinates of the inner and outer contours were relatively far apart in color space (i.e., the chromatic contrast in the contour pair was relatively large). In the second experiment, results showed that increasing the colorimetric purity of the outer and inner contours increases the shift in chromaticity of the WCE; however, no additional gain in effect magnitude was obtained when the colorimetric purity increased beyond a value corresponding to an equal vector length between the inner and outer contours. This experiment cannot distinguish between a dependence on symmetry in the colorimetric purity of the contours or a compressive nonlinear relation between overall contrast and effect magnitude. Finally, the WCE is a contrast-dependent effect (Devinck et al., 2005), but the results of the last experiment indicated that an L-M-cone-modulated pattern is perceptually stronger for eliciting the WCE than an S-conemodulated pattern when the WCE is scaled in chromatic discriminability.

## Relation with previous color induction studies

Our results on the chromatic composition of the induction pattern in the WCE are largely consistent with earlier work on the study of color induction. The chromatic direction of the inducing area was studied by Tiplitz-Blackwell and Buchsbaum (1988) in simultaneous color contrast. They showed that as the color of the surrounding area becomes more similar to that of the induced area, chromatic induction decreases. The effects of saturation were investigated in relation to simultaneous color contrast, which, according to Kirschmann's (1890) fifth law, increase with an increase in saturation of the inducing color. However, some studies indicate that simultaneous color contrast effects increase slightly with an increase in saturation of the inducing color (Jameson \& Hurvich, 1959; Kinney, 1962), although other evidence is not consistent with these findings (Valberg, 1974). Our first two experiments show that the chromatic composition of the induction area influences chromatic assimilation in a similar fashion to previous studies of simultaneous color contrast. Some previous results indicated that contrast along the $\mathrm{L}-\mathrm{M}$-cone axis affects other induction patterns, whereas the influence of S-cone stimulation is relatively weak (Barnes et al., 1999; Singer \& D’Zmura, 1994). Consequently, we might conclude that the chromatic compositions that yield the strongest assimilation effects in the WCE share similar properties to the chromatic composition of patterns that produce strong induction effects.

## Chromatic-luminance processing

The experiments presented here demonstrate that the WCE is most pronounced when a number of intersecting constraints are satisfied in the chromatic- and luminancecontrast relations between the two contours and the background. As expected, when the chromaticity of one contour is similar to that of the other $($ Experiment 1 , color direction $=$ 0 ) or to the background (Experiment 2, vector length $=0$ ), the strength of the WCE is greatly reduced. Thus, we can conclude that chromatic contrast between the two inducing contours and between the contours and the background is important for a robust WCE. The results from Experiment 3 confirm that WCE can be obtained when the contours are equiluminant, but as our earlier study demonstrated, the magnitude of the effect decreases with decreasing luminance contrast between the contours (Devinck et al., 2005; Pinna et al., 2001). Additionally, we show here that for maximal color spreading, chromatic contrast along an $\mathrm{L}-\mathrm{M}$ axis is required between the contours. Thus, the WCE depends on a rather particular combination of both chromatic and luminance contrast between the contours and between the contours and the background. However, even under nonoptimal stimulus arrangements in the WCE display, color spreading is still perceived. It is well known that color and luminance information are multiplexed in the visual system (De Valois, 2004; De Valois \& De Valois,
1975). This pattern of results is consistent with the idea that the WCE depends on the operation of mechanisms tuned selectively to particular luminance-chromatic conjunctions.

## Relation to previous color assimilation model

Jameson and Hurvich $(1975,1989)$ suggested that chromatic contrast and assimilation depend upon the diameters of both center and surround regions of the underlying receptive fields. Indeed, when the stimulus components are smaller than the receptive field center, assimilation occurs because the inducing area close to the induced area is weighted strongly in the center of the receptive field. Moreover, when the image elements are larger, assimilation gives way to contrast because of the inhibitory surround of the receptive field. Consequently, this transition should depend on stimulus width. Previous research suggests a transition from contrast to assimilation at about 3 to 6 cycles/deg, depending on the width of the stimulus (Fach \& Sharpe, 1986; Smith et al., 2001). This model has been extended by Monnier and Shevell $(2003,2004)$ and Shevell and Monnier (2005) based on an S-cone antagonistic centersurround $(+S /-S)$ receptive field. Such neurons are not found in the retina (Dacey, 2000) but have been reported in the visual cortex (Conway, 2001; Solomon, Peirce, \& Lennie, 2004). The transition from assimilation to contrast suggested by Jameson and Hurvich $(1975,1989)$ might also occur in S-cone spatial antagonism.
The WCE appears to involve different mechanisms at a different level of processing than are needed to explain previously described color assimilation effects. Although larger color assimilation effects are seen with decreasing distance between the inner components of the inducing contours in the WCE, assimilation is still seen in relatively large patterns in which the assimilated area is much larger than would be expected from classical accounts of contrast versus assimilation (Devinck et al., 2006; Pinna et al., 2001). Consequently, classical receptive field organization does not fully explain the WCE. However, a hypothesis related to color filling-in derived from receptive field organization might be proposed. A classical explanation is that a neuronal mechanism detects the contours and generalizes it to the enclosed area by way of a long-range signal. Moreover, this hypothesis might be extended with "symbolic" color representation, assuming that the signals from edge are integrated at a higher level to produce the response for the color of the surface (von der Heydt, Friedman, \& Zhou, 2003).

The WCE presents an additional challenge to any complete model of chromatic assimilation. The strength of the apparent color spreading seen in this effect depends on a conjunction of chromatic and luminance contrast. Cortical cells sensitive to border ownership are candidates for explaining this characteristic of the WCE. These cells respond, for example, to a gray-orange border but not to an orangegray border (Zhou, Friedman, \& von der Heydt, 2000).

This asymmetry of response may lead to spreading via longrange connections to impart not only the coloration but also associated properties defining figure-ground organization (Pinna, Werner, \& Spillmann, 2003; von der Heydt \& Pierson, in press). It is interesting that many of these cells are orientation selective, perhaps explaining why the WCE is more effective with wiggly contours. Cells mediating border ownership (perhaps with opposite polarity on the opposite side of the figure) must provide a barrier so that the illusory coloration defines a surface or object on a nonfigural ground to complete the filling-in.

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