The Watercolor Illusion and Neon Color Spreading: A Unified Analysis of New Cases and Neural Mechanisms
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Abstract

Coloration and figural properties of neon color spreading and the watercolor illusion are studied using phenomenal and psychophysical observations. Coloration properties of both effects can be reduced to a common limiting condition, a nearby color transition called the "two-dots limiting case", that clarifies their perceptual similarities and dissimilarities. The results are explained by the FACADE neural model of biological vision. The model proposes how local properties of color transitions activate spatial competition among nearby perceptual boundaries, with boundaries of lower contrast edges weakened by competition more than boundaries of higher contrast edges. This asymmetry induces spreading of more color across these boundaries than conversely. The model also predicts how depth and figure-ground effects are generated in these illusions.
1. Introduction: A Current View of a Seminal Discovery of DeValois
Russell DeValois and his colleagues discovered many seminal neurobiological data that have been influential in developing concepts about how the visual cortex sees. The Thorell et al. (1984) study helped to inspire and support modeling concepts that were developed at around the same time. This important article reported data from macaque monkey which showed that "simple cells...are distinguished by relatively narrow color specificity" (p. 761). In contrast, "complex color cells...responded uniformly to many (or, in the extreme, all) equiluminant wavelength changes". The RFs of many of these cells (15/31, 48%) were composed of overlapping color-regions" (p. 762) and "these cells always responded with the same polarity to all colors tested. This was in keeping with one of the criterial features of complex cell behavior: their lack of phase specificity" (p. 764). Thorell et al. (1984) went on to conclude that these complex cells "must surely be considered color cells in the broadest sense. They clearly use color information to detect the presence of spatial patterns" (p. 768).

At around this time, Cohen and Grossberg (1984) and Grossberg and Mingolla (1985a, 1985b) were introducing their concepts that the visual cortex computes perceptual boundaries and surfaces in parallel processing streams. This conclusion was derived primarily from a perceptual analysis, so Grossberg and his colleagues searched for neurobiological evidence to confirm or deny that this actually happens. One timely piece of evidence was the Thorell et al. (1984) study, which supported the early prediction that these boundaries and surfaces are processed by the interblob and blob streams, respectively, from V1 to V4. It should be emphasized that the prediction of parallel boundary and surface streams differs in significant, indeed profound, ways from the prediction that parallel cortical streams compute orientations and colors. Within the boundary/surface conception, complex cells in V1 pool over opposite polarities and colors as part of the process of computing good boundary signals. Because of this pooling, however, the prediction was made that "all boundaries are invisible", or amodal, within the boundary stream. This conclusion followed from the fact that, because boundaries pool over opposite luminance polarities and colors, they cannot represent the difference between light and dark, or between different colors. Grossberg and his colleagues thus concluded that the property which Thorell et al. (1984) reported about "color cells in the broadest sense" was exactly what was needed to build good boundary signals. However, Grossberg and colleagues also predicted that the activities of these boundary cells were, in themselves, invisible or amodal, and therefore did not carry a visible color signal. Visible colors were predicted to be represented within the surface stream, whose interactions with the boundary stream define the regions within which visible surface lightnesses and colors are restricted. The present article shows how this insight can be used to provide a unifying explanation of recent data about neon color spreading and the waterfall illusion, two classes of phenomena which enable visible colors of the surface stream to be dissociated from figural properties that are initiated in the boundary stream.

2. Neon color spreading
Varin (1971) studied a "chromatic spreading" effect induced when four sets of concentric black circumferences are arranged in a cross-like shape and are partially composed of blue arcs that create a virtual large central blue circle (see Figure 1a). The central virtual circle appears as a ghostly transparent veil or as a chromatic translucent diffusion of bluish tint spreading among the boundaries of the blue arcs. The chromatic spreading fills the whole illusory circle induced by the terminations of the black arcs (see Bressan et al., 1997, for a review).
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Figure 1. The neon color spreading: The central virtual circle (Figure 1a) and the inset virtual diamond shape (Figure 1b) appear as a ghostly overlapping transparent veil of bluish tint spreading among the boundaries of the blue components.

The neon effect was independently reported in 1975 by van Tuijl (see also van Tuijl and de Weert, 1979), who named it “neon-like color spreading”. Van Tuijl used a lattice of horizontal and vertical black lines, where segments creating an inset virtual diamond shape had a different color (e.g., blue). The perceptual result is a delicately tinted transparent diamond-like veil above the lattice (see Figure 1b). The common geometrical property of the known cases of neon color spreading is the continuation of one line in a second line differently colored or, otherwise stated, a single continuous line varying at a certain point from one color to another. Neon color spreading manifests two basic phenomenal properties: coloration and figural effects, which are discussed below.

2.1. Coloration effects in neon color spreading. The phenomenology of coloration effect within neon color spreading points out the following properties, mostly depending on the luminance contrast between the two inducing lines. (i) The color is perceived as a diffusion of a certain quantity of pigment of the inset chromatic segments. (ii) The appearance of the spreading color (Erscheinungweise, Katz, 1911, 1930) is diaphanous and glows like a smoggy neon upon the background or (most under achromatic conditions) like a shadowy, foggy, dirty or filmy transparent veil. (iii) When the inset virtual figure is achromatic and the surrounding inducing elements chromatic, the illusory veil appears tinted not in the achromatic color of the embedded elements, as expected, but in the complementary color of the surrounding elements; for example, the achromatic components appear to spread reddish or yellowish color when the surrounding components are, respectively, green or blue (van Tuijl, 1975).

2.2. Figural effects in neon color spreading. The previous coloration qualities are strongly linked to the figural effects of neon color spreading. Phenomenally, (i) the illusory neon region has a depth stratification: it typically appears in front of the component elements; (ii) the illusory region is perceived as a transparent film; (iii) by reversing the relative contrast of inset vs. surrounding components, the depth stratification reverses as well; for example, when the surrounding elements have less contrast than the inset ones, as illustrated in Figure 2, the inset components appear as a background rather than as a foreground (Bressan, 1993b); (iv) the illusory region may assume different figural roles or may become different objects; for example, a “light”, a “veil”, a “shadow” or a “fog”; (v) neon color spreading illustrates a
“phenomenal scission” (Spaltung, Koffka, 1935; Metzger, 1954) of an elevated transparent colored veil and underneath components that appear to amodally continue without changing in color.

Figure 2. Figural effect of the neon color spreading: When the surrounding elements have less contrast than the inset ones, the inset components appear as a background rather than as a foreground.

3. Watercolor illusion
The “watercolor illusion” is a long-range spread of color (up to 45° visual angle) diffusing from a thin colored line running parallel and contiguous to a darker chromatic contour and imparting a strong figural effect across large regions (Pinna, 1987; Pinna, Brelstaff and Spillmann 2001; Pinna, Werner and Spillmann, 2003; Spillmann, Pinna and Werner, 2004, Pinna, 2005a). In Figure 3, purple undulating contours flanked by orange edges are perceived as undefined irregular curved shapes evenly colored by a light veil of orange tint spreading from the orange edges. All the chromatic combinations of the two lines produce similar effects (see Pinna, 1987; Pinna, Brelstaff and Spillmann 2001).
Figure 3. The watercolor illusion: purple undulated contours flanked by orange edges are perceived as undefined irregular curved shapes with a plain volumetric effect evenly colored by a light veil of orange tint spreading from the orange edges.

In Figure 4, different number-pointed stars are now perceived evenly colored of the same illusory faint orange as in Figure 3. The different results of Figure 3 and 4, although both figures have the same geometrical structure, depend on the inversion of the purple and orange lines: the purple/orange line arrangement of Figure 3 become the orange/purple of Figure 4. This reversion affects both the coloration and figural effects of the watercolor illusion: what in Figure 3 appears as illusory tinted and segregated as a figure, in Figure 4 appears as an empty space without a clear coloration.
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3.1. Coloration effects in the watercolor illusion. The phenomenology of the coloration effect within the watercolor illusion highlights some properties that appear analogous and some different from those of neon color spreading: (i) as in neon color spreading, the illusory color is perceived as a spreading of some quantity of tint belonging to the orange line and giving rise to a more dilute orange (yellow) coloration; (ii) the coloration does not appear transparent as in neon color spreading, but opaque and belonging to a solid impenetrable object; (iii) the coloration appears epiphanous and as a surface color (Katz, 1930); (vi) like neon color spreading, the watercolor illusion produces a complementary color when one of the two juxtaposed lines is achromatic and the other chromatic (Pinna, 2005b).

3.2. Figural effects in the watercolor illusion. Besides the coloration effect, the watercolor illusion determines a unique figural effect that competes with the classical Gestalt principles of grouping and figure-ground segregation (Wertheimer, 1923; Rubin, 1915, 1921). All else being equal, Pinna et al. (2001) and Pinna (2005a) demonstrated that the watercolor illusion determines figure-ground segregation more strongly than the Gestalt principles of proximity, good continuation, pragnanz, closure, symmetry, convexity, past experience, and similarity. It was also shown (Pinna, 2005a) that the watercolor illusion includes a new principle of figure-ground segregation, the *asymmetric luminance contrast principle*, stating that, all else being equal, given an asymmetric luminance contrast on both sides of a boundary, the region whose luminance gradient is less abrupt is perceived as a figure relative to the complementary more abrupt region, which is perceived as a background. This phenomenal and physical asymmetry.
across the boundaries makes the figural effect due to the watercolor illusion stronger than in classical figure-ground conditions, and prevents reversibility of figure-ground segregation. The asymmetric luminance contrast principle strengthens Rubin’s principle of unilateral belongingness of boundaries (Rubin, 1915): The boundaries belong only to the figure and not to the background, which appears as an empty space without a defined shape.

The main figural qualities of the watercolor illusion are: (i) the illusory figure has a univocal (poorly reversible) depth segregation similar to a rounded surface with a bulging and volumetric effect; (ii) the resulting surface appears thick, solid, opaque and dense; (iii) as shown in Figures 3 and 4, by reversing the colors of the two parallel lines, figure-ground segregation reverses as well; in these two figures, the border ownership is also reversed: the boundaries belong only to one region and not to the other; (iv) as in neon color spreading, the figural effect of the watercolor illusion may be perceived in terms of phenomenal scission but with a different mode of appearance; that is, as a figure showing a strong depth segregation and appearing as a volumetric rounded object within a three-dimensional space, while the perceived variation of color, going from the boundaries to the center of the object, may be seen as a gradient of shading, as if light were reflected onto a volumetric and rounded object, so that the variation of color appears to be the homogeneous color of the object. Object and light are the two split emergent components of the scission.

Summing up, neon color spreading differs from the watercolor illusion both in the appearance of the coloration (respectively, transparent vs. solid and impenetrable, and diaphanous vs. epiphanous) and in the figural effects (respectively, transparent vs. opaque and dense appearance, and appearance as a “light”, a “veil”, a “shadow” or a “fog” vs. rounded thick and opaque surface bulging from the background).

4. Neon color spreading and watercolor illusion: similarities and differences
Despite the specific differences, the two illusions are phenomenally similar in their strong color spreading and clear depth segregation. We suggest that, while the similarities may be attributed to the local nearby transition of colors that are common to both illusions, the differences may be attributed to the global geometrical boundary conditions that differ in the two illusions, notably, the continuation of a segment of a different color in neon color spreading and the juxtaposition of at least two lines in the watercolor illusion.

If this is true, then the differences between the two illusions can be reduced under modified geometrical conditions and, by reaching a limiting case, they can be eliminated. The questions to answer in this Section are thus: can the watercolor illusion assume coloration and figural properties similar to those of neon color spreading? Can the two illusions be reduced to a simple limiting case based on local nearby transitions of colors where coloration and figural effects are still perceived?

4.1. Coloration and figural variations of the watercolor illusion and neon color spreading.
By increasing the width of one of the two juxtaposed lines of the watercolor illusion to such an extent that the line becomes a surface, the watercolor illusion manifests different coloration and figural effects. Under these conditions, the surface may be segregated independently from the colored fringes. The resulting coloration does not assume surface color properties, but properties belonging to the background: it is perceived diaphanous like a foggy coloration diffusing everywhere in the background, or as a colored light (see Figure 5).
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Figure 5. A light blue coloration spreading from the inset square of elements appears surrounded by a red spreading. The coloration effect is not accompanied by a figural effect with a plain volumetric property, but it appears diaphanous like a foggy veil of color.

In Figure 6, the coloration effect gives to the illusion star a fuzzy luminous quality. While in Figure 5 the coloration belongs to the background, in Figure 6 it is a property belonging to the figure; however, the star does not manifest the strong surface appearance peculiar to Figures 3 and 4: its inner surface appears brighter and yellowish, foggy and smooth.

Figure 6. The illusionary coloration of the star appears fuzzy and luminous, and manifests a poor surface appearance.

A fuzzy surface coloration, but with a more volumetric figural effect, is illustrated in Figure 7. The columns bulge in depth even if they appear softly and nebulously colored.
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Figure 7. The columns bulge in the 3D space even if they appear softly and nebulously colored.

In Figure 8, the watercolored frame appears transparent, as in neon color spreading.

Figure 8. A transparent watercolored frame.
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In Figure 9, a comparison between quasi-equiluminant conditions and high contrast differences between the two juxtaposed color lines, induces different coloration and figural effects: around the quasi-equiluminant conditions, the coloration appears not as a surface color, but as an ethereal soft coloration without clear figural or background properties; around the high contrast differences, the figural effect and the surface color properties are restored.

Take together, these figures suggest that, in the watercolor illusion: (i) the modes of appearance of coloration are strongly related to boundary conditions that induce specific figural effects; (ii) by changing the boundary conditions, coloration and figural properties are seen that are analogous to those of neon color spreading; (iii) given this variety of appearances on the basis of different conditions, a simpler set of boundary conditions, or limiting case, can unify both effects using local transitions of colors, and can help to explain similarities and dissimilarities of the two illusions.
4.2. Towards a limiting case. Figure 10a shows a case of neon color spreading where purple surrounding arcs continue in orange arcs. The inset square annulus appears not to glow, as in Figure 1, but is rather perceived as a transparent orange veil. This difference in appearance of both coloration and figural effects is possibly due to the high contrast between the two colors relative to each other.

**Figure 10.** Four conditions that gradually introduce a limiting case: (i) The neon color spreading defined by the continuation of lines of different color (Figure 10a); (ii) a condition in between neon color spreading and watercolor illusion, where the orange inset arcs are reduced to short dashes (Figure 10b); (iii) a condition once again in between neon color spreading and watercolor illusion, where the purple surrounding arcs of Figure 10a are reduced to short dashes; (iv) the two-dots limiting case obtained by reducing both purple and orange arcs to short dashes and considered as the basis for a common neural model to account for the neon color spreading and the watercolor illusion (Figure 10c).

Because neon color spreading and the watercolor illusion are, respectively, defined by the continuation and juxtaposition of lines, the two illusions can be gradually combined, as illustrated in Figures 10b and 10c, and reduced to the limiting case in Figure 10d. Geometrically, in Figure 10b, the orange inset arcs are reduced to short dashes, creating a condition in between neon color spreading and the watercolor illusion: from the neon color spreading point of view, the inducing elements are lines that continue in short dashes, but from the watercolor point of view, the termination of each inducing arc has a juxtaposed short dash. A clear coloration effect is perceived, not weaker than that of Figure 10a, but it has a
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diaphanous and poor surface appearance and a figural effect describable as a fuzzy illusory square annulus that is yellowish and brighter than the background. This phenomenal result is similar to that of Figures 5 and 6. Note that the reduction of dashes to dots with the same diameter as the width of the purple arcs or even smaller does not change the strength of these effects.

The opposite geometrical condition, once again in between neon color spreading and the watercolor illusion, is illustrated in Figure 10c. Here, the purple surrounding arcs of Figure 10a are reduced to short dashes. Under these conditions, a coloration effect weaker than that of Figure 10a is perceived.

The percepts of Figures 10b and 10c suggest that local nearby transitions of colors may be responsible for the coloration and figural effects in both illusions, even if the coloration and figural effects change their mode of appearance (Figure 10b) or their strength (Figure 10c). If this is true, then by reducing both purple and orange arcs to short dashes, the coloration and figural effects should be still perceived (see Figure 10d). By reducing the dashes to dots, the strength of these effects does not change. It has been already shown that the watercolor illusion occurs not only by using juxtaposed lines but also by using juxtaposed chains of dots (see Pinna et al., 2001). Under these conditions both coloration and figural effects become weaker and weaker as the density of the dots becomes sparser and sparser.

We suggest that the two-dots juxtaposition may represent a limiting case for neon color spreading and the watercolor illusion. More specifically, (i) the two-dots limiting case can be considered as the phenomenal basis for the coloration and figural effects in both illusions. (ii) Given these basic conditions, the specific mode of appearance of coloration and figural effects in the two illusions may be elicited by different local and global distributions of nearby transitions of colors that create different boundary organizations. (iii) This limiting case has the advantage of providing support for a simple common neural model (see Section 5). Coloration and figural effects may derive from parallel processes: at a feature processing stage, the small interaction area around and between the two dots produces the color spreading common to both illusions, and at a parallel boundary processing stage, the different geometrical structures in both illusions organize the color spreading to generate different figural effects.

Despite these advantages, Figures 10b, c and d raise two sorts of issues. On the one hand, the geometrical reduction causes changes in both the strength and the mode of appearance of the coloration and figural effects. A systematic measurement is needed to evaluate how the strength of coloration changes by progressively reducing the length of the inducing purple arcs. This is the topic of the experiment in Section 4. As regards the modes of appearance of the coloration and figural effects, little variations suffice to induce large qualitative effects that are difficult to quantify and predict, as shown in Figures 3-9 for the watercolor illusion.

On the other hand, to appropriately assume the two-dots juxtaposition as a limiting case, the strength of its color spreading has to be compared with that induced by other phenomena related to neon color spreading, such as the chromatic assimilation of the inner orange arcs of Figure 10a when the purple surrounding arcs are removed (Redies and Spillmann, 1981; Bressan, 1993a, 1993b). Under these conditions, the white space in between the arcs of the square annulus appears orangish, as if the white regions assimilate the color of the arcs. A comparison between the two kinds of color spreading is needed to show that the coloration induced by the two-dots limiting case has a different nature compared to that of the assimilation phenomenon. This comparison is also the topic of the next experiment.
5. Experiment: Neon color spreading and watercolor illusion combined in a new limiting case

Bressan (1993a, 1993b) proposed that assimilation and neon spreading may obey the same basic diffusion mechanism in inducing the coloration effect, and that the difference between the two effects is the phenomenal scission of the coloration from the plane of the figure in the form of a transparent layer. Assimilation does not create this kind of scission. The best perceptual condition for obtaining the phenomenal scission is the inset of colored drawings (e.g., orange arcs creating the square annulus of Figure 10a) in the blank area in continuation with the outer drawing (e.g., purple arcs of Figure 10a) that would otherwise produce a strong illusory figure (Bressan, 1993a; Bressan et al., 1997).

The questions to be answered in this experiment are: Given the watercolor illusion and more specifically the two-dots limiting case, can chromatic assimilation still be considered as a basic effect for neon color spreading? Is the illusory figure and, as a consequence, the transparent phenomenal scission really needed to cause neon color spreading? Is the strength of the coloration effect due to the two-dots limiting case sufficient to explain the coloration of neon color spreading and of the watercolor illusion?

As illustrated in Figures 10b and 10d, our hypothesis is that assimilation may not be needed to induce the coloration effect of neon color spreading, and, due to incomparable geometric constructions between the three illusions, assimilation cannot be considered as a basic effect for either neon color spreading or the watercolor illusion. A common element based on nearby transitions of colors is structurally preferable. However, assimilation may play a role in neon color spreading, but not necessarily in summing up its coloration effect to the one induced by the limiting case. The experimental results can clarify this point.

Furthermore, illusory contours do not necessarily play any role in neon color induction. In fact, as illustrated in Figure 10c, after removing the inner orange arcs the small dashes do not produce any illusory figure (apart from an emergent boundary that may contain the spread of color beyond the square annulus), even though they produce a plain coloration. In addition, the role of illusory contours is further weakened because the strength of the coloration of Figure 10b is about as strong as the one of Figure 10a. Each small orange dash weakens illusory contour formation and brightness induction due to the purple arcs (Kennedy, 1978; Sambin, 1987; Shipley and Kellman, 1990). The fact that the coloration effect in Figures 10a and 10b is approximately the same (see Figure 11), but the illusory contours for the two cases have different strength, illustrates once again that coloration and figural effects are due to different processes.

Reducing both neon color spreading and the watercolor illusion to the two-dots limiting case, as illustrated in Figure 10d, suggests that coloration effects depend on nearby color transitions, while the figural differences between the two illusions may depend on how the global geometrical structure (e.g., size or length of each dot or line, and their spatial arrangement) interacts with these color transitions to create context-sensitive perceptual differences.

5.1. Subjects. Fifteen naive subjects participated in the experiment. All observers had normal or corrected-to-normal vision.

5.2. Stimuli. The stimuli were obtained by varying Figure 10a in the following four conditions. (i) Three levels of length of purple arcs -- not reduced to dashes as in Figure 10a, reduced to dashes of about 1.5 deg and reduced to dashes of about 8.1 arcmin; by varying the length of the purple arcs, the role of phenomenal scission, illusory contours and assimilation is varied. (ii) Two levels of length of the orange arcs -- not reduced to dashes, as in Figure 10a, and reduced to dashes of about 8.1 arcmin; by changing the length of the orange arcs, the
strength of the coloration due to the two-dots limiting case is tested. (iii) Assimilation of orange arcs obtained by removing the purple components of Figure 10a; under these conditions, the strength of the coloration due to the assimilation can be compared with that induced by neon color spreading and the watercolor illusion. (iv) Assimilation of short orange dashes obtained by removing the purple arcs when the orange arcs are reduced to the minimum length of 8.1 arcmin; this is a control condition to evaluate if any coloration effect is perceived when only the orange components of the two-dots limiting case are shown.

The stroke width of the purple and orange arcs was approx 6.5 arcmin. The CIE x,y chromaticity coordinates of the chromatic components of the patterns were: (purple) 0.30, 0.23; (orange) 0.57, 0.42. Stimuli were presented on a white background and on a computer screen under Osram Daylight fluorescent light (250 lux, 5600° K). The overall size of the stimuli was about 12.4X12.4 deg, the largest side of the square annulus was about 6.85 deg, and the width of the square annulus was about 1.15 deg.

5.3. Procedure. Subjects viewed the stimuli with freely moving eyes using a chin-and-forehead rest positioned at 50 cm from the pattern. Magnitude estimation was used to quantify the perceived strength of the perceived coloration on an 8-point scale. The upper value “8” was defined by the coloration perceived in the inner edges of a square annulus created with wiggly purple and orange continuous contours and having about the same size of the square annulus of the stimuli, whereas the lower value “1” was defined by the complete absence of coloration obtained by removing the orange fringe from the upper modulus (see above the graph in Figure 11). Subjects were allowed to exceed the upper modulus, in case one of the experimental stimuli should surpass the square annulus reference. The eight stimuli were presented consecutively to each observer in a random order.

There was a training period preceding each experiment to familiarize subjects with the color spreading in neon color spreading, the watercolor illusion, chromatic assimilation, and with the task. During practice, subjects viewed some examples of neon color spreading, watercolor illusion and assimilation different from the stimuli to familiarize them with these coloration effects. Observation time was unlimited.

5.4. Results and Discussion. Mean coloration ratings for each stimulus are plotted in Figure 11. The results clearly showed that, by shortening the purple arcs when the orange arcs are not reduced (see stimuli 1, 2 and 3 in the abscissa of Figure 11), the strength of the coloration effect decreases very little, less than 1 point of the magnitude scale ($F_{2,39}=3.81, p<0.05$). This result confirms previous results reported by Redies and Spillmann (1981) and Redies, Spillmann and Kunz (1984).
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Figure 11. Mean coloration ratings for four stimuli conditions: (i) Three levels of length of purple arcs; (ii) two levels of length of the orange arcs; (iii) chromatic assimilation of arcs obtained by removing purple components; (iv) assimilation of short orange dashes obtained by removing purple components. Above the graph, lower and upper values (1-8) used for the magnitude estimation are illustrated.

On the contrary, by shortening the purple arcs when the orange arcs are reduced to short dashes (see stimuli 4, 5 and 6 in the abscissa of Figure 11), the strength of the coloration effect increases within a small magnitude range scale of less than 1 point \( (F_{2,39}=3.49, p<0.05) \). Significantly, no differences in the strength of the coloration were reported by the subjects between the two opposite conditions, the longest purple and orange arcs of stimulus 1 and the shortest purple and orange arcs of stimulus 6. This result clearly suggests the effectiveness of the two-dots limiting case as a good candidate to explain the coloration effects in neon color spreading. Furthermore, because the strength of the coloration in the watercolor illusion is directly proportional to the density of the dots (data not shown, see Pinna et al., 2001) and because a continuous line can be considered as the highest density of dots, the gap of the coloration strength between stimulus 6 and the maximum coloration rating (see above the graph in Figure 11) supports the effectiveness of the two-dots limiting case as a bridge even for the watercolor illusion.
Both assimilation conditions (iii, see stimulus 7 in the abscissa of Figure 11) and (iv, see stimulus 8 in the abscissa of Figure 11) confirm the basic role played by the two-dots limiting case. In fact, by removing the purple components and therefore by removing the nearby color transitions, the strength of the coloration effect abruptly drops significantly (no statistics are needed) up to 2.7 in the assimilation of arcs (stimulus 7) and significantly (no statistics are needed) up to 1.1 in the assimilation of short dashes (stimulus 8), where the coloration is to be considered absent. These results suggest that even if orange arcs induce some coloration or chromatic assimilation, this effect is much weaker than (it does not sum up to) the coloration perceived in neon color spreading or in the limiting case, and thus seems to be a different phenomenon.

The experimental results suggest that the coloration effect within neon color spreading and the watercolor illusion can be understood by considering the two-dots limiting case as the basis for a common neural mechanism useful to account for both illusions. However, the two illusions present many phenomenal dissimilarities, described in Sections 1, 2 and 3 and not studied in the experiment, that may depend on the geometrical differences (continuation vs. juxtaposition) elicitig singular local color interactions and figural organizations.

We suggest (see Section 5) that coloration and figural effects may derive from parallel processes, indeed from parallel cortical streams: at a feature processing or surface formation stream, the small interaction area around and between the two dots produces the color spreading common to both illusion; and at a parallel boundary processing stream, the distinct geometrical structures present in both illusions produce the complex phenomenology of figural effects reported in Section 3. Color spreading may itself arise in two steps that involve an interaction between both the boundary and the surface streams (see Section 5): First, lateral inhibition can weaken the boundaries that surround the colored regions such that the weaker boundaries formed by smaller image contrasts are inhibited more, and second, color can spread through the weakened boundaries into the surrounding regions. The next section proposes how the FACADE neural model of 3D vision and figure-ground separation can more completely explain the experimental results as well as other properties of neon color spreading and the watercolor illusion.

6. A neural model unifies the explanation of neon and watercolor effects

6.1. Boundary completion and surface filling-in. The distinct coloration and figural effects suggest that different mechanisms give rise to these properties. The FACADE model (Grossberg, 1994, 1997) proposes how parallel boundary grouping and surface filling-in processes are carried out, respectively, by a Boundary Contour System (BCS) and a Feature Contour System (FCS) (Cohen and Grossberg, 1984; Grossberg and Mingolla, 1985a, 1985b; Grossberg and Todorovic, 1988). These two processes are predicted to be realized by the cortical interblob and blob streams, respectively, within cortical areas V1 through V4. The boundary and surface processes exhibit complementary properties (Grossberg, 2000): Boundaries form inwardly between similarly oriented contrasts, and are insensitive to contrast polarity or, in other words, pool contrast information at each position from opposite contrast polarities. Boundaries pool opposite contrasts so that they can form around objects on textured backgrounds. In particular, a boundary can continuously surround an object even if its contrast relative to the background reverses multiple times as the object boundary is traversed. Because of this contrast-pooling property, all boundaries are predicted to be amodal within the interblob cortical stream wherein they form. Visible colors and brightnesses, including neon color spreading and watercolor colorations, are predicted to be a property of the surface formation stream. Surfaces fill-in outwardly from individual lightness or color inducers in an unoriented way using a process that is sensitive to contrast polarity. Surface filling-in is contained by boundaries, which act as barriers, or gates, that restrict the spread of color or
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brightness. This hypothesis implies that, whenever surface colors are seen at locations far from their inducers, they must have spread there via surface filling-in. Moreover, if surface color does manage to spread to positions beyond which they occur in a scene or image, then the boundaries which might otherwise have contained their spread must be broken or otherwise weakened to permit the leakage of color beyond them.

6.2. Spatial competition weakens boundaries in a contrast-sensitive way. Typically, if a boundary is broken or weakened at a position where it might otherwise be expected to occur, this is due to some form of competition within the boundary system. Indeed, the BCS was predicted to include both spatial and orientational competition in order to explain a wide range of data about perceptual grouping. The main effect in the watercolor illusion, and more specifically the two dots-limiting case, can be explained by a process of spatial competition where stronger inputs to the boundary system occur at the edges of higher contrast colored lines than at lower contrast ones. This spatial competition provides an answer to the following questions: Why does a large luminance contrast difference between inducing lines show the strongest coloration effects? Why is there an asymmetry in the amount of color spreading from two inducing lines such that the color of the line with less luminance contrast relative to the background spreads proportionally more than the color of the line with more luminance contrast? This happens in the BCS because the spatial competition is stronger from the boundaries of higher contrast edges to those of lower contrast edges than conversely. The boundaries of the lower contrast edges are thus weakened more by competition than the boundaries of the higher contrast edges. Hence more color can spread across these boundaries than conversely. A similar idea was used to explain why neon color spreading is sensitive to the relative contrasts of the edges at which neon color is released (Grossberg and Mingolla, 1985a). Such a spatial competition has been modeled to occur between layers 6 and 4 of cortical areas V1 and V2 (Grossberg, 1999b; Grossberg and Raizada, 2000; Raizada and Grossberg, 2003). This argument does not imply that the lower contrast boundaries are entirely suppressed. If they were, then the color of the lower contrast edge could not be distinguished from the watercolor that it causes. A key property of competitive and cooperative interactions in the BCS is that they preserve their analog sensitivity in response to the intensity of the inputs that drive them. This property, which is called analog coherence, is robustly realized by the laminar circuits that carry out grouping in cortical areas V1 and V2, as well as by the BCS model of these cortical boundary interactions (Grossberg, 1999b; Grossberg, Mingolla, and Ross, 1997; Grossberg and Raizada, 2000).

An implication of this competition hypothesis is that any boundary that can produce a similar weakening of a nearby, less contrastive, boundary at a colored region of prescribed size can cause a similar amount of color spreading from that region. This property can explain the approximately equal chromatic effects in cases 1 through 6 in Figure 11, despite the difference in the length of the purple and orange contours. The main effect is a local one whereby the more contrastive boundaries due to the purple regions inhibit the less contrastive boundaries due to the contiguous orange regions.

The watercolor illusion, as in Figures 3 and 4, derives its strength from the fact that a more contrastive and less contrastive edge are parallel to one another over a significant spatial extent. Thus the total effect is derived from color leakage across the entire length of the weaker boundary, among others.

6.3. Cooperative boundary groupings contain color spreading. This competition effect is not sufficient to explain all aspects of neon color spreading and the watercolor effect. One basic additional property that must be explained is how the color that spreads from spatially discrete or continuous inducers can be contained within prescribed regions of space. For the
watercolor illusion in Figures 3 and 4, continuous boundaries exist whereby to contain the spreading color. For the neon color spreading and limiting cases of Figures 10 and 11, there are no explicit boundaries within the images themselves. The brain creates these boundaries. This is achieved through a cooperative process whereby boundary groupings are formed and completed, as during the formation of illusory contours, and also through the manner in which the competitive and cooperative boundary and surface processes interact to generate 3D boundaries and surfaces that exhibit figure-ground separation effects.

Boundary completion, including illusory contour formation, was predicted by the BCS to depend upon a long-range oriented cooperation process whereby boundaries could form across image locations which receive no bottom-up contrastive signals. This cooperative process was predicted to obey a bipole property whereby the cooperating cells could fire, even if they received no direct bottom-up input, if they received (almost) colinear inputs with (almost) their preferred orientation from positions on both sides of their receptive field. Since these original predictions were made, neurophysiological, anatomical, and perceptual experiments have provided supportive evidence, and it has been possible to interpret both the competitive and the cooperative BCS mechanisms in terms of identified cells within the laminar circuits of cortical areas V1 and V2. Since these original predictions were made, neurophysiological, anatomical, and perceptual experiments have provided supportive evidence, and it has been possible to interpret these BCS mechanisms in terms of identified cells within the laminar circuits of cortical areas V1 and V2. This laminar cortical BCS model is called the LAMINART model. Several recent articles review these data and the laminar circuits in which BCS mechanisms are proposed to be realized (Grossberg, 1999b, 2003; Grossberg and Howe, 2003; Grossberg, Mingolla, and Ross, 1997; Grossberg and Raizada, 2000; Grossberg and Williamson, 2001; Grossberg and Yazdanbakhsh, 2005; Raizada and Grossberg, 2001, 2003).
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Figure 12. Some known cortical connections that are joined together in the LAMINART model of bottom-up, horizontal, and top-down interactions within visual cortical areas V1 and V2. See Raizada and Grossberg (2001) for summaries of supportive anatomical and neurophysiological data. Inhibitory interneurons are shown filled-in black. (a) The LGN provides bottom-up activation to layer 4 via two routes. First, it makes a strong connection directly into layer 4. Second, LGN axons send collaterals into layer 6, and thereby also activate layer 4 via the 6 → 4 on-center off-surround path. The combined effect of the bottom-up LGN pathways is to stimulate layer 4 via an on-center off-surround, which provides divisive contrast normalization of layer 4 cell responses. The balance between the excitatory and inhibitory layer 6 inputs to the layer 4 on-center are approximately balanced. As a result, the on-center receives a modulatory, but not driving, input. (b) Connecting the 6 → 4 on-center off-surround network to the layer 2/3 grouping circuit: like-oriented layer 4 simple cells with opposite contrast polarities compete (not shown) before generating half-wave rectified outputs that converge onto layer 2/3 complex cells in the column above them. Layer 2/3 contains long-range oriented recurrent connections to other layer 2/3 cells. A balance between excitation via long-range horizontal connections and short-range disynaptic inhibitory interneurons helps to control which layer 2/3 cells will fire, as does interlaminar feedback: Layer 2/3 cells send activation to enhance their own positions in layer 4 via the 6 → 4 on-center, and to suppress input to other layer 2/3 cells via the 6 → 4 off-surround. There exist direct layer 2/3 → 6 connections in macaque V1, as well as indirect routes via layer 5. (c) V2 repeats the laminar pattern of V1 circuitry, but at a larger spatial scale. In particular, perceptual groupings form using the V2 horizontal layer 2/3 connections, which have a longer range than the connections in layer 2/3 of V1. V1 layer 2/3 projects up to V2 layers 6 and 4, just as LGN projects to layers 6 and 4 of V1. Higher cortical areas send attentional feedback into V2 which ultimately reaches layer 6, just as V2 feedback acts on layer 6 of V1. Feedback paths from higher cortical areas straight into V1 (not shown) can complement and enhance feedback from V2 into V1. Top-down attention can also modulate layer 2/3 pyramidal cells directly by activating both the pyramidal cells and inhibitory interneurons in that layer. The inhibition tends to balance the excitation, leading to a modulatory effect. These top-down attentional pathways tend to synapse on apical dendrites in layer 1, which are not shown, for simplicity. (Reprinted with permission from Raizada and Grossberg (2001).)

For present purposes, the most important hypothesis is the following: The bipole property is predicted to be realized by cells in layer 2/3 of cortical area V2 that interact together via long-range horizontal connections (Figures 12b and 12c). The spatial competition from layer 6-to-4 of V2 (Figures 12a and 12b) directly influences the input strengths from layer 4 that activate the long-range horizontal connections in layer 2/3 of V2 that form
perceptual boundaries. When the spatial competition weakens the activities of layer 4 cells, the perceptual boundaries in layer 2/3 that would otherwise form in response to these layer 4 inputs are correspondingly weakened. As a result, color within the surface stream can flow more easily across those boundaries.

A sensitivity to relative contrast has earlier been used to explain why neon color spreading is sensitive to the relative contrasts of the edges at which neon color is released (Grossberg and Mingolla, 1985a). Here again, interacting competitive and cooperative boundary grouping processes played a key role. The main idea was again that boundaries at positions of lower contrast are weakened more than spatially contiguous boundaries at positions of higher contrast, as at the orange lines that abut the more contrastive purple lines in Figure 10. Another factor in the explanation of neon color spreading is the ability of the BCS to form illusory contours that are perpendicular (among other orientations) to the inducing lines that initiate spreading, and to thereby contain the filling-in process within the square annular regions in Figure 10.

The BCS predicts that these illusory contours are formed by the same cooperative-competitive interactions that weaken the boundaries through which neon color can spread (Grossberg and Mingolla, 1985a). The first step in forming these illusory contours is the generation of small boundaries, called end cuts, at line ends. These boundaries form due to the way in which spatial competition interacts with competition between orientations at each position (Grossberg, 1994; Grossberg and Mingolla, 1985a). Several such end cut boundaries can form at each line end, and they have orientations that are almost perpendicular to that of the inducing line. Like-oriented end cuts that are colinear across position can use bipole cooperation to form illusory contours. In Figure 10, these illusory contours are approximately perpendicular to the purple line ends and pass through the positions where the lines change color, thereby forming a square annular boundary that can contain the spreading orange color. These illusory contours can be quite sharp, despite the fuzziness of the end cut orientations, because bipole cooperation also interacts via feedback with the spatial and orientational competition to inhibit weaker cell responses. Such boundary and surface interactions have elsewhere been used to explain a variety of additional data about neon color spreading (Grossberg, 1987a, 1994, 1999a; Grossberg and Mingolla, 1985a; Grossberg and Swaminathan, 2004; Grossberg and Yazdanbakhsh, 2005).

6.4. Why assimilation is weaker than neon. This explanation also clarifies why the assimilation effect in cases 7 and 8 in Figure 10 are weaker than the neon and watercolor illusion effects. Consider case 7 for definiteness. The ends of the orange lines can create end cuts that can form a bounding illusory contour, again in the form of a square annular boundary. Here, too, the bipole cooperation interacts via feedback with the spatial and orientational competition. It can hereby weaken the boundaries at the ends of the orange lines a little, but not nearly so much as the more contrastive purple boundaries. As a result, some color can spread into the square annulus. In case 8, the inducers are so short that they create very weak, if any, end cuts and a weak, if any, illusory contour. Any assimilation that can occur will be correspondingly weak.

6.5. 3-D surfaces and figure-ground separation in the watercolor illusion. Figure 3, 4, 7, and 8 illustrate the fact that the watercolor illusion can generate percepts of rounded 3-D surfaces and can lead to figure-ground separated percepts of transparent surfaces lying above a background surface. FACADE theory proposes how 2-D monocular properties of the BCS and FCS may be naturally embedded into a more comprehensive theory of 3-D vision and figure-ground separation that was introduced in Grossberg (1987b, 1994, 1997) and further developed in a series of quantitative studies to explain several different types of perceptual
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and neural data (Cao and Grossberg, 2004; Grossberg and Howe, 2003; Grossberg and Kelly, 1999; Grossberg and McDoughlin, 1997; Grossberg and Pessoa, 1998; Grossberg and Swaminathan, 2004; Grossberg and Yazdanbakhsh, 2005; Kelly and Grossberg, 2000; McDoughlin and Grossberg, 1998).

In particular, FACADE theory proposes how brain processes that have evolved in order to represent the world in three-dimensions also enable us to perceive two-dimensional images as figures and backgrounds in depth. Some of these figure-ground mechanisms enable partially overlapping, occluding, and occluded image parts to be separated and completed in depth. The same mechanisms shed light on how the watercolor illusion can support a figural percept. In Figures 3 and 4, for example, the watercolor illusion segregates the colored frame in depth and gives it the appearance of a rounded figural surface. This rounded percept becomes stronger as the contrast ratio between the two colored lines is increased, as Figure 9 illustrates.

Several factors contribute to these percepts within FACADE theory. One factor is that there are depth-specific and color-specific networks within the surface stream where filling-in occurs. These networks are called Filling-In Domains, or FIDOS. FACADE theory proposes how depth-specific boundaries can selectively capture color signals to fill-in at one depth but not others. Surface filling-in within a particular FIDO is seen at a prescribed relative depth from the observer. This fact helps to explain how the achromatic and chromatic filled-in surfaces of a watercolor illusion get separated from each other, but it is not sufficient to explain which surface will appear as figure and which as ground.

The determination of figure and background can be traced to how boundaries interact with surface inducers to selectively fill-in FIDOs that represent different depths. In particular, when two colored lines of different contrast are contiguous, as with the purple and orange lines in Figures 3 and 4, then three parallel rows of boundaries are generated, usually of progressively decreasing boundary strength. Such an array generates a spatially sparse version of a boundary web, or spatial array of boundaries that can restrict filling-in within relatively small surface regions. Earlier modeling studies predicted how a boundary web can elicit a percept of a rounded surface in depth (Grossberg, 1987a; Grossberg and Mingolla, 1987). This prediction was successfully tested in experiments using depth-from-texture images by Todd and Akerstrom (1987). In their data, the worst correlation between human psychophysical judgments of 3D shape-from-texture and model predictions was .985.

The main idea behind this predictive success can be summarized as follows, before it is applied to explain watercolor effect figural properties. Consider a 2-D shaded ellipse. How does such a 2-D image generate a percept of a 3-D curved surface? The 2-D image activates multiple filters, each sensitive to a different range of spatial scales (see the bottom-up pathways to layer 4 in Figures 12a and 12c). Other things being equal, larger filters need bigger inputs to fire than do smaller filters. Likewise, larger filters can, other things being equal, binocularly fuse more binocularly disparate images, representing closer objects, than can smaller filters. Smaller filters can only binocularly fuse less binocularly disparate images, and thus farther objects. In addition, larger filters can respond to a wider range of disparities than can smaller filters. As a result, an object at a given depth with respect to an observer can initially be represented by multiple spatial scales. These disparity-selective properties of multiple-scale filters often go under the name of the size-disparity correlation (Julesz and Schumer, 1981; Kulikowski, 1978; Richards and Kaye, 1974; Schor and Tyler, 1981; Schor and Wood, 1983; Schor et al., 1984; Tyler, 1975, 1983).

How does the brain decide which combination of multiple scale filters will ultimately represent the depth of an object? The multiple-scale filters input to grouping cells, via layer 4-to-2/3 connections, which use the same cooperative-competitive interactions that have already been mentioned to select and complete boundary representations that are sensitive to different
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depths. These competitive interactions include the spatial competition that helps to explain how the watercolor effect occurs. Then, as already mentioned, the winning depth-selective boundaries selectively capture color inputs at FIDOs that fill-in the captured color at the corresponding depth, while also bounding the regions within the color can spread. If some of these boundaries are weakened, as in the contrast-sensitive spatial competition described above, then color can flow out of a region to the extent that the boundary has been weakened.

Now consider how multiple scales may respond to a shaded ellipse. Other things being equal, smaller scales can fire more easily nearer to the bounding edge of the ellipse. As the spatial gradient of shading becomes more gradual with distance from the bounding edge, it becomes harder for smaller scales to respond to this gradient. Thus, other things being equal, larger scales tend to respond more as the distance from the bounding edge increases. As a result, the regions nearer to the center of the ellipse look closer due to the size-disparity correlation.

A similar thing happens, albeit with a more spatially discrete filter input, in response to a watercolor image such as the ones in Figures 4 and 5. Here, just as in response to a shaded ellipse, there is a spatial array of successively weaker filter responses as the distance increases from the most contrastive edge of the display. These successively weaker filter responses activate boundary and surface processes much as one would expect from a spatially discrete version of a shaded ellipse, and these processes can generate a rounded appearance using the same size-disparity correlation mechanisms. A new property of the watercolor effect, which is due to the discrete changes in successive boundary contrasts, is that the spatially disjoint boundaries can weaken each other via spatial competition and thereby allow surface color to spread within the depth-selective boundaries that are formed in response to the multiple-scale filter responses. That is why the interior of the watercolor region can look a little closer to the observer than the bounding edge. Because of this perceived depth difference, a region suffused with the watercolor illusion can have a stronger figural quality than one filled with a uniform color, which tends to look flat.

6.6. Transparency in the watercolor illusion. Figure 8 illustrates how the watercolor effect can create transparent percepts. In this figure, the contrast of the watercolor bounding contour is greater than that of the vertical boundary, thereby creating a stronger boundary around the watercolor region. This property is enough to initiate a figure-ground separation process whereby the watercolor boundary can be seen in front of the vertical boundary. See Grossberg and Yazdanbakhsh (2005) or Kelly and Grossberg (2000) for an explanation of how this happens. Because the conditions for the watercolor illusion are also present—namely, the parallel purple and orange lines—these nearer boundaries can fill-in yellowish surface color due to the spatial competition among the watercolor boundaries that was described above. The two gray surfaces can also fill in at the same positions, but on a FIDO that represents a slightly farther depth plane. Hence, a transparent surface percept is seen.

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6. References


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