

Neon color spreading: a review

Paola Bressan

Dipartimento di Psicologia Generale, Università di Padova, Via Venezia 8, 35131 Padova, Italy; e-mail: paola-bressan@psico.unipd.it

Ennio Mingolla

Department of Cognitive and Neural Systems, Boston University, 677 Beacon Street, Boston, MA 02215, USA

Lothar Spillmann

Arbeitsgruppe Hirnforschung, Institut für Biophysik und Strahlenbiologie, Hansastrasse 9, 79104 Freiburg, Germany

Takeo Watanabe

Department of Psychology, Boston University, 64 Cummington Street, Boston, MA 02215, USA

1 Introduction

This paper is about a phenomenon that combines a delicate beauty with a profound significance for understanding visual perception. The neon-like glow of a color that escapes the boundaries of a real figure and fills the surrounding area until it is halted by the boundaries of an illusory figure has an ethereal quality unlike any other brightness and color effect. It also has substantial implications regarding the way in which our visual system uses seemingly incomplete stimuli to generate meaningful percepts, segregate objects from their backgrounds, and provide them with color and depth.

As it so often happens in science, the effect was discovered and then independently rediscovered in the span of a few years. In 1971, Dario Varin of the University of Milan published a monograph on 'chromatic contrast and diffusion' whose front cover is reproduced in figure 1. A circular transparent veil can be seen to extend over four sets of concentric rings partly composed of blue arcs. It has a subtle bluish tinge and is luminescent, as if it emitted a weak light, or as if it were a colored spot of light cast by some off-screen lamp. This veil is illusory, in the sense that a point-by-point description of the reflectance spectrum of the white background would not reveal any changes corresponding to it.



Figure 1.

Varin's work was written in Italian and had little international circulation, but four years later Harrie van Tuijl of the University of Nijmegen described an analogous illusion that was to take root. This time there were no concentric circles but a lattice consisting of horizontal and vertical black lines in which a number of segments arranged in the shape of a diamond had been replaced by segments of a different color. As a result of this operation, a delicately tinted, glowing diamond emerged within the lattice. There was no need for especially elaborate drawings either: indeed, the luminescent form showed up in full in the barest of patterns, the Ehrenstein figure, that is four black radial lines separated by a central gap (Ehrenstein 1941/1987). A clearly delineated bright illusory disk is normally perceived here, but if the inner endpoints of the lines are connected by a colored cross the disk becomes translucent and misty, as in figure 2. In part because of the tinge, in part because of the glow, van Tuijl (1975) named the phenomenon neonlike color spreading.

As a rule, colors appear firmly attached to visual surfaces and well contained within their boundaries. Neon color spreading seems to defeat this solid perceptual fact. Also, illusory contours certainly look much more flimsy and insubstantial than real, contrast-based contours. Neon color spreading seems to defeat this solid perceptual fact too. Why does color flow out of the colored segments in the first place? And why do illusory contours succeed in blocking the spreading where the real segment contours have gone amiss? In this article, we deal with these questions from four different angles: phenomenology, psychophysics, physiology, and modeling.

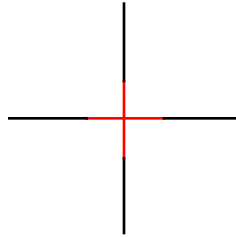


Figure 2.

2 Phenomenology: Perceptual qualities of neon color spreading

A classic neon spreading figure is, in essence, a perceptually incomplete black pattern where the parts of the lines that are missing have been replaced by colored segments. Before the segments are put in the right places, the illusory figure looks white, compact, opaque, thick, and sharply outlined. Once the segments bridge the gaps, the illusory figure becomes colored, tenuous, transparent, almost immaterial, and fuzzy.

2.1 Color

The illusory color comes apparently from the segments, as if by local dilution of a slight amount of pigment. Much as one would expect from previous experiences with dyes that wash out, the embedded segments do look more vague and less vivid than non-embedded identical segments presented nearby. The color leaves the segments, diffuses beyond their immediate surrounds and fills, entirely and evenly, the illusory area. There is one exception to this rule. If the colored segments are too long (or the gaps are not properly aligned, so that no illusory figure shows up), color diffusion is confined to a narrow streak alongside the segments. If the segments are even longer (about 1 centimeter or more at arm's length), the tinted area becomes quite small and is only perceived at the junction between the colored segment and the black line. Redies et al (1984) have called this local effect neon flanks.

The colored segments need not have a hue. Grey segments embedded in black lines will give rise to a perfectly good achromatic version of neon color spreading, sometimes called neon brightness spreading. In the familiar case where the segments have less contrast than the rest of the pattern, the illusory figure will normally be seen as a spot of misty light or a semi-transparent filter, as in figure 3a. When the lines have less contrast than the segments, as in figure 3b and 3c, the illusory figure will either resemble a tinted clear piece of plastic or a patch of light or shade, and in the second case it may appear behind the pattern rather than in front (Bressan 1993b).



Figure 3.

Colored patterns coupled with achromatic segments make for truly extraordinary effects (see figure 4). Under these circumstances the illusory figure becomes tinted not in the color of the segments (grey, in this case), but in the color complementary to that of the external lines, say yellowish when the lines are blue or pinkish when they are green (van Tuijl 1975). Here, the fact that the illusory color comes from the segments is not obvious to the eye; indeed, it is not even obvious that such color could have originated within the figure at all.

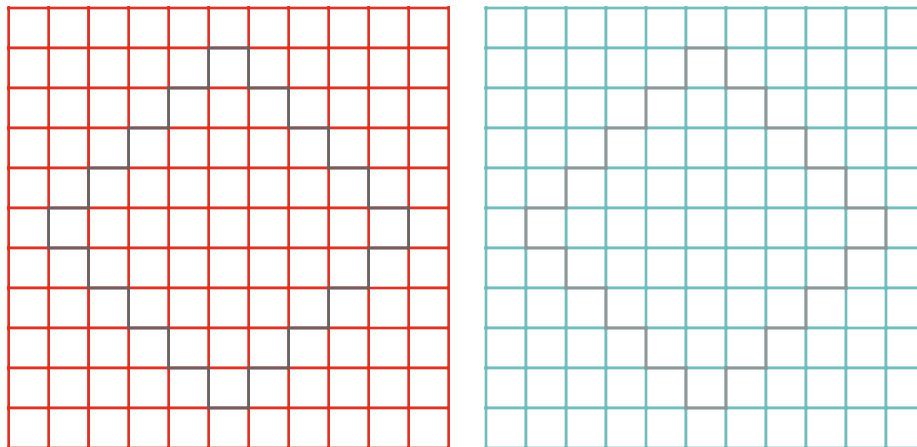


Figure 4.

2.2 Transparency

A neon spreading figure appears transparent. The pattern lines look continuous and complete, although some are seen as if directly, while others are seen as if through a veil, be it light or shade or diaphanous matter. Sometimes the segments and lines appear consistent with a transparent overlay, as in figure 1 where the concentric circles might look black and partly covered by a bluish veil. Sometimes the percept is inconsistent with physical

transparency, as in figure 2 where the cross behind the pinkish overlay appears red rather than black. Neon spreading is observed nonetheless, but so is perceptual transparency, which in favorable conditions is known to survive even when there is a striking color difference between the portion of the figure seen directly and the one seen through the overlay (e.g., Metelli et al 1980). It seems to be of little importance that this corresponds to a highly unrealistic occurrence in a world of fog, water, shadows and other physically transparent things.

2.3 Glow

Though a large part of the beauty of neon spreading figures is in their glow, not all neon spreading figures glow. If one takes a photographic negative of figure 1, for example, the effect survives but the luminescence dissolves. In general, dark neon spreading in achromatic patterns (resulting, regardless of the background color, whenever segments are darker than lines) has a dim quality, and is often described as smoke-grey, or dusky, or shadowy.

3 Psychophysics: Conditions for the occurrence of neon color spreading

3.1 Figure

Many different bicolored drawings will let neon spreading figures sprout if the spatial arrangement of lines and segments is right. Redies and Spillmann (1981) showed that the Ehrenstein neon pattern of figure 2 will tolerate deformations, amputations, fractures, twisting, and other disturbances only up to a certain amount. The illusion is most powerful when lines and segments are continuous, collinear, and equally thick, and progressively weakens as they become more and more separated along these dimensions. There seems to be a magical number here corresponding to the largest tolerable separation, since for gaps, lateral misalignments, vernier offsets due to rotation, or differences in stroke width all bigger than 2 minutes of arc, neon spreading disappears. The effect also disappears if the subjective figure is encircled by a ring or if the colored segments are too long (longer than 35 minutes of arc in foveal viewing, about twice this value in extrafoveal viewing), whereas stretching or shortening the black lines seems to matter little, even when it means reducing them to mere dots.

On the other hand, Bressan (1993a) has suggested that the visual system may actually tolerate wide departures from these constraints, provided that the stimulus supports perceptual transparency. She demonstrated that, as long as lines and segments are still seen as part of the same structure, neon spreading occurs for colored segments well above the

critical length (spanning, actually, a few degrees of arc) and persists despite figural stops, lateral misalignments, or dissimilar stroke widths. The question of why such conditions should normally be so crucial for neon spreading thus may be answered by noticing that their violation normally disrupts perceptual transparency.

The link between neon color spreading and transparency has been manifest from the earliest references in the literature. This relation touches not only on phenomenology (neon spreading figures appear transparent), but also on psychophysics, and has some bearing not only on the figural, but also on the depth and color conditions for neon spreading, as we will now see.

3.2 Depth

If the perceived depth stratification is incompatible with a transparent overlay, neon color spreading vanishes. This has been shown, for example, by altering the apparent depth of the inner colored cross in stereograms of the Ehrenstein pattern (Nakayama et al 1990). When the colored cross is made to appear in front (in which case it looks like a transparent film, covering part of the underlying cross), neon spreading is enhanced compared to the coplanar condition. When, however, the inner cross is perceived behind (appearing as an opaque figure partly seen through a cross-shaped aperture), the spreading of color is much reduced and the neon effect is lost. The same point was made by an earlier experiment (Meyer and Dougherty 1987), where flicker-induced depth was used to have the colored regions appear either as foreground or as background. In order to yield neon spreading, the colored elements had to be phenomenally in front of (and partly covering) the inducing areas.

However, an exception to this rule has been reported. Bressan and Vallortigara (1991) filled aligned gaps in a pattern of concentric black circles with red arcs. When this pattern was rotated in the frontal plane about the common center of the circles, all observers saw a pink, neon-like bar moving *behind* uniformly black circles. Here is a case in which the neon-colored region does not appear in front of, nor partly covering, the inducing lines. These data support the argument that the essence of neon spreading consists in the perceptual detachment of the illusory color from the plane of the figure (Bressan 1993a). This may be obtained via depth stratification through motion as well as via depth stratification through the formation of a transparent overlay.

3.3 Color

The chromatic and achromatic cases have been studied separately, and brightness neon spreading, probably on the grounds of being the simplest, has been (systematically) examined first. In grey figures, the basic rule is that the luminance of the segments must be

in between the luminances of the embedding lines and of the background. Thus, on a white background grey segments will 'bleed' when embedded in darker lines, but will not if the lines are lighter.

This simple hierarchy has been demonstrated to hold both for lattice patterns with diamonds (van Tuijl and de Weert 1979) and for Ehrenstein figures with crosses (Nakayama et al 1990). It has later been shown, however, that in patterns like that of figure 1 neon spreading can occur with any possible luminance hierarchy, provided that the luminance differences between segments, lines, and background support transparency (Bressan 1993b). In this case, grey segments may also 'bleed' when embedded in slightly darker lines on a black background (figure 3b) and in slightly lighter lines on a white background (figure 3c), thereby infringing the luminance conditions. Bressan has claimed that, exactly as it happens with figural conditions, the luminance conditions for neon spreading simply represent the luminance prerequisites for perceiving a transparent subjective figure. This interpretation has the merit of solving the seeming contradiction between data, since it is easy to see that figural cues suggesting a superimposed transparent layer are poorer (and then, tolerance of adverse color conditions may be lower) in either figure 2 or lattice-and-diamond patterns than in figure 1.

As is the case between patterns, the relation of the effect with contrast appears to vary within structurally identical figures, too, and depends on whether they are grey or colored. Working with chromatic Ehrenstein neon configurations, Ejima et al (1984) found not only that the arms could have a lower contrast than the cross, but that the effect reached at equiluminance was not much increased by increasing the contrast of the arms. On the contrary, when the contrast ratio between arms and cross was too large (larger than eight to one) the illusory color became extremely weak. Neon spreading, then, does not need the contrast of the lines to be higher than that of the segments, but the vigor of the effect is indeed modulated by contrast.

A red cross gives rise to an excellent spreading when it joins bluish-green arms, but not when it joins orange arms. If both the pattern and the segments are colored, in fact, neon spreading depends on the relation between the two hues, being most vivid when they are complementary to each other, feeble or even absent when they are alike (Ejima et al 1984). Bressan (1995) has interpreted these results as supporting the idea that the color which spreads in the illusory area is a mixture between the color of the segments and the color complementary to the lines. When the red color of the cross mixes with the red color induced in the cross by greenish arms, the result will be a maximally saturated, strong, easily visible mixture. Reddish arms, instead, will induce in the cross a greenish color which, added to the red of the cross, will produce a desaturated mixture, that is an extremely washed-out color that will be hard to detect. (When additively mixed, complementary colors cancel each

other out.) The antecedents of this idea can be found in Grossberg and Mingolla's (1985) model and are outlined in section 6.

4 Relation of neon color spreading to other perceptual phenomena

4.1 Assimilation

If one rules a piece of white paper with sufficiently thin blue lines, the white space between the lines will appear bluish. It is as if the white area partly 'absorbed' or 'assimilated' the color of the elements which lie on it. The illusory color, however, shows no glow; it looks opaque and on the same plane as the inducing elements. Neon spreading and assimilation, then, are distinguishable phenomena that emerge in different inducing patterns: the blue lines only need an appropriate thickness and arrangement for simple assimilation, but require other lines (that are continuous, collinear, and of a different color) for neon spreading. The difference in stimulus conditions required for the two phenomena has been taken to imply that they are actually produced by different mechanisms (Redies and Spillmann 1981), but this is not necessarily the case. Bressan (1993a, 1993b) has suggested that neon spreading and assimilation might share the same basic 'diffusion' mechanism (which provides the illusory color), and that the only difference between the two could be the presence (neon spreading) or absence (assimilation) of perceptual scissioning of the illusory color from the plane of the figure. Assimilation, in other words, would turn into neon spreading whenever it takes place within a surface that satisfies the conditions for transparency. Note that this calls exactly for the presence of elements which are continuous, collinear, and of a different color relative to the target elements. The illusory tinge, then, rather than merging with the solid background color, would become a translucent layer, assuming the 'vagueness' and the special floating quality of the neon effect.

4.2 Illusory contours

In general, neon spreading occurs when colored segments are inserted in the blank area of a drawing that would otherwise produce a plain illusory figure. In the absence of illusory contours, however, color spreading persists, though it has no clear boundary, and is reduced in extent (Watanabe and Sato 1989, Watanabe and Takeichi 1990). Watanabe and Sato (1989), for instance, made illusory contours disappear by making the cross and the arms in a neon Ehrenstein figure equiluminant. In this case, the diameter of the neon-like area shrank to about half of what it was when the pattern was not equiluminant. This suggests that illusory contours play a role not in generating the spreading, but in delimiting and shaping it. Bressan (1993a) has shown that, under certain conditions, such a function can also be

accomplished by real, rather than illusory, contours. Neon color spreading within real contours may be not as spectacular as within illusory contours, but it retains transparency and color, and, in part, vagueness and luminescence. Cases of perceptual transparency obtained with lines of different widths and causing the medium to become ‘milky’, as those described by Bozzi (1975), may well be regarded as early instances of achromatic neon color spreading taking place inside physically delimited surfaces.

Takeichi, Shimojo and Watanabe (1992) showed that when the colored cross is presented to one eye and the black arms to the other, so that they are perfectly aligned in the fused image, the resulting percept exhibits illusory contours but no color spreading. On the other hand, when one eye sees the horizontal component of the figure (horizontal colored segment embedded in horizontal black arms) and the other eye sees its vertical component (vertical colored segment embedded in vertical black arms), a fully-formed neon disk appears, even though each component by itself only induces narrow neon flanks. It is therefore likely that local color spreading is generated before the fusion of information from the two eyes; illusory contours are, evidently, generated after (or at) the site of binocular fusion. It is as if local color spreading were ‘captured’ and diffused inside the area bounded by illusory contours. The final effect appears then to be the result of an interaction between operations occurring at different stages of visual information processing.

4.3 Motion and depth

Neon color spreading can be enhanced, and in some cases even triggered, by motion. Bressan and Vallortigara (1991) reported enhancement under conditions of both stereokinetic and translatory motion. In either case it is the neon surface that appears to move, and not the colored segments. The same holds for stroboscopic motion: when two black crosses are lying side by side and a smaller colored cross is made to appear and disappear alternately on the center of either cross, one sees a luminous, delicately tinted disk jumping left and right in front of two uniformly black crosses (Bressan, unpublished data).

Some configurations induce neon color spreading only as a result of motion. The first report dates back to Wallach’s (1935) classical work on the barberpole illusion. The effect is obtained with a set of lines that are red in their upper half and black in their lower half. When in motion behind an aperture, the lines can look black along their whole length, in which case a reddish transparent veil seems to cover the red sections. Concomitantly, there is a change in the direction in which the lines appear to displace. The colored elements do not need to be physically in motion in order to let their color flow out. For example, if a circular patch of green dots in a field of red dots is set in apparent motion by changing from red to green the dots at its leading edge and from green to red the dots at its trailing edge, subjective contours delimiting the moving patch appear, and a greenish color spreads

throughout the illusory area (Cicerone et al 1995). In this case, no green spreading is noticeable in the static configuration, and the color diffuses within an area defined by apparent motion only.

Neon color can also spread on curved surfaces, and pervade three-dimensional illusory objects. Bressan and Vallortigara (1991) obtained such an object by rotating in the frontal plane, about its center, a pattern of concentric black circles with aligned gaps, half of which had been replaced by red arcs. The stereokinetic transformation produced a half-white and half-reddish three-dimensional rod, slanted in depth and pivoting about the center of the circles. The neon-like half appeared to move behind (and the subjective, opaque half in front of) a plane of stationary black circles. Here, color spreading was also present in the static display, but in that case it filled one half of a flat stripe lying over the circles. The passage from a two- to a three-dimensional object, and the corresponding change of a surface color into a volume color, required apparent motion in depth.

A related transformation can be obtained through binocular disparity rather than stereokinesis. One example involves a modification of the paradigm of Carman and Welch (1992), who introduced binocular disparity, along with slight changes in orientation, into the vertical edges of the gaps in the Kanizsa figure, producing a three-dimensional, cylindrical illusory surface. Kojo et al (1995) inserted wedge-shaped colored sectors to complete the missing parts of such a figure, finding that neon color spreading was perceived on the cylindrical surface. This shows that neon spreading interacts with the visual system's representation of smoothly curved surfaces in depth.

4.4 Texture and disparity

Visual features other than color and brightness can diffuse in configurations analogous to those that give rise to neon color spreading. Watanabe and Cavanagh (1991) reported that when a peripherally viewed textured (instead of colored) cross is embedded in an Ehrenstein pattern, the texture appears to spread outside the cross and fill the illusory figure. Takeichi, Watanabe and Shimojo (1992) observed that apparent depth of small dots signaled by uncrossed binocular disparity spread within the area defined by an illusory contour. These findings suggest that the presence of illusory contours may trigger or strengthen the diffusion not only of color and brightness, but also of texture and depth. It is as yet unclear, however, how neon color spreading and the filling-in of features such as texture, disparity, or motion are related.

5 Physiology: The neural basis of neon color spreading

Neon color spreading has helped to unlock the doors of understanding of certain visual processes; however, our knowledge of its neural basis is incomplete. We deal here with the available neurophysiological data concerning the main aspects of the neon spreading effect: illusory contours, apparent contrast reduction, color diffusion.

5.1 Illusory contours

A neurophysiological model that could account for the emergence of illusory contours has been proposed by Peterhans et al (1986). These authors suggest that illusory contours bridging the gap between two aligned inducers may be explained by end-stopped cells in the primary visual cortex in conjunction with a hypothetical grouping mechanism. Grossberg and Mingolla (1985) had earlier proposed that the spatial inhibition underlying end-stopping, combined with inhibition among cells tuned to differing orientations, produced ‘end-cutting’, that is, enhanced activity in cells whose orientational tuning had a peak in the orientation perpendicular to that of a thin line whose end fell into the cells’ receptive fields. End-stopped cells have elongated receptive fields with an excitatory region in the middle and inhibitory zones at their ends. Cells can be double end-stopped, with inhibitory zones at both ends, or single end-stopped, with an inhibitory zone on only one end. End-stopped cells are optimally stimulated by an oriented line (or edge) falling into their central discharge region. When the line exceeds this length and continues into an inhibitory end-zone, the response is diminished.

In the model of Peterhans et al (1986), completion of illusory contours in a horizontal direction occurs between pairs of end-stopped cells that are themselves tuned to vertically oriented edges or lines. Thus, in the Kanizsa square configuration, the ‘inducers’ of an illusory contour are not the horizontal segments that are collinear with the illusory contour, but the perpendicular edges where the curved outer contour of a three-quarter disk terminates. Activity at spatially disjoint pairs of such end-stopped cells can activate a gating mechanism in V2, through a multiplicative interaction of activity triggered by those end-stopped cells. Grossberg and Mingolla (1985) had called their version of such a gating mechanism a ‘cooperative bipole cell’. In the Peterhans et al (1986) model, the output of the gating cell signals illusory contours. This output can then be combined with the output of cells signaling ‘real’ contours to form an integrated perceptual representation of real and illusory contours.

The grouping of inputs from end-stopped cells is reminiscent of the psychophysical notion of dissimilation. This idea emerged from the observation that small ‘brightness buttons’ at the ends of lines may give rise to line-end contrast and brightness induction (Frisby and Clatworthy 1975). By spreading orthogonally, these brightness buttons are assumed to connect up with others to form an illusory boundary (Day and Jory 1978).

Kennedy (1979) pointed out that the effect of brightness buttons may be subliminal for single lines, but noticeable as several line ends are near each other, especially if an illusory figure is also induced. Section 6.2 describes an alternative view of the operation of physiological mechanisms that may underlie brightness buttons and their role in illusory contour formation.

5.2 Apparent contrast reduction

When embedded in black lines, the colored segments look paler than when presented in isolation. This effect can also be explained by end-zone inhibition (Redies et al 1984, Redies 1989). When a colored segment falls into the excitatory area of the hypercomplex receptive field and the black adjoining lines extend into the inhibitory zones, the discharge rate of the cell will be reduced and, as a consequence, the apparent contrast of the colored segment will be less. Neurophysiological experiments have shown that end-stopping is most pronounced when the lines falling into the excitatory and inhibitory regions of the receptive field are continuous and collinear, whereas separation, lateral displacement, and angular tilt weaken it (Kato et al 1978). These receptive field properties are the same as the structural constraints that govern the perception of neon spreading (see section 3.1).

Contrast reduction, in conjunction with the spread of neon color, might serve to enhance the discontinuity between two black lines and a gray or colored segment inserted into the gap. Redies et al (1984) called this 'line-gap enhancement'. By making the colored connection more conspicuous, changes in luminance or wavelength of the line would be more easily discerned. A striking example of line-gap enhancement is the observation that a neon halo can be seen even if the color of the connecting line is too dim to be perceived, for instance when the pattern is observed from a distance. The halo would reveal a discontinuity within the seemingly uniform line that would otherwise escape attention.

An opposite interpretation is also possible. Bressan (1993a, 1993b), for instance, has proposed that the spread of color serves to homogenize, rather than differentiate, regions of different color whenever they appear to belong to the same object. By perceptually 'lifting' the color off the connecting segment and into an elevated plane, scission would generate the percept of a colored, transparent film through which the line underneath could continue unchanged. In this way phenomenal unity would be preserved. Such an interpretation makes sense in an environment where irregular patches of the visual scene are often illuminated differently from others. (Think of the filtering of light in a forest.)

5.3 Neon flanks and color diffusion

We know very little about the way in which neon color spreads from a thin colored line into a large illusory area. Chromatic aberration and eye movements cannot explain the effect, as

neon color is absent when the colored connecting segments are presented alone. Redies et al (1984) have suggested that neon spreading is a form of lateral extension of local neon flanks, in the sense that some assimilative mechanism may cause the narrow streaks of illusory color to spread once they have formed. In fact, neon flanks are more basic than color spreading since they appear first (flanks are observed even with a single junction), and disappear later (flanks are still observed when the colored segment have become too long to sustain spreading).

The available neurophysiological data account neither for the emergence of neon flanks nor for their hypothetical spreading. The first might be related to the formation of brightness buttons at the ends of lines. Color diffusion, instead, might be the end result of some kind of synergistic, rather than antagonistic, interaction among cells. Both neuronal spatial integration within receptive fields and receptive fields without center-surround antagonism have been discussed (de Weert 1991); however, the neurophysiological basis of assimilation is not well understood.

To account for what happens in the brain when we observe a neon color spreading pattern, then, we expect to find some neuronal mechanism that produces color signals at inappropriate places, probably through diffusion of brightness and color. The next section describes how such a mechanism might work.

6 Analysis of neon color spreading using a model of early vision

6.1 Spreading as metaphor and mechanism

The expression ‘neon color spreading’ suggests a physical metaphor for the propagation or transport of signals of hue, saturation, or brightness. Little is known about the physiological mechanisms that could accomplish spreading. One may think of a physical process of cortical diffusion: an excited cell will pass a signal to its neighbors and its neighbors will in turn pass it to their neighbors, and so on. Much as it happens with a drop of ink in a glass of water, at some point the activity will have diffused everywhere, unless some tangible barrier gets in the way. Even in its simplest form a mechanism like this can explain why, in figure 1, we see color where no color exists; why such color is of the same hue as the embedded segments, but of less saturation; and why it is uniform. The metaphor also suggests that the illusory contours that restrict the spreading act as the surface of the glass: the color diffuses inside, but cannot escape. How the diffusion of activation among cortical cells is physically implemented in the brain is, however, still an open matter. Transmission by action potentials might be too slow to sustain rapid perceptual filling-in, and this concern led Stephen Grossberg to propose cortical circuits including speedy electrotonic propagation of

cell potentials by gap junctions (Grossberg 1984). While such signal transmission occurs in retinæ of many species, no evidence of cortical analogs has been reported to date. Conversely, if the time required for filling-in in neon color spreading is comparable to that required for brightness induction (a rather sluggish process, according to Rossi and Paradiso 1997), then propagation of signals by action potentials would be fast enough to mediate the perceptual effect.

In the neon effect, illusory contours may bound regions of neon color, while real contours are incapable of restricting color to its proper place. Because of this paradoxical reversal of the efficacy of real and illusory contours in acting as delimiters for the perceived color of surface regions, neon color spreading was of central importance in the development of the Boundary Contour System (BCS) and Feature Contour System (FCS) of Grossberg and Mingolla (1985). The BCS and FCS are complementary systems, in the sense that neither alone can adequately describe a visual percept. In terms of the example of ink diffusion in a glass of water, the FCS determines the color of the ink from measures of local luminance, contrast, and wavelength, while the BCS determines the form of the sides of the glass. In neon color spreading, the sides of a glass that ‘should’ contain color become porous, while a larger ‘illusory glass’ is constructed that restricts the color that diffuses out.

The BCS begins with oriented contrast filtering operations of the sort believed to be performed by simple and complex cells of the visual cortex. Successive stages of competitive (inhibitory) and cooperative (excitatory) interactions among units (‘cells’) sensitive to oriented edges act to enhance the activity of units for which local and contextual information are compatible; at the same time, they suppress the activity of units for which local and contextual information conflict. Specifically, the BCS includes a stage of inhibition among contour-extracting cells sensitive to similar orientations of contrast at nearby positions of perceptual space. Cells receiving such inhibition are end-stopped, as described in section 5. Such competition among cells explains how, under the proper conditions of orientational alignment and spatial juxtaposition of edges, inducer boundary signals can inhibit boundary signals of the neon segment, thereby making the boundaries permeable. Note that inhibition among BCS units does not diminish the color signal originating in the neon segment in the FCS. If boundaries are made sufficiently permeable, however, the color signal originating from the neon segment may diffuse into the neighboring region, where mixture with an induced brightness, described in the next section, results in a desaturated appearance. The permeability of boundaries in the neon effect may vary between partial and nearly complete; in the former case, the color signal in the neon segments will be stronger than that which diffuses out of the segments.

The same BCS mechanisms that are responsible for inhibiting the boundaries of the neon segment also help to reorganize the local information for boundary position and

orientation at the junctions formed where the collinear sides of inducer and neon segments abut. For example, in the neon cross configuration, signals for boundaries perpendicular to the orientation of the inducer and neon segments are amplified. Note that the same mechanisms that underlie the formation of illusory contours roughly perpendicular to line ends are also involved in inhibiting the boundaries of the neon segment, thereby permitting spreading in neon configurations. The BCS also includes a stage of completion of boundaries, mediated by cooperative bipole cells, so that those amplified signals may be grouped to form illusory contours which surround the area in which the neon color spreads.

6.2 Brightness boosting: putting the 'glow' in neon spreading

Neon color often appears to glow, with an amplified brightness accompanying the illusory hue. This brightness increase appears related to brightness increments in plain illusory figures. Consider the Ehrenstein pattern and its neon counterpart of figure 2. The Ehrenstein pattern alone induces a brightness increase within the illusory figure; the neon variation appears to be a combination of a similar brightness increase with a color diffusion.

Recently, Gove et al (1995) have proposed that formation of brightness buttons at line ends may be accomplished by a local circuit that feeds back the signals from cells of V1 onto cells in the lateral geniculate nucleus (LGN). Specifically, feedback from end-stopped cells of V1 can amplify the response of center-surround cells in the LGN when the ends of thin lines fall within the receptive fields of the LGN cell. If a thin dark line end falls in the surround of an on-center, off-surround cell in the LGN, the cell's 'on' response would be amplified by the feedback. The visible effects of such enhanced LGN cell activities, subject to processing by later mechanisms, are brightness buttons.

The simplest example of diffusion of brightness button signals and the subsequent containment of those signals by illusory contours occurs in the classical Ehrenstein illusion. A similar analysis explains the enhanced brightness or glow of the neon region in the neon cross configuration of figure 2, insofar as the effects of increased brightness and flowing color may be additive (Bressan 1995). The desaturation of color observed at the transition between a colored cross and the black inducers may result from the superposition of a brightness button generated at the inducer line end.

Bressan (in preparation) has recently noted that certain combinations of colors for inducers and neon segments produce neon color that is not identical to that of the neon segment. Instead, the spreading color appears to be a mixture of the color of the segments with a color that is complementary to that of the inducers. For example, magenta lines with red neon segments produce yellow neon spreading. Yellow is the result of the additive mixture of red and green, where red is the color of the segments and green is the color complementary to magenta. Within the BCS/FCS framework, this effect can be analyzed as a

generalization of the brightness button effect for dark achromatic inducers. That is, the inducing line produces, just outside its end, a button of complementary color signal in the FCS representation, which then combines with the color of the segments to produce the neon color spreading effect.

The study of neon color spreading began as an unambitious exploratory venture by a few perceptual psychologists, who were initially attracted by the mere existence of this visual illusion, by its beauty, and perhaps its paradoxical nature. The developments of such curiosity represent a remarkable example of how the phenomenologist's observations and queries can inspire and assist psychophysical investigation, neurophysiology, modeling, and theory construction in vision research.

Acknowledgements. The authors are very grateful to the Rockefeller Foundation for making possible the writing of this manuscript, through its support of a Team Residency at the Bellagio Study and Conference Center. Thanks are also due to S. Lehar, D. Hoffman, W. H. Ehrenstein, J. S. Werner, C. Redies, D. Todorovic', and C. M.M. de Weert for their comments on the paper. Ennio Mingolla was partially supported by the Office of Naval Research (N00014-95010597, N00014-95-1-0409, and N00014-95-1-0657). Lothar Spillmann was supported in part by grant SP 67/4-1 from the German Research Council. Takeo Watanabe was supported in part by the National Science Foundation SBR-9631573.

References

- Bozzi P, 1975 "Osservazioni su alcuni casi di trasparenza fenomenica realizzabili con figure a tratto" in *Studies in Perception. Festschrift for Fabio Metelli* Ed. GB Flores d'Arcais (Milano: Martello) pp 88-110
- Bressan P, 1993a "Neon color spreading with and without its figural prerequisites" *Perception* **22** 353-361
- Bressan P, 1993b "Revisitation of the luminance conditions for the occurrence of the achromatic neon color spreading illusion" *Perception & Psychophysics* **54** 55-64
- Bressan P, 1995 "A closer look at the dependence of neon color spreading on wavelength and illuminance" *Vision Research* **35** 375-379
- Bressan P (in preparation) "Chromatic induction in neon color spreading figures"
- Bressan P, Vallortigara G, 1991 "Illusory depth from moving subjective figures and neon color spreading" *Perception* **20** 637-644
- Carman G J, Welch L, 1992 "Three-dimensional illusory contours and surfaces" *Nature* **360** 585-587
- Cicerone C M, Hoffman D D, Gowdy P D, Kim J S, 1995 "The perception of color from motion" *Perception & Psychophysics* **57** 761-777
- Day R H, Jory M K, 1978 "Subjective contours, visual acuity, and line contrast" in *Visual Psychophysics and Physiology* Eds JC Armington, J Krauskopf, BR Wooten (New York: Academic Press) pp 331-340
- de Weert C M M, 1991 "Assimilation versus contrast" in *From Pigments to Perception* Eds A Valberg, BB Lee (New York: Plenum Press) pp 305-311

- Ehrenstein W, 1941/1987 "Modifications of the brightness phenomenon of L Hermann" in *The Perception of Illusory Contours* Eds S Petry, GE Meyer (1987; New York: Springer) pp 35-39 (translated by A Hogg from "Über Abwandlungen der L Hermannschen Helligkeitserscheinung" *Zeitschrift für Psychologie* **150** 83-91)
- Ejima Y, Redies C, Takahashi S, Akita M, 1984 "The neon color effect in the Ehrenstein pattern: Dependence on wavelength and illuminance" *Vision Research* **24** 1719-1726
- Frisby J P, Clatworthy J L, 1975 "Illusory contours: Curious cases of simultaneous brightness contrast?" *Perception* **4** 349-357
- Gove A, Grossberg S, & Mingolla E, 1995 "Brightness perception, illusory contours, and corticogeniculate feedback" *Visual Neuroscience*, **12**, 1027-1052.
- Grossberg S, 1984 "Outline of a theory of brightness, color, and form perception" in *Trends in Mathematical Psychology* Eds E Degreef, J van Buggenhaut (Amsterdam: Elsevier/North Holland) pp 5559-5586
- Grossberg S, Mingolla E, 1985 "Neural dynamics of form perception: Boundary completion, illusory figures, and neon color spreading" *Psychological Review* **92** 173-211
- Kato H, Bishop P O, Orban G A, 1978 "Hypercomplex and simple/complex cell classification in cat striate cortex" *Journal of Neurophysiology* **41** 1071-1095
- Kennedy J M, 1979 "Subjective contours, contrast and assimilation" in *Perception and Pictorial Representation* Eds C Nodine, DF Fisher (New York: Praeger) pp 167-195
- Kojo I V, Liinasuo M E, Rovamo J M, 1995 "Neon colour spreading in three-dimensional illusory objects" *Investigative Ophthalmology & Visual Science* **36** 665
- Metelli F, Masin S C, Manganelli A M, 1980 "Partial transparency" *Atti dell'Accademia Patavina di Scienze, Lettere ed Arti* **92** 115-169
- Meyer G E, Dougherty T, 1987 "Effects of flicker-induced depth on chromatic subjective contours" *Journal of Experimental Psychology: Human Perception and Performance* **13** 353-360
- Nakayama K, Shimojo S, Ramachandran V S, 1990 "Transparency: Relation to depth, subjective contours, luminance, and neon color spreading" *Perception* **19** 497-513
- Peterhans E, von der Heydt R, Baumgartner G, 1986 "Neuronal responses to illusory contour stimuli reveal stages of visual cortical processing" in *Visual Neuroscience* Eds JD Pettigrew, KJ Sanderson, WR Levick pp 343-351
- Redies C, 1989 "Discontinuities along lines: Psychophysics and neurophysiology" *Neuroscience & Biobehavioral Reviews* **13** 17-22
- Redies C, Spillmann L, 1981 "The neon color effect in the Ehrenstein illusion" *Perception* **10** 667-681
- Redies C, Spillmann L, Kunz K, 1984 "Colored neon flanks and line gap enhancement" *Vision Research* **24** 1301-1309
- Rossi AF, Paradiso MA, 1997 "Temporal limits of brightness induction and mechanisms of brightness perception" *Vision Research* **37** in press
- Takeichi H, Shimojo S, Watanabe T, 1992 "Localization of the process for color filling-in in the neon color spreading" *Perception* **21** 313-324
- Takeichi H, Watanabe T, Shimojo S, 1992 "Illusory occluding contours and surface formation by depth perception" *Perception* **21** 177-184

- Tuijl H F J M van, 1975 "A new visual illusion: Neonlike color spreading and complementary color induction between subjective contours" *Acta Psychologica* **39** 441-445
- Tuijl H F J M van, Weert C M M de, 1979 "Sensory conditions for the occurrence of the neon spreading illusion" *Perception* **8** 211-215
- Varin D, 1971 "Fenomeni di contrasto e diffusione cromatica nell'organizzazione spaziale del campo percettivo" *Rivista di Psicologia* **65** 101-128
- Wallach H, 1935 "Über visuell wahrgenommene Bewegungsrichtung" *Psychologische Forschung* **20** 325-380
- Watanabe T, Cavanagh P, 1991 "Texture and motion spreading, the aperture problem, and transparency" *Perception & Psychophysics* **50** 459-464
- Watanabe T, Sato T, 1989 "Effect of luminance contrast on color spreading and illusory contour in the neon color spreading effect" *Perception & Psychophysics* **45** 427-430
- Watanabe T, Takeichi H, 1990 "The relation between color spreading and illusory contours" *Perception & Psychophysics* **47** 457-467