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THE ART OF SEEING AND PAINTING

Stephen Grossberg*

Department of Cognitive and Neural Systems
and
Center of Excellence for Learning in Education, Science, and Technology
Boston University
677 Beacon Street, Boston, MA 02215
Phone: 617-353-7858/7857
Fax: 617-353-7755

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All correspondence should be addressed to
Professor Stephen Grossberg
Email:steve@bu.edu

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Abstract

The human urge to represent the three-dimensional world using two-dimensional pictorial representations dates back at least to Paleolithic times. Artists from ancient to modern times have struggled to understand how a few contours or color patches on a flat surface can induce mental representations of a three-dimensional scene. This article summarizes some of the recent breakthroughs in scientifically understanding how the brain sees that shed light on these struggles. These breakthroughs illustrate how various artists have intuitively understand paradoxical properties about how the brain sees, and have used that understanding to create great art. These paradoxical properties arise from how the brain forms the units of conscious visual perception; namely, representations of three-dimensional boundaries and surfaces. Boundaries and surfaces are computed in parallel cortical processing streams that obey computationally complementary properties. These streams interact at multiple levels to overcome their complementary weaknesses and to transform their complementary properties into consistent percepts. The article describes how properties of complementary consistency have guided the creation of many great works of art.

Running Title

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Key Words

Complementary computing, visual cortex, perceptual grouping, surface filling-in, figure-ground perception, amodal boundaries, perspective, T-junctions, opponent colors, neon color spreading, watercolor illusion, chiaoscuro, complementary consistency, Impressionism, Fauvism, Matisse, Monet, Hawthorne, Hensche, Leonardo da Vinci

1. Introduction

Many painters have struggled to understand how we see a 3D world, and to express their insights on flat canvases or other 2D surfaces. Cavanagh (2005) has noted that "discrepancies between the real world and the world depicted by artists reveal as much about the brain within us as the artist reveals about the world around us" (p. 307). This article will summarize how the insights of various artists reflect different organizational principles about how the brain sees. The article does not, however, focus on discrepancies between the real world and the world depicted by artists. Rather, I summarize brain organizational principles and mechanisms that reflect different artistic efforts. A recent cortical model of how the brain sees clarifies these organizational principles and mechanisms and enables the nature of artists' struggles to be clearly articulated.

The foundational model is called the FACADE model, or Form-And-Color-And-DEpth model, of 3D vision and figure-ground perception (Grossberg, 1987b, 1994, 1997; Grossberg and McLoughlin, 1997; Grossberg and Pessoa, 1998; Kelly and Grossberg, 2000; McLoughlin and Grossberg, 1998). More recently, the FACADE model has been further developed as the 3D LAMINART model to show how the layered circuits of visual cortex realize processes of 3D vision and figure-ground perception, and to thereby explain and predict even more perceptual and brain data (Cao and Grossberg, 2005; Grossberg, 1999; Grossberg and Howe, 2003; Grossberg and Swaminathan, 2004; Grossberg and Yazdanbakhsh, 2005)

My discussion will address aspects of the following basic question that needs to be answered whenever one considers painting: Why can brain designs that represent the 3D world of our daily experience also respond to 2D pictures with conscious 3D representations of what the pictures depict? Without this brain capacity, the world of pictorial art, whether expressed by paintings, movies, or TV, could not exist. This is a huge topic, and I will only sample some highlights here. Before turning to artistic examples, I will ground my discussion with some basic discoveries from the FACADE and 3D LAMINART models about how the brain sees.

2. Complementary Computing of Boundaries and Surfaces

What are the perceptual units that are used by the brain to build visible percepts? Our modeling work predicted in the mid-1980s (Grossberg, 1984; Cohen and Grossberg, 1984; Grossberg and Mingolla, 1985a, 1985b; Grossberg and Todorovic, 1988), and many subsequent experiments have supported, the claim that *boundaries* and *surfaces* are the brain's perceptual units, notably 3D boundaries and surfaces. Although this seems like a simple enough answer, actually it represented a radical break with previous views of visual perception.

This was a radical break because it is part of a major paradigm shift in understanding how the brain works. It also introduced into vision some conclusions which seem shocking to the non-specialist, because the properties of boundaries and surfaces are far from obvious. These shocking conclusions reflect, moreover, just the sorts of issues with which artists have had to cope to make great paintings.

The new paradigm is what I have called *complementary computing* (Grossberg, 2000). Complementary computing contradicts the previously popular hypothesis that the brain sees by using *independent modules*. The notion of independent modules tried to deal with the realization that visual properties (e.g., form, color, motion, depth) require specialized processes to be computed. Many scientists therefore proposed that our brains possess independent modules, as in a digital computer, to process these different properties. The brain's organization into distinct anatomical areas and processing streams supports the idea that brain processing is specialized. However, specialization does not imply independence. Independent modules should be able to fully compute a property like form, color, motion, or depth on its own. Unfortunately, this is not true: During visual perception, strong interactions are known to occur between perceptual qualities (e.g., Egusa, 1983; Faubert and von Grunau, 1995; Kanizsa, 1974; Pessoa *et al*., 1996; Smallman and McKee, 1995). In particular, form and motion can interact, as can brightness and depth, among other combinations of qualities.

This mutual dependence of perceived properties is one of the hardest things for vision scientists to explain. It is also one of the hardest things for an artist to embody in a painting. I know at least one *plein air* artist who has said that if, while she is painting a scene, a car drives into the scene and parks, then she has to start painting the scene all over again. This artist's comment vividly illustrates that specialization does not imply independence.

Figure 1

Cortical anatomy shows that there exist several processing streams in the visual brain (DeYoe and van Essen, 1988), and these streams have been assumed to carry out specialized processing, such as form, color, motion, and depth processing (Figure 1). However, even at the cortical level, the simple view of independent modules is not supported. Indeed, cells in different streams often share many properties in common. Complementary computing clarifies this situation by asserting that certain pairs of processing streams compute complementary properties, indeed that boundaries and surfaces are computed in complementary streams, with the LGN-(V1 interblob)-(V2 interstripe)-V4 stream computing boundaries, and the LGN-(V1 blob)-(V2 thin stripe)-V4 stream computing surfaces. The ability of cells in one stream to compute one sort of property (e.g., a perceptual boundary) prevents it, in principle, from computing a complementary property (e.g., a perceptual surface). The streams need to interact at multiple stages of processing to overcome their complementary weaknesses. A neurophysiologist who records a cell in one stream would therefore have considerable difficulty separating properties that are computed directly in that stream from properties that are projected to the stream from cells in the complementary stream.

The hyphenated name Form-And-Color-And-DEpth (FACADE) attempts to express the fundamental fact that the perceptual qualities of form, color, and depth can mutually influence one another, and that these properties are multiplexed at individual cells within the visual cortex. The name FACADE also expresses the idea that, due to this interaction, we can understand how the world looks vividly "real" without falling into the trap of Naïve Realism.

Figure 2

Some of the shocking conclusions about boundaries and surfaces include the following. Suppose that you are asked: "Why do we bother to see?" You might very well answer: "We see things in order to recognize them." However, it is easy show that this claim is false, by providing a counterexample to it. In Figure 2a, the vertical boundary that forms between the offset gratings of horizontal lines is consciously recognized, but not visibly seen. However, if we can recognize things without seeing them, then why *do* we see?

Figure 2a shows that "some boundaries are invisible." Actually, in a sense that is clarified below, "all boundaries are invisible," at least within the boundary stream. Visibility is a property of the complementary surface stream. Some of the other surprising conclusions of this sort of analysis include: All line ends are illusions. Continuous boundaries form discontinuously. Some surface colors are invisible. And, as an answer to the question of why we see, if not to recognize: Visible surface colors are used for reaching.

Before going on, you might express the concern: "This may be interesting, but what does it have to do with painting?" I claim that, in fact, a core struggle of great artists such as Matisse, the Impressionists and many other *plein air* painters concerned artistic implications of the fact that "all boundaries are invisible."

3. All Boundaries are Invisible

Perceptual boundaries are also called groupings. They take many forms (see Figure 3), but all of these forms have begun to be explained as the outcome of a single type of perceptual grouping process. Figures 4a and 4b illustrate some grouping properties using illusory contour percepts of Kanizsa squares. We see boundaries forming *inwardly* between cooperating pairs of incomplete disk (pac man) inducers to form the square's sides. These boundaries are *oriented* collinearly between like-oriented inducers.

Figure 3

The square boundary in Figure 4b can be both seen and recognized because of the enhanced illusory brightness of the Kanizsa square. The square boundary in Figure 4a can be recognized even though it cannot be seen; that is, there is no brightness or color difference on either side of the boundary. Figure 4b shows that *some* boundaries can be recognized even though they are invisible. Our recent vision models predict that *all* boundaries are amodal, or invisible, within the boundary stream.

Figure 4

The boundary in Figure 4a is invisible because its vertical boundaries form between black and white inducers that possess opposite contrast polarity on the gray background. The same is true of the boundary around the gray square in Figure 4c. Figure 4c illustrates how, by pooling signals from opposite contrast polarities at each position, the brain can build a boundary around the entire square, even though it lies in front of a textured background whose contrasts with respect to the square reverse along the boundary. The brain does this by pooling opposite contrast polarity signals at every boundary position. Pooling of opposite polarities renders the boundary system output *insensitive* to contrast polarity. The boundary stream cannot represent visible colors or brightnesses, because its outputs cannot signal the difference between dark and light. In summary, "all boundaries are invisible" to enable the visual cortex to build boundaries around objects as a key step in object recognition.

If boundaries are invisible, then how do we see anything? The FACADE and 3D LAMINART models predict that visible properties of a scene are represented by the surface processing stream. A key step in representing a visible surface is called *filling-in*. Why does a surface filling-in process occur? An early stage of surface processing compensates for variable illumination, or "discounts the illuminant," in order to prevent illuminant variations, which can change from moment to moment, from distorting all percepts. Discounting the illuminant attenuates color and brightness signals except near regions of sufficiently rapid surface change, such as edges or texture gradients, which are relatively uncontaminated by illuminant variations. Later stages of surface formation fill in the attenuated regions with these relatively uncontaminated color and brightness signals, and do so at the correct relative depths from the observer through a process called *surface capture*. One struggle that many artists face is how to represent surface colors "out there in the world," even though all they can consciously see are the results of discounting the illuminant within their own brains.

Figure 4d shows an example of surface filling-in that is called neon color spreading (Grossberg and Mingolla, 1985a; Van Tuijl, 1975). Filling-in spreads *outwardly* from the individual blue inducers in all directions. Its spread is thus *unoriented*. The FACADE and 3D LAMINART models predict that signals from the boundary stream to the surface stream define the regions within which filling-in is restricted. Without these boundary signals, filling-in would dissipate across space, and no visible surface percept could form. Filling-in can lead to visible percepts because it is *sensitive* to contrast polarity. The complementary properties of boundary completion and surface filling-in are summarized in Figure 4.

4. Matisse Realized that All Boundaries are Invisible

Invisible boundaries indirectly assure their own visibility through their interactions with the surface stream. Within the surface stream, boundaries trigger the filling-in of lightness and color within their contours, and restrict the spreading of lightness and color to the surface region that they bound. In addition, the same visual stimuli activate both the boundary and the surface streams, in parallel. Thus, a visual scene or painting activates both the boundary and the surface streams in parallel, the boundary stream generates an emergent perceptual grouping, and this grouping controls the filling-in of potentially visible surface lightnesses and colors within the surface stream. These facts about brain processing have influenced the creative struggles and decisions of many artists.

In particular, every artist faces the choice of whether to actually draw the boundaries around the surfaces that his or her painting will represent, or to allow the brain to create these boundaries through the process of amodal perceptual grouping, as it does in response to the images in Figure 3. Figure 3b is particularly instructive, because it illustrates how the brain can respond to a spatially discrete pattern of 2D texture elements with a 3D representation of a smooth surface.

Figure 5

Matisse, among others, struggled with this issue for many years. Later in his life, when his health led him to work with paper cut outs, he wrote about "the external conflict between drawing and color…Instead of drawing an outline and filling in the color…I am drawing directly in color" (Matisse, 1947/1992). Matisse was already "drawing directly in color" in his paintings from the Fauve period, as illustrated in his painting from 1905 called The Roofs of Collioure (Figure 5). Matisse realized instinctively that, if he painted directly with appropriately shaped color patches, these patches would induce the formation of amodal boundaries within the brain of the viewer. These boundaries, in turn, would capture the inducing colors to form the surface representations of color and form that enable the viewer to understand the painting (Figure 6).

Figure 6

How does “drawing directly in color” change how a painting looks? If instead of drawing directly in color, Matisse drew visible contours around his surfaces, and did so in a dark color, then these contours could darken the surface colors of the entire scene, via a process of color assimilation. Color assimilation occurs due to mechanisms whereby boundaries control the filling-in of surface color. See Kelly and Grossberg (2000) for an explanation of how this can happen. Matisse, however, wanted to create bright, glowing surface colors, which were a goal of the entire Fauve movement to which he belonged. He therefore figured out how to prevent the darkening and other distorting effects of visibly drawn contours, without preventing a viewer from perceiving the surface representations that are needed to understand his paintings. An intuitive understanding of the fact that “all boundaries are invisible” was one result of this struggle.

A striking example of color assimilation due to visible contours is the watercolor illusion of Pinna (Figure 7). Pinna and Grossberg (2005) have explained this variant of color assimilation using the competition that occurs between nearby boundaries when one boundary is stronger than the other. The stronger boundary is induced by a larger contrast in the scene. A stronger boundary can inhibit a nearby weaker boundary more than conversely. The color that the weaker boundary would otherwise contain can then partially spread, and be assimilated, into the contiguous surface.

Figure 7

5. The Impressionists and the Cape Cod School of Art

Many other artists have also struggled with how to represent object surfaces without drawing explicit boundaries around them, including the leading members of the Cape Cod school of art, Charles Hawthorne (Hawthorne, 1938/1960) and his most famous student, Henry Hensche (Hensche, 1988; Robichaux, 1997). The Cape Cod school championed painting *en plein air* and was thus especially concerned with representing the vivid colors of natural scenes. Their statements below, which were aimed at teaching the art of seeing and painting, reflect some of the same themes that concerned Matisse. Hawthorne (1938/1960) wrote: “Beauty in art is the delicious notes of color one against the other…all we have to do is to get the color notes in their proper relation” (p. 18). “…put down spots of color…the outline and size of each spot of color against every other spot of color it touches, is the only kind of drawing you need bother about…Let color make form—do not make form and color it. Forget about drawing…” (pp. 25-26). “You don’t hear me say much about drawing. It is because I think drawing the form, and painting, are better separated. The first thing is to learn to see color” (pp. 41-42). Hensche further developed these concepts and put them into a historical context in which Monet played a pivotal role: “When Monet came along…he revolutionized the ‘art of seeing.’ …it was the method of expressing light in color, and not value, to allow the key of nature to show clearly…The landscape helped Monet determine how color expressing the light key was the first ingredient in a painting, not drawing” (Robichaux, p. 27). “The untrained eye is fooled to think he sees forms by the model edges, not with color…Fool the eye into seeing form without edges” (Robichaux, p. 31). “Every form change must be a color change” (Robichaux, p. 33).

6. Surface Filling-In of Impressionist Paintings and SAR Images

Although the Impressionists pioneered an enhanced understanding of the role of color in painting, each painter expressed this insight in a unique way. We are all aware of how

Impressionist paintings of such artists as Monet can perceptually disintegrate into meaningless jumbles of color spots as they are approached and their individual color elements become more visible, yet when viewed from a sufficient distance are organized by the brain into vibrant colored surfaces that have a clear and often exquisite scenic meaning.

The role of amodal emergent boundaries is critical in being able to make sense of an Impressionist painting, notably the fact that boundaries form more vigorously in response to statistically significant distributions of contrast and color across space. As in the case of the watercolor illusion, the stronger boundaries inhibit weaker boundaries that would otherwise form. Boundary sensitivity to statistical groupings of contrast and color is needed to form percepts of an Impressionist painting because the painted surface is often densely covered with small spots of color. Surviving boundaries group together statistically significant combinations of these contrast and color spots to generate a form-sensitive plexus of boundaries, or *boundary web* (Grossberg, 1987a; Grossberg and Mingolla, 1987; Grossberg, Kuhlmann, and Mingolla, 2006; Pinna and Grossberg, 2005). Then the colors fill-in within the compartments of the boundary web, mixing within each compartment.

Figure 8

A similar effect can be seen when the LAMINART vision model processes images that are derived from an artificial sensor, such as Synthetic Aperture Radar, or SAR. In a SAR image, there is a great deal of granularity in the input image, much as in an Impressionist painting. Figure 8 illustrates a SAR simulation from Mingolla, Ross, and Grossberg (1999). Figure 8a is the input image, which contains five orders of magnitude in the SAR power return. This image would look entirely black were it not for some image enhancement due to the reproduction process. Figure 8b shows the image after it has been normalized without saturating its relative contrasts. This *contrast normalization* property is a result of discounting the illuminant. Here the granularity, or pointilistic nature, of the image is evident. Figure 8c shows the emergent boundaries that are derived from the contrast-normalized image, and Figure 8d shows the filled-in surface representation, which shows a top-down view of a country scene in which a bridge crosses a highway in an area filled with trees and grass. Figure 8d is created when the contrast-normalized input to the surface stream in Figure 8b is gated by the boundaries in Figure 8c and thereupon fills-in until it hits a boundary. This happens within multiple scales of processing that are all lumped together in Figure 8. In contrast to the granularity in Figure 8b, the surface representation of Figure 8d exhibits smoothly shaded forms. The conversion from granular texture to smooth form derives from the use of boundary-gated filling-in to smooth over input differences within each boundary compartment, and to differentiate inputs between boundary components, much as the brain does in response to an Impressionist painting.

7. 2D Image to 3D Percept: Multiple Scales, Binocular Disparity, Chiaroscuro, and Perspective

The ability of amodal boundary webs to group together statistically regular combinations of contrast and color also helps to explain the percept that is generated by the image in Figure 3b. Two basic problems must be solved for the brain to achieve this result: (1) Patterns of spatially discrete 2D texture elements need to be transformed into a spatially smooth surface representation of 3D shape. (2) Changes in the statistical properties of texture elements across space need to induce corresponding changes in the perceived 3D shape of this surface representation. This can be achieved by the FACADE model when multiple filters of different orientation preference and spatial size, or scale, process the 2D image. Several filters can respond to the same texture features, but in different ways. Filter orientation and size determine what properties of the texture can be detected by each filter.

Why are there multiple filter sizes? This is because the brain needs to construct cells that are sensitive to different *binocular disparities*. Binocular disparity describes the positional differences of an object's projections on an observer's left and right retinas, and is a strong cue for perceiving depth of objects that are at sufficiently near depths (Howard and Rogers, 2002; Julesz, 1971; Tyler, 2004). For distant objects, monocular cues, such as T-junctions, may be used to determine relative depth when one object is nearer than another object, and occludes parts of the farther object (Howard and Rogers, 2002). Occlusion can also elicit strong 3D percepts when we view 2D images (Figure 9). In addition to being perceived at a farther depth, the visible parts of an occluded object are often perceptually linked together behind the occluder by amodal boundary and surface representations (Grossberg, 1994).

Figure 9

For the moment, we concentrate on the fact that bigger scales can more easily compute larger binocular disparities than smaller scales, other things being equal, although bigger scales can also compute a larger range of disparities than smaller scales. It is also often the case that objects tend to subtend a larger region of the retina, and to create larger binocular disparities, when they are closer to an observer than when they are far away. This tendency for larger scales to represent nearer objects is called the *size-disparity correlation* (Julesz and Schumer, 1981; Kuffler, 1978; Prince *et al.*, 2002; Prince and Eagle, 1999; Richards and Kaye, 1974; Schor and Tyler, 1981; Schor and Wood, 1983; Schor *et al.*, 1984; Smallman and MacLeod, 1994; Tyler, 1975, 1983). The differential activation of multiple scales occurs in response to 2D pictures as well as to 3D scenes, which clarifies how pictures can represent the 3D world. It needs to be emphasized, however, that these multiple-scale filter activations are ambiguous if only because larger scales can represent a larger range of disparities than can smaller scales. Thus, multiple scales can be activated, but to different degrees, by objects at each depth.

The FACADE model clarifies how this ambiguous multiple-scale representation of shape is disambiguated using cooperative and competitive boundary interactions (Grossberg, 1987b, 1994, 1997; Grossberg and Mingolla, 1987) that, in concert with scale-to-depth and depth-to-scale maps (Grossberg, 1994), carry out coherent perceptual groupings within depths. These maps link together all of the multiple-scale filters that can respond to the same narrow range of depths with a boundary representation that represents that depth range, and conversely. Across-depth competition helps to select the most strongly activated 3D boundary representations, while suppressing weaker boundary representations. These processes take place within multiple depth-selective boundary webs before the boundary representations regulate the filling-in of a smooth 3D surface representation that is what we see. Grossberg, Kuhlmann, and Mingolla (2006) used these ideas to quantitatively simulate challenging percepts and data about 3D shape-from-texture, including percepts such as the one in Figure 3b.

3D shape-from-shading can also be explained by similar mechanisms, except that, with a shaded image, the inducers of the boundary web are not separated in space. The percept of blue columns bulging in 3D space that is derived from viewing Figure 7 can be explained using these mechanisms, as can the related percept of the blue regions as being the "figures" of the image, and the white regions the "background" (Pinna and Grossberg, 2005). Indeed, the painterly technique of *chiaroscuro*, whereby a skillful use of light and dark paints create the illusion of 3D shape, achieves the illusion of a bulging 3D figure instead of the actual 2D painted surface. Leonardo da Vinci was one of the first painters to master the chiaroscuro technique, whose creation of a 3D percept may also be explained by how differentially activated multiple-scale filters give rise to a 3D boundary web that captures surface color at different depths.

The same sorts of multiple-scale boundary representations can be used to explain how *perspective* in a 2D picture can generate a 3D percept of increasing depth (Figure 9b), as has been used with great effect since the time of Renaissance painters. The bigger scales, other things being equal, create a percept of a nearer surface, while the smaller scales create a percept of a surface that is farther away. The ambiguity in the multiple-scale representation must here too be eliminated by scale-to-depth and depth-to-scale maps, cooperative-competitive boundary interactions, and the filling-in of slanted surface representations. How the brain fills-in percepts of surfaces that are slanted in depth was first simulated in Grossberg and Swaminathan (2004).

Figure 10

Chiaroscuro, perspective, and T-junctions are all employed in the Mona Lisa of Leonardo da Vinci, each contributing in its own way create the 3D appearance of the figure and to project it in front of the landscape background (Figure 10). The chiaroscuro and perspective effects can be explained in the manner summarized above. Let us briefly consider how T-junctions help to create a percept of a figure in front of its background. Here again the complementarity of boundaries and surfaces plays an important role.

8. Bipole Cells, T-junctions, Figure-Ground Perception, and Pictorial Depth

First, we need to briefly summarize theoretical and experimental evidence for how perceptual boundaries are formed, and how they are completed in response to pictures and scenes with spatially separated inducers, as in Figure 3. Perceptual boundaries, or groupings, may be formed by cells in layer 2/3 of cortical area V2, among other places. Long-range excitatory connections exist among the cells in this layer, and provide an anatomical substrate for forming perceptual groupings, including the illusory contours of the Kanizsa square, as well as the groupings which represent ecologically important scenic cues such as shading, texture, and depth (Figure 3). These connections tend to exist between cells which are tuned to the similar orientational preferences that are aligned, or co-linear, across space. Left to themselves, these excitatory connections could lead to an uncontrollable spread of excitation across the cortex.

Figure 11

In addition to the long-range excitatory connections, there are shorter-range inhibitory connections. These inhibitory connections are activated by the excitatory connections and also terminate on the cells that send out the long-range excitatory connections (Figure 11). This inhibition is balanced against the excitation in order to realize a property for perceptual grouping that I have called the *bipole property* (Cohen and Grossberg, 1984; Grossberg, 1984; Grossberg and Mingolla, 1985a, 1985b) A cell that obeys the bipole property can fire if it gets approximately co-linear excitatory inputs from approximately co-oriented cells on both sides of its receptive field, even if it does not directly receive a bottom-up input. This is what happens, for example, when an illusory contour is formed in response to a Kanizsa square (Figure 3a). A bipole cell can also fire in response to a bottom-up input alone. This can happen, for example, when a bipole cell is directly activated by an oriented contrast, such as a short edge in a picture or scene. Finally, a bipole cell can respond to a bottom-up input plus any combination of long-range signals from nearby bipole cells. This is what happens, for example, in response to the extended contours of the pac men figures in Figure 3a that induce the illusory contour: The direct input comes from the oriented contrast at the location of the bipole cell, while additional inputs come from the cells that respond to other positions on the pac men.

The bipole property allows perceptual boundaries to form *inwardly* between pairs or greater numbers of inducers, as in the Kanizsa square of Figure 3a, but *not outwardly* from individual inducers, which would allow boundaries to form uncontrollably from individual specks of contrast in a scene. This balance of excitation and inhibition is also important during cortical development: Without the balanced inhibitory interactions, the growth of the long-range excitatory connections during development could proliferate uncontrollably if inhibition were too weak, or could be suppressed entirely if inhibition were too strong; see Grossberg and Williamson (2001) for model simulations.

Cortical cells with the bipole property were discovered at around the same time that we predicted them. Cells with these properties were reported in cortical area V2 of monkeys in the classical experiments of von der Heydt, Peterhans, and Baumgartner (1984) and in subsequent experiments from this laboratory; e.g., Peterhans and von der Heydt (1989). Later psychophysical experiments have also supported this receptive field structure; e.g., Field, Hayes, and Hess (1993) and Kellman and Shipley (1991). See Grossberg (2003) for a review of additional experimental evidence about bipole cells.

Figure 12

Bipole cells do not respond only to their preferred orientation and positions. Due to the manner in which they develop from visual experience, they receive excitatory connections from a range of positions that are close to their preferred co-linear locations, and also from a range of orientations that are close to their preferred orientation. Likewise, inhibition is received from a range of positions near the bipole, and acts particularly strongly on orientations other than their preferred orientation (Figure 12). These basic bipole properties enable the brain to react to T-junctions in a scene or picture.

Consider the inputs received by bipole cells where the top of the T in Figure 12 meets its stem. The bipole cells whose orientation preference is co-linear with the T top receive excitatory inputs from both sides of the T top. In contrast, the bipole cells whose orientation preference is co-linear with the T stem receive excitatory inputs from only one side of the T stem. The more active bipole cells at the T top can therefore inhibit the bipole cells along the T stem more than conversely. The inhibition along the T stem can completely inhibit boundary cells along the T stem at locations near the T top.

This break in the boundary is called an *end-gap*. The end-gap allows lightness and color signals to flow out of the figural region that would otherwise have been formed by the T stem. This flow of color initiates the separation of figures from their background, and tends to push the background to a perceived depth that is farther away than the figure. This happens due to feedback interactions between the boundary and surface streams that help to create a *consistent percept* in response to the *complementary* *properties* of the boundary and surface streams (Figure 13). I call this property *complementary consistency*.

Figure 13

For present purposes, I consider only the question of whether there is any direct evidence that competing boundaries can create end-gaps, that lightness and color can flow through these gaps, and that such a flow can influence figure-ground percepts? Neon color spreading provides an excellent classical example of how boundaries can create end-gaps and how color can flow through these gaps. In response to the image in Figure 4d, for example, the end-gaps form at the positions where the black and blue lines join. Grossberg and Mingolla (1985a) provided the first explanation of how this happens, and Grossberg (1994) provided the first explanation of how 3D percepts of neon can occur. Recent experiments have shown how a lightness or color flow through an end-gap can trigger a figure-ground percept, while also influencing perceived lightness or color (Dresp *et al.*, 2002; Tse, 2005). Several articles explain how this may happen (Grossberg, 1997; Grossberg and Yazdanbakhsh, 2005; Kelly and Grossberg, 2000). Pinna and Grossberg (2005) explain how neon color spreading and the watercolor illusion (Figure 7) may be given a unified explanation.

These conclusions provide some comfort to those who reasonably worry how the brain can embody competences, like figure-ground separation, that might otherwise seem too difficult to be discovered by Darwinian selection during brain evolution. FACADE theory provides an explanation of figure-ground separation that uses processes which seem much simpler than figure-ground perception itself. In other words, figure-ground perception may now be understood as an emergent property of simple processes. One key process is the way in which bipole cells form perceptual groupings. The balance between excitation and inhibition that realizes the bipole property also enables end-gaps to form at T-junctions. In addition, simple feedback interactions between the boundary and surface streams help to create consistent percepts in response to complementary properties (see Grossberg, 1997).

9. Equiluminance and Undulating Percepts

Great painters used a wide range of insights about how the brain sees to paint effective works of art. Monet, for example, created some paintings in which adjoining areas of the painting are almost *equiluminant*, such as his paintings called Impression:Sunrise (http://webexhibits.org/colorart/monet.html) and Near Argenteuil (see Figure 14 and http://webexhibits.org/colorart/monet2.html). The former painting can create the impression of sun undulating in the sky, and the latter can create the impression of red poppies quivering in a green field. The concept of equiluminance illustrates another aspect of boundary/surface complementarity.

Figure 14

Within the boundary stream, indeed already at complex cells of cortical area V1, an early stage of boundary formation (see Figure 13b), inputs are pooled over opposite contrast polarities and all opponent colors as part of the process of computing good boundary signals. The data of Thorell, DeValois, and Albrecht (1984) support this claim. Their important article reported data from macaque monkey that 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…were composed of overlapping color-regions" (p. 762). The pooling process at complex cells helps to build boundaries from essentially all sources of achromatic and chromatic contrastive signals that the brain can compute. Such pooling is also the basis for the prediction that "all boundaries are invisible," since light-dark and dark-light contrasts are pooled, as well as red-green, green-red, blue-yellow, and yellow-blue contrasts. It is of historical interest that Thorell *et al.* (1984) did not draw this conclusion. Instead, they asserted that 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). FACADE theory claims that complex cells are not color cells. Rather, they are boundary cells which, at least within the boundary stream, do not give rise to any visible color percept. In order to see, the surface stream does not lump all of these signals together. Rather, it elaborates them into separate opponent and double-opponent achromatic and chromatic channels that are the basis of visible achromatic and chromatic surface percepts.

When adjoining regions of a painting are equiluminant, then many of the contrastive signals that input to complex cells at the region boundaries are either zero or very small. If they were all zero, then there would be no boundary, and lightness and color would spread across both regions by filling-in and cancel out as in the Ganzfeld. This does not happen because the balance point of all the opponent pairs of signals (e.g., light-dark vs. dark-light, red-green vs. green-red, blue-yellow vs. yellow-blue) are not identical. However, at equiluminance, boundaries are weak and therefore labile. Boundary lability is, I claim, one factor that contributes to the impression of an undulating sun and quivering poppies.

Using opponent colors such as red and green at both sides of a boundary facilitates this effect, because equiluminance can then more easily be balanced across the several channels that contribute to the boundary, thereby creating a particularly weak boundary between the opponent colored regions.

10. Opponent Colors, Antagonistic Rebound, and Balance

Why are there opponent colors in the first place, with all their implications for color contrast in paintings? To explore this issue fully would take us beyond the scope of this article, but some comments can be made. A clue about how to think about this is that opponent colors can lead to *negative aftereffects*. For example, after one views a red patch of color for awhile, if one looks at a white piece of paper, a green aftereffect is experienced. Such an aftereffect is an example of an *antagonist rebound*; that is, offset of cells that code red causes an antagonist rebound of activation in the opponent cells that code green.

Opponent colors are not the only features that have an opponent organization and that experience antagonistic rebounds. If one observes an image for awhile with lines radiating like spokes of a wheel from a central point, and then looks at a blank white piece of paper, an antagonistic rebound occurs in which lines perpendicular to the spokes appear and seem to be organized in concentric circles. This is the MacKay illusion. If one looks at water running downward for awhile and then looks at a blank white piece of paper, an antagonistic rebound occurs in which motion seems to be moving upward. This is the Waterfall illusion. In addition to antagonistic rebounds in vision, they occur in many other brain systems. For example, offset of a sustained fearful cue can elicit a wave of relief, whereas removal of a desired food can elicit a wave of frustration. Why do opponent processes exist throughout the brain, and what functional role does antagonistic rebound play?

My colleagues and I have been developing Adaptive Resonance Theory, or ART, to explain such phenomena for the past thirty years; e.g., Grossberg (1976, 1978, 1980, 1984, 1991) and Carpenter and Grossberg (1991, 1993). ART clarifies another type of complementary computing in the brain. This one has to do with how the brain balances between expected vs. unexpected events, or familiar vs. unfamiliar events. ART shows how this balance enables the brain to learn quickly about a changing world without experiencing catastrophic forgetting.

Within ART, antagonistic rebounds play an important role in causing the rapid and context-sensitive *reset* of brain states in response to changing inputs. Such a reset process helps to *rebalance* sensory, cognitive, emotional, and motoric representations in response to rapidly changing environmental inputs, and to thereby enable the brain to response to new information in as unbiased a way as possible. When there is a mismatch between a learned expectation and a visual or other sensory cue, reset can also drive a *memory search* for more appropriate learned categories with which to represent the unexpected or unfamiliar event.

The opponent processing circuits in which such antagonistic rebounds occur are called *gated dipoles*. Gated dipoles also seem to represent all brain circuits where on-cells (cells activated by the original input) and off-cells (cells activated by the antagonistic rebound) coexist, and where offset of a previously active on-cell can cause an antagonistic rebound that activates the corresponding off-cell. Gated dipoles have been used to explain a wide variety of behaviors about animal and human cognitive-emotional learning and decision-making. See Grossberg (2000) and Grossberg and Seidman (2006) for how imbalanced gated dipoles may contribute to schizophrenia and autism, respectively.

In summary, even the seemingly relatively simple phenomenon of opponent colors reflects a general brain design that embodies a type of complementary computing. Tipping the balance between opponent colors can tend to cause aftereffects that can influence the percepts that we see, both in the world and in paintings.

8. Concluding Remarks: Complementarity and Art

This article indicates how a variety of artists, including Renaissance painters, Fauvists, Impressionists, and members of the Cape Cod School of painting, have developed an artistic understanding of rather deep properties of how the brain sees. Their insights included an intuitive understanding of the complementary properties of 3D perceptual boundaries and surfaces.

All of these artists seemed to understand that a given spot of contrast or color in a picture can activate both the cortical boundary stream and the cortical surface stream in parallel, before these streams process their shared inputs in complementary ways. Some artists, such as Fauve painters like Matisse, and Cape Cod School artists like Hawthorne and Hensche, exploited the fact that “all boundaries are invisible” to “paint in color.” They thereby created luminous surface color percepts, without the darkening effects of explicit edges. Other artists, such as Impressionists like Monet, exploited the fact that perceptual boundaries sense the statistical distribution of color spots to create the frames within which lightness and color flow, and thereby mix colors, to generate perceived surface form and color.

Artists since the Renaissance understood how to use perspective cues to generate a percept of depth by exploiting the different reactions of oriented filters of different size, whose differential activation of depth-selective boundaries can create depthful boundary and surface percepts in much the same way as a 3D scene does. These artists also understood how T-junctions can separate figures from their backgrounds. However, they could not understand that the same bipole cell receptive fields that create perceptual groupings are also sensitive to T-junctions, and can trigger the initial steps of figure-ground perception that are completed by feedback between the boundary and surface streams that ensures complementary consistency. Insights about equiluminant boundaries and how they can influence color percepts, and about the organization of opponent colors, with their attendant antagonistic rebounds, also reflect the complementary organization of the brain. In this sense, many artists can be viewed as masters of how the brain achieves complementary consistency, and with it the balance that radiates from many of the greatest works of art.

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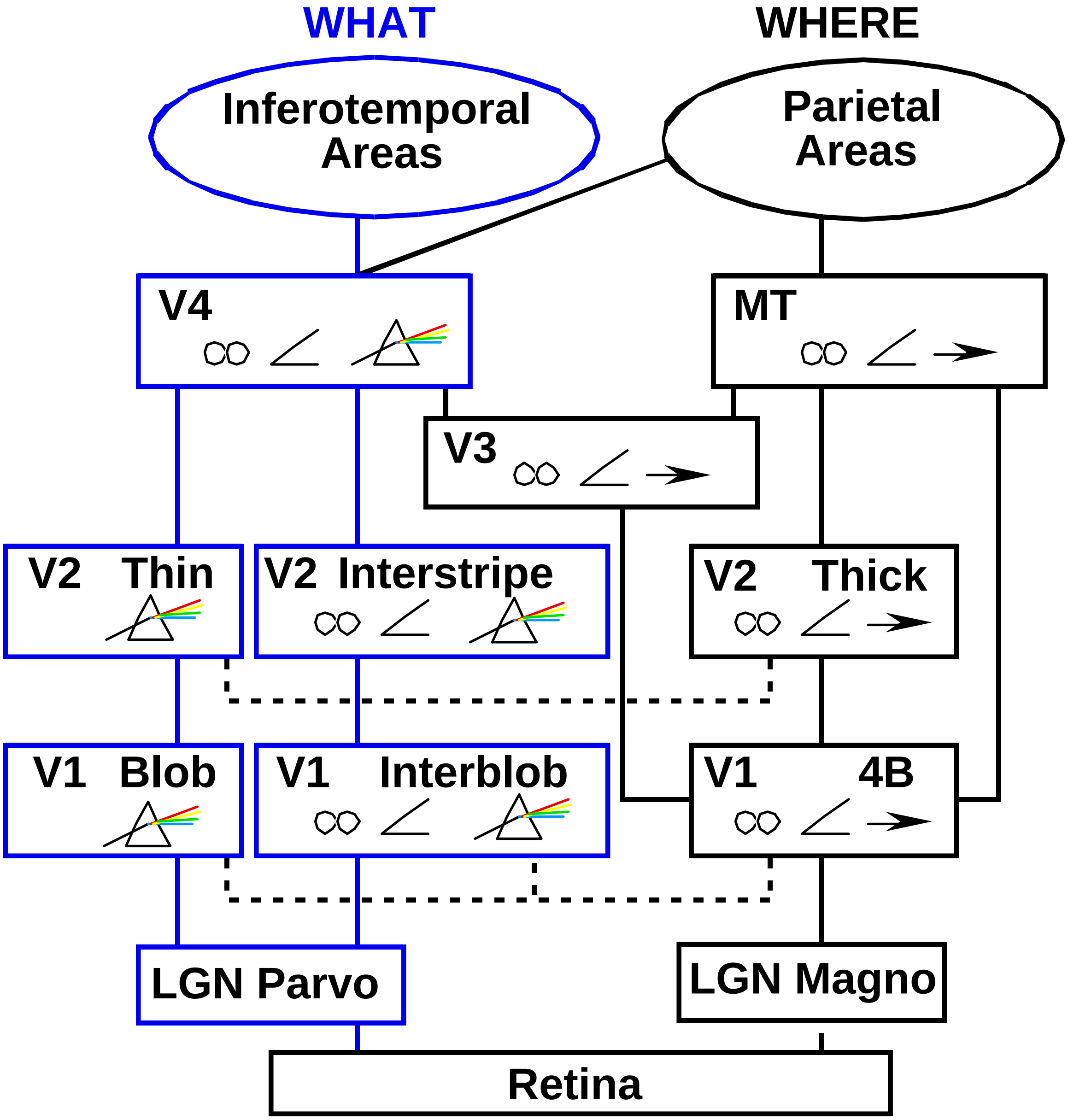

Figure 1

Figure 1. Schematic diagram of anatomical connections and neuronal selectivities of early visual processing areas in the macaque monkey. The LGN Parvo-(V1 Interblob)-(V2 Interstripe)-V4 stream is predicted to compute perceptual boundaries. The LGN Parvo-(V1 Blob)-(V2 Thin Stripe)-V4 stream is predicted to compute perceptual surfaces. LGN = lateral geniculate nucleus (parvocellular [parvo] and magnocellular [magno] divisions). Divisions of visual areas VI and V2: blob = cytochrome oxidase blob regions, interblob = cytochrome oxidase-poor regions surrounding the blobs, 4B = lamina 4B, thin = thin (narrow) cytochrome oxidase strips, interstripe = cytochrome oxidase-poor regions between the thin and thick stripes, thick = thick (wide) cytochrome oxidase strips, V3 = Visual Area 3, V4 = Visual Area(s) 4, and MT = middle temporal area. Areas V2, V3, V4, and MT have connections to other areas not explicitly represented here. Area

V3 may also receive projections from V2 interstripes or thin stripes. Heavy lines indicate robust primary connections, and thin lines indicate weaker, more variable connections. Dotted lines represent observed connections that require additional verification. Icons: rainbow = tuned and/or opponent wavelength selectivity (incidence at least 40%), angle symbol = orientation selectivity (incidence at least 20%), spectacles = binocular disparity selectivity and/or strong binocular interactions (V2; incidence at least 20%), and right-pointing arrow = direction of motion selectivity (incidence at least 20%). [Adapted with permission from "Concurrent processing streams in monkey visual cortex," by E. A. DeYoe and D. C. van Essen, 1988, Trends in Neurosciences, II, p. 223. Copyright 1988 by Elsevier Science.]

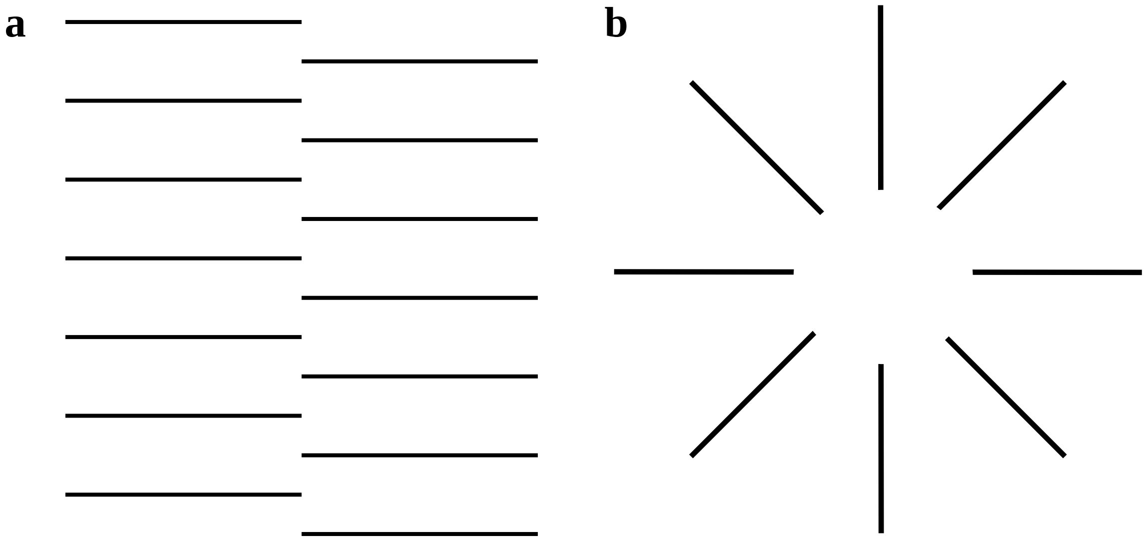

Figure 2

Figure 2. (a) The offset black horizontal lines induce a percept of a vertical boundary that can be recognized even though it does not generate a visible brightness or color difference. (b) The circular illusory boundary of the Ehrenstein disk is visible because it induces an illusory brightness difference between the disk and its surround.

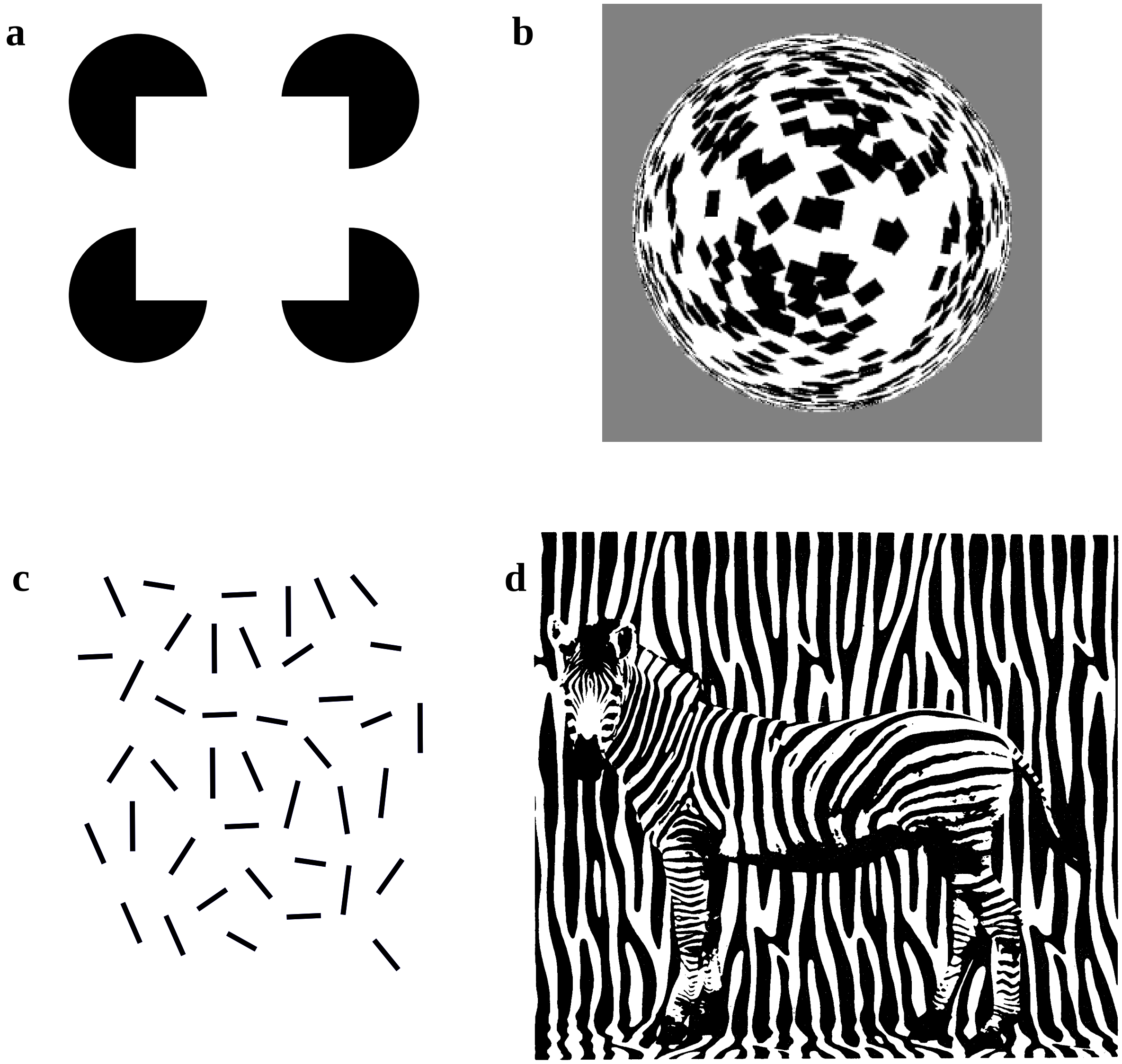

Figure 3

Figure 3. Examples of perceptual grouping: (1) an illusory square emerges from the four pace men to be seen as the well-known Kanizsa square. (b) a discrete texture in a 2D picture can generate a percept of a continuous 3D surface by differentially activating multiple-scales of boundary webs. (c) colinear lines can pop-out from a field of randomly oriented lines by being linked by an emergent boundary. (d) an emergent boundary can separate the figure of the zebra from the background. T-junctions between the zebra and the background can help to push the background behind the zebra figure. See text for further discussion.

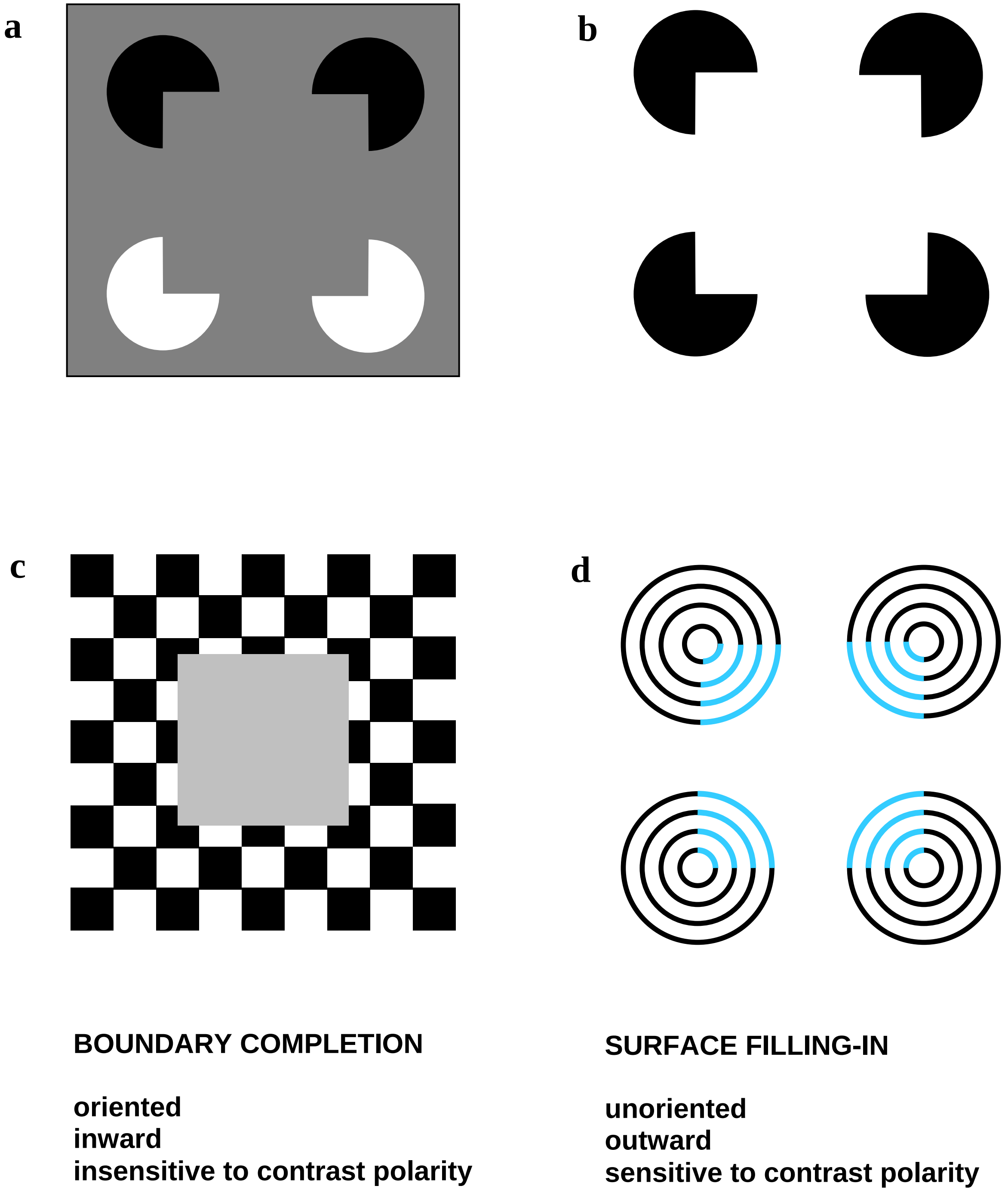

Figure 4

Figure 4. (a) opposite-contrast Kanizsa square shows that opposite contrast polarities can group together, as well as same contrast polarities, and that both sorts of groupings are

part of the same boundary completion process. Because two pac men are darker than the background gray, and the other two are lighter than the background gray, they induce lightening and darkening effects that cancel out, thereby creating an invisible, or amodal, Kanizsa square that is recognized but not seen. (b) same-contrast Kanizsa square is visible because all four black pac men induce brightness signals within the square that creates a brighter square after surface filling-in. (c) pooling of opposite contrast along the square borders illustrates how the brain can build an object boundary around a textured background and thus why “all boundaries are invisible.” (d) neon color spreading vividly illustrates the computationally complementary properties of boundary completion and surface filling-in that are summarized at the bottom of the figure.

Figure 5

Figure 5. The Roofs of Collioure was painted by Matisse in 1905.

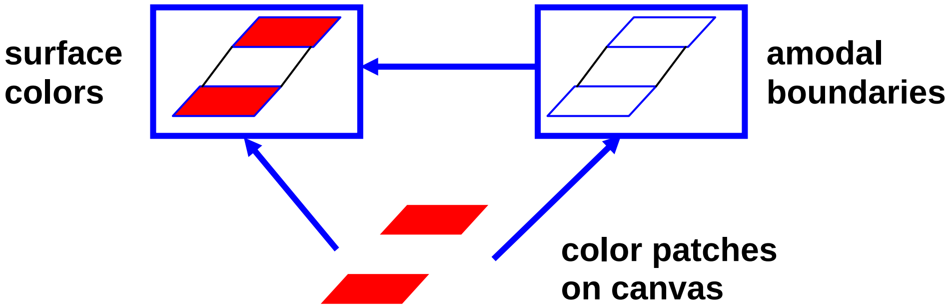

Figure 6

Figure 6. The Roofs of Collioure in Figure 5 illustrates how Matisse "paints in color" without using explicitly drawn edges that could darken the painting's perceived colors. These color patches generate amodal boundaries that can capture the surface colors into surface percepts that have a meaning to viewers.

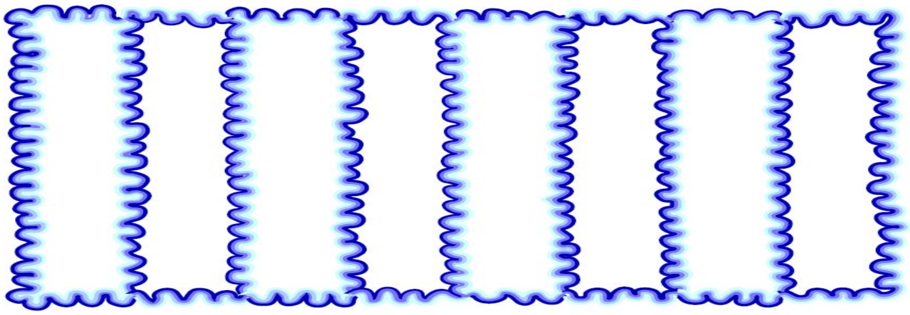

Figure 7

Figure 7. The columns bulge in the 3D space even if they appear softly and nebulously colored. [Reprinted with permission from Pinna and Grossberg (2005).]

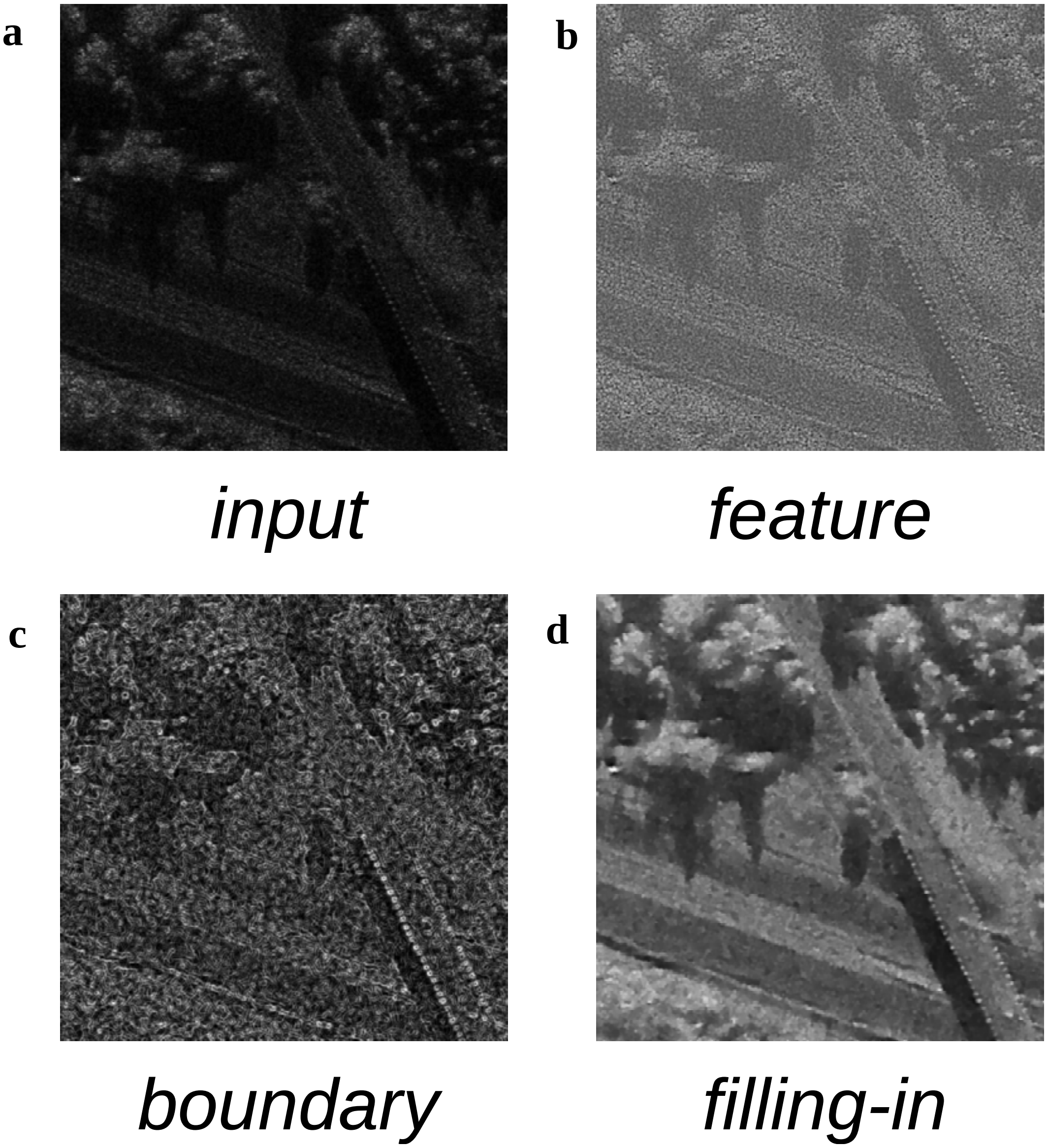

Figure 8

Figure 8. Processing of a Synthetic Aperture Radar (SAR) image by the boundary completion and surface filling-in mechanisms: (a) unprocessed SAR imagine of upstate New York scene consisting of a highway with bride overpass in a wooded area with grass. This image represents five orders of magnitude of power in the radar return. It would look almost entirely black were it not for enhancement due to figure reproduction. It also includes a lot of multiplicative noise and sparse high-intensity pixels. (b) the contrast-normalized image due to "discounting the illuminant." (c) the boundary representation that is generated in response to the image in (b), after responses of

multiple boundary scales are combined. (d) the filled-in surface representation after the results of multiple filling-in events are pooled in response to the multiple boundary scales. Note that the “pointilistic” nature of the image in (b) is now replaced by smoothly defined surface forms. [Reprinted with permission from Mingolla, Ross, and Grossberg (1999).]

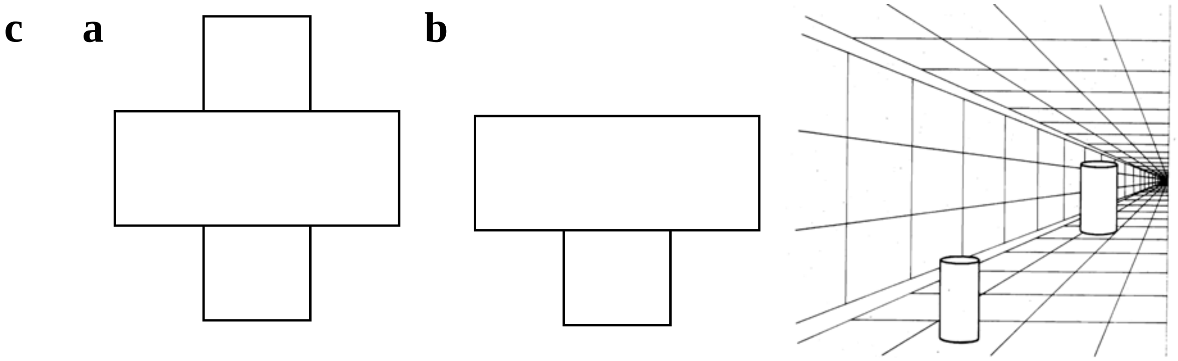

Figure 9

Figure 9. (a) The horizontal bar typically appears to lie in front of a partially occluded vertical bar that is amodally completed behind it. (b) Where only one vertical bar exists. its upper horizontal edge still seems to belong to the horizontal bar. This property of "border ownership" can be explained by how bipole cells break the boundary where a T-junction stem joined a T-junction top. Such end-cuts are predicted to initiate figure-ground separation. (c) the corridor illusion: Due to the spatial gradients within the figure, the smaller pasrallelograms look further away than the larger ones. Correspondingly, the upper cylinder looks larger than the lower cylinder, although both cylinders are the same size. [Reprinted with permission form From Sight and Mind: An Introduction to Visual Perception by L. Kaufman. 1974. New York: Oxford University Press. Copyright 1974 by Oxford University Press.]

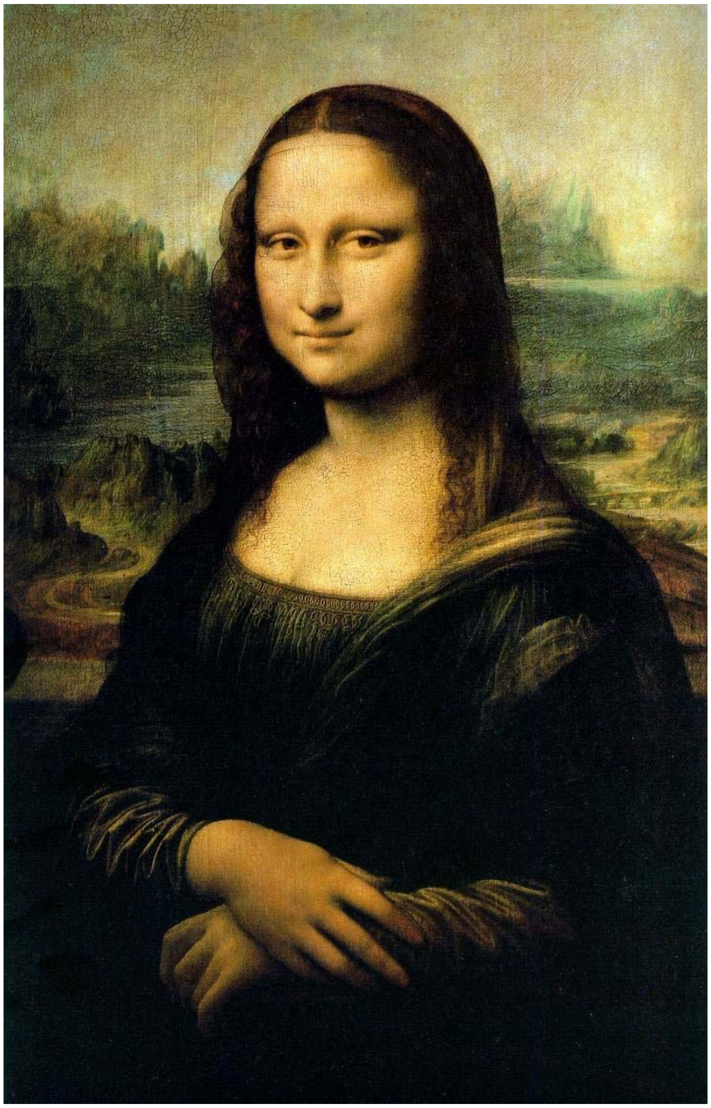

Figure 10

Figure 10. The Mona Lisa of Leonardo da Vinci, circa 1503 – 1507, contains exquisite examples of chiaroscuro to create a percept of a 3D shape in the subject, and of multiple scales and T-junctions, among other factors, to create the impression of a background at a greater distance.

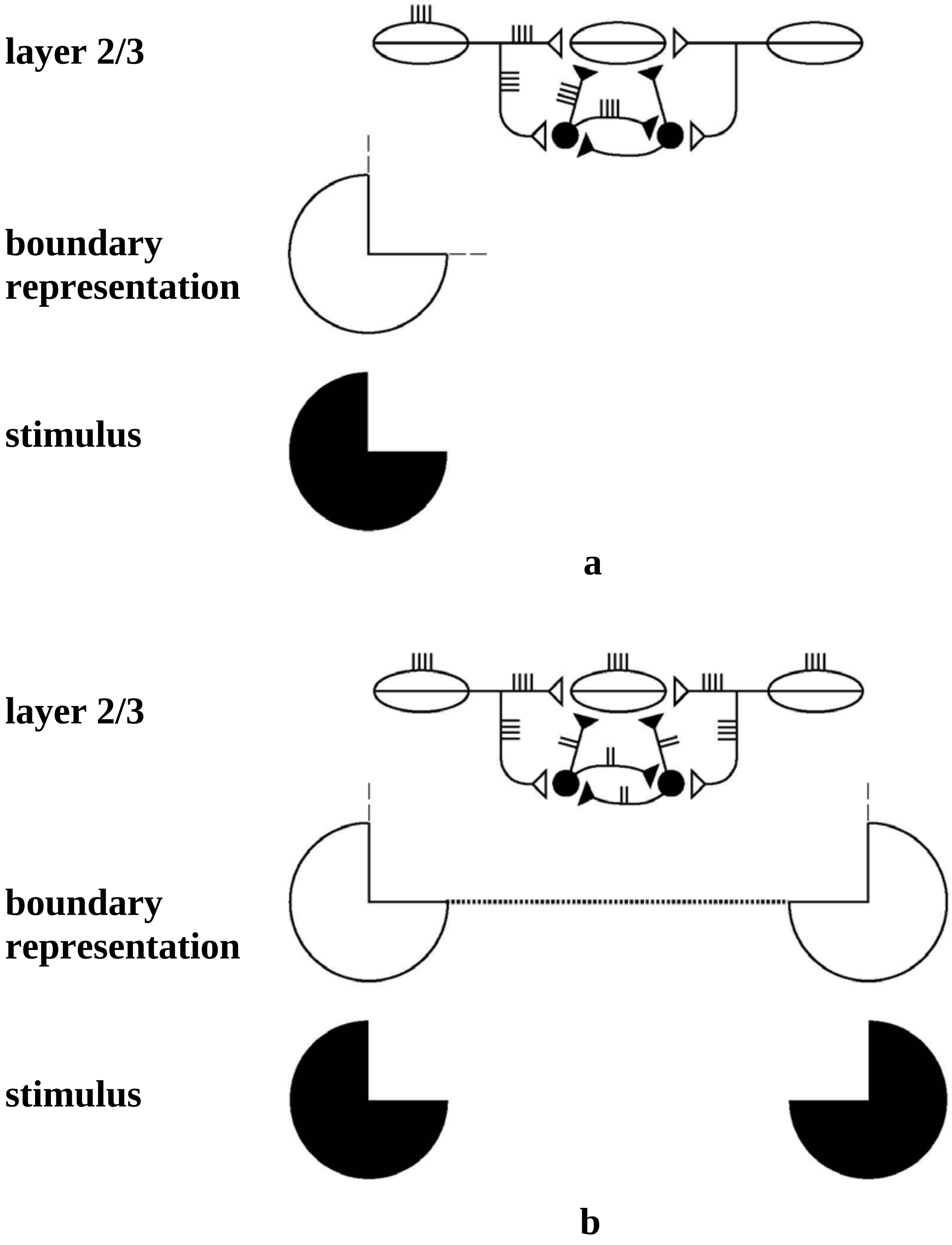

Figure 11

Figure 11. Schematic of the boundary grouping circuit in cortical layer 2/3. Pyramidal cells with colinear, coaxial receptive fields (shown as ovals) excite each other via long-range horizontal axons (Bosking *et al.*, 1997; Schmidt *et al.*, 1997), which also give rise to short-range, disynaptic inhibition via pools of interneurons, shown filled-in black (McGuire *et al.*, 1991). This balance of excitation and inhibition helps to implement the

bipole property. (a) Illustration of how horizontal input coming in from just one side is insufficient to cause above threshold excitation in a pyramidal cell (henceforth referred to as the target) whose receptive field does not itself receive any bottom-up input. The inducing stimulus (e.g., a Kanizsa ‘pacman’) excites the oriented receptive fields of layer 2/3 cells, which send out long-range horizontal excitation onto the target pyramidal. This excitation brings with it a commensurate amount of disynaptic inhibition. This balance of “one-against-one” prevents the target pyramidal cell from being excited above-threshold. The boundary representation of the solitary pacman inducer produces only weak, sub-threshold colinear extensions (thin dashed lines). (b) When two colinearly aligned inducer stimuli are present, one on each side of the target pyramidal cell receptive field, a boundary grouping can form. Long-range excitatory inputs fall onto the cell from both sides, and summate. However, these inputs fall onto a shared pool of inhibitory interneurons, which, as well as inhibiting the target pyramidal, also inhibit each other (Tamas *et al.*, 1998), thus normalizing the total amount of inhibition emanating from the interneuron pool, without any individual interneuron saturating. The combination of summating excitation and normalizing inhibition together create a case of “two against-one”, and the target pyramidal is excited above-threshold. This process occurs along the whole boundary grouping, which thereby becomes represented by a line of suprathreshold-activated layer 2/3 cells (thick dotted line). Boundary strength scales in a graded analog manner with the strength of the inducing signals. [Reprinted with permission from Grossberg and Raizada (2000).]

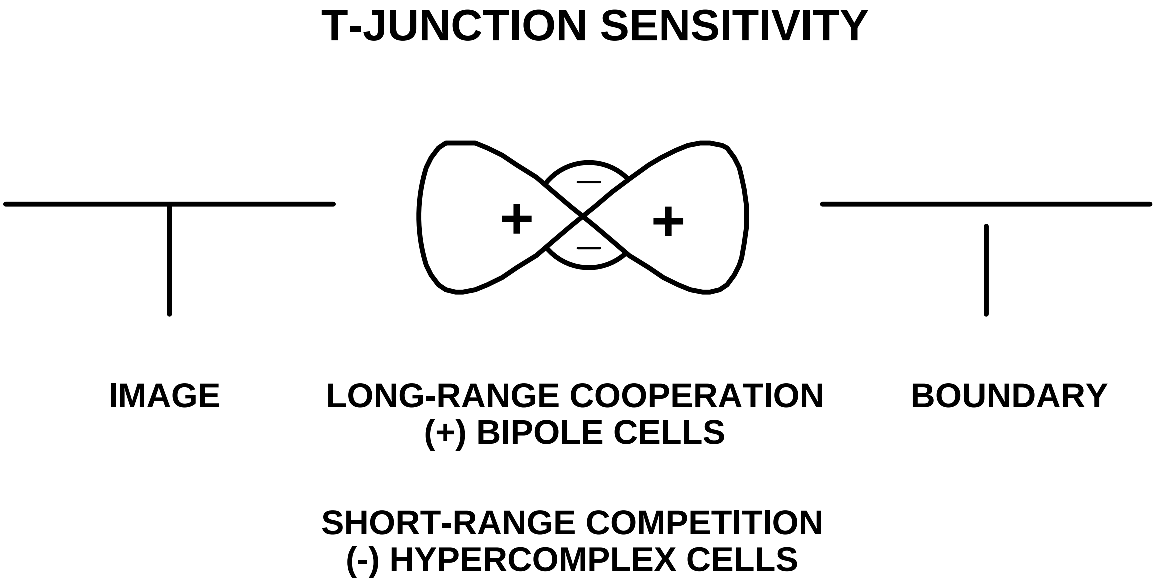

Figure 12

Figure 12, T-Junction Sensitivity: (a) T-junction in an image. (b) Bipole cells provide long-range cooperation (+), and work together with inhibitory interneurons that provide cells provide short-range competition (-). (c) An end-gap in the vertical boundary arises because, for cells near where the top and stem of the T come together, the top of the T activates bipole cells along the top of the T more than bipole cells are activated along the T stem. As a result the stem boundary gets inhibited whereas the top boundary does not. [Reprinted with permission from Grossberg (1997).]

a

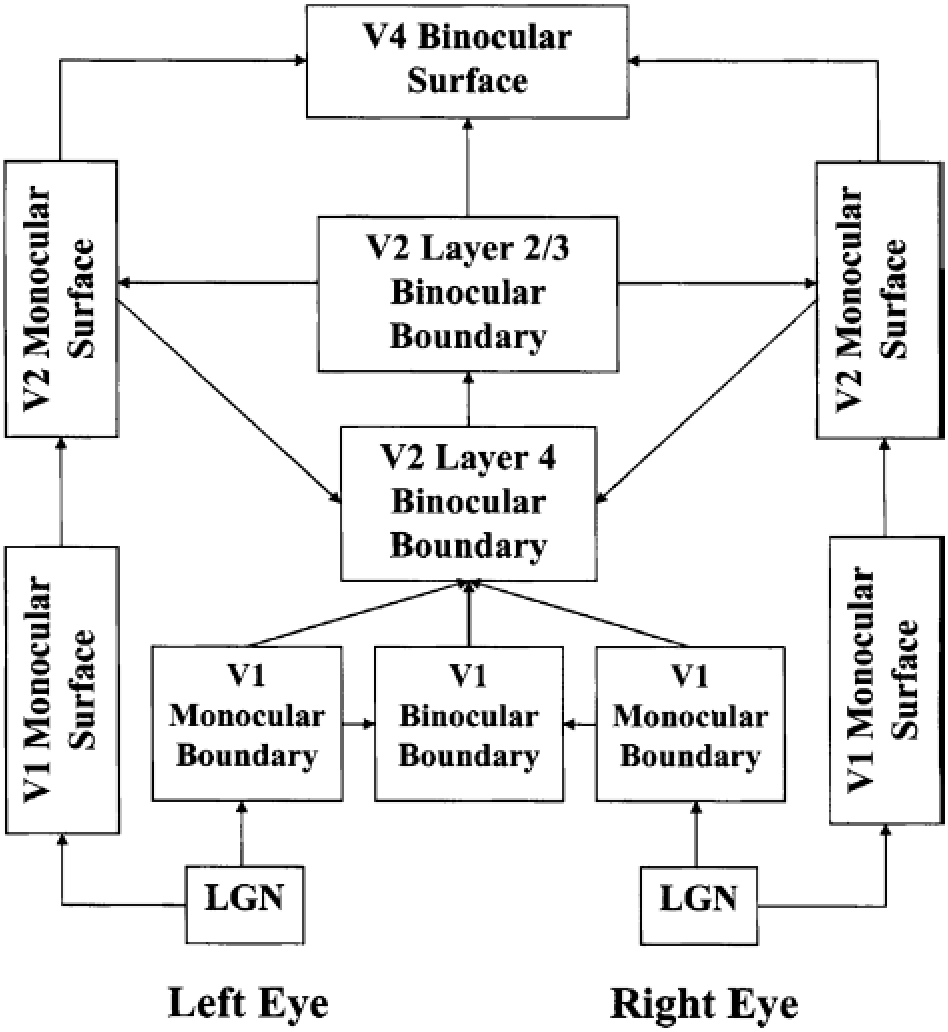

Figure 13 a

Figure 13. **(a)** 3D LAMINART macrocircuit. It illustrates the interactions between model components Retina/LGN and cortical areas V1, V2, and V4.

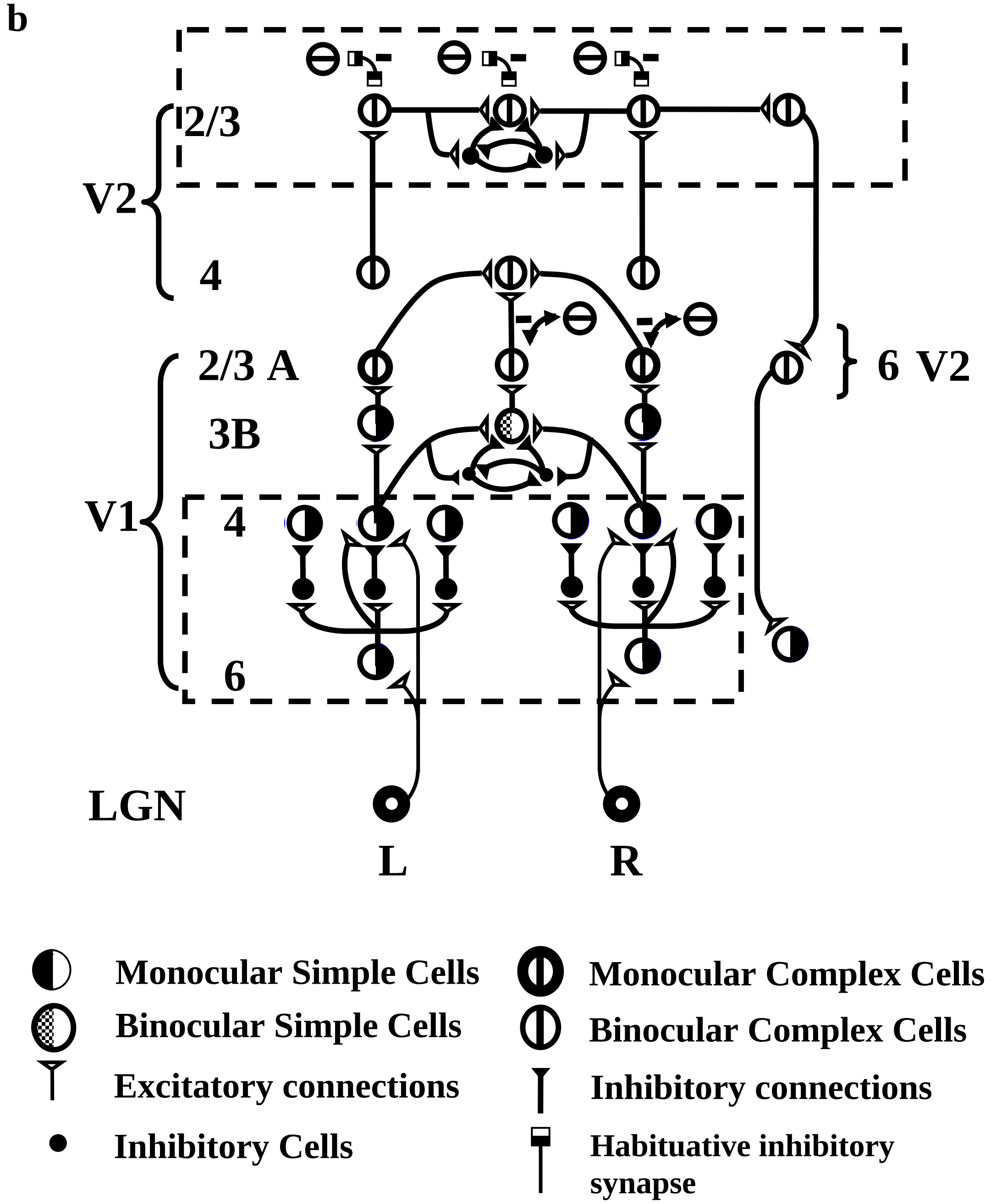

Figure 13 b

Figure 13. (b) Model circuit diagram. The model consists of a boundary stream that includes V1 interblobs, V2 pale stripes, and part of V4, and computes 3D perceptual groupings in different scales; and a surface stream that includes V1 blobs, V2 thin stripes, and part of V4, and computes 3D surfaces that are infused with lightnesses in depth. These two streams both receive illuminant-discounted signals from Retina/LGN cells, and interact with each other to overcome their complementary deficiencies and create consistent 3D boundary and surface percepts, in the cortical area V4. Also, 3D boundary and surface representations formed in the pale stripes and thin stripes of cortical area V2,

respectively, are amodally completed, and provide neural support for the object recognition process in the inferotemporal cortex.

Figure 14

Figure 14. In the painting Near Argenteuil by Monet, 1973, the red poppies and the green field are painted to be almost equiluminant (at least in the original painting). This creates weak boundaries between them and facilitates an occasional impression of the boundaries moving in a country breeze.