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Surface and boundary interactions in visual cortex

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Boston University Center for Adaptive Systems and
Department of Cognitive and Neural Systems
677 Beacon Street
Boston, MA 02215

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Stephen Grossberg*
Department of Cognitive and Neural Systems
and
Center for Adaptive Systems
Boston University
677 Beacon St.
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Correspondence should be addressed to:
Stephen Grossberg
Department of Cognitive & Neural Systems
Boston University
677 Beacon Street
Boston, MA 02215
Phone: 617-353-7858
Fax: 617-353-7755
E-mail: steve@bu.edu
http://www.cns.bu.edu/Profiles/Grossberg

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Complementarity: A Global View of Brain Organization

In order to discuss the role of filling-in in the brain, it is helpful to caste this issue within a larger framework that clarifies more global properties of brain organization. This is useful because, I would contend, filling-in can only be fully understood within such a global framework. In one traditional view, our brains are proposed to possess independent modules, as in a digital computer. For this view, we see by processing perceptual qualities such as visual form, color, and motion using different modules. This view's supporters sometimes turn to the well-known fact that the brain is organized in parallel processing streams. Figure 1 schematizes how at least three such processing streams within the visual cortex are activated by light impinging on the retina. One such stream goes from the retina through a processing stage called LGN parvo (classified due to its "parvocellular" cell type) to the cortical processing stages V1 blob, then V2 thin stripe, then V4, and then inferotemporal cortex. Another such stream goes from retina through LGN parvo, then through V1 interblob, V2 interstripe, then V4, and again on to inferotemporal cortex. A third stream goes from retina through LGN magno (classified due to its "magnocellular" cell type) to cortical processing layer 4B in area V1, then to V1 thick stripes, then MT, and then parietal cortex. More will be said about the role that these streams play in vision, and more specifically in filling-in, in a moment.

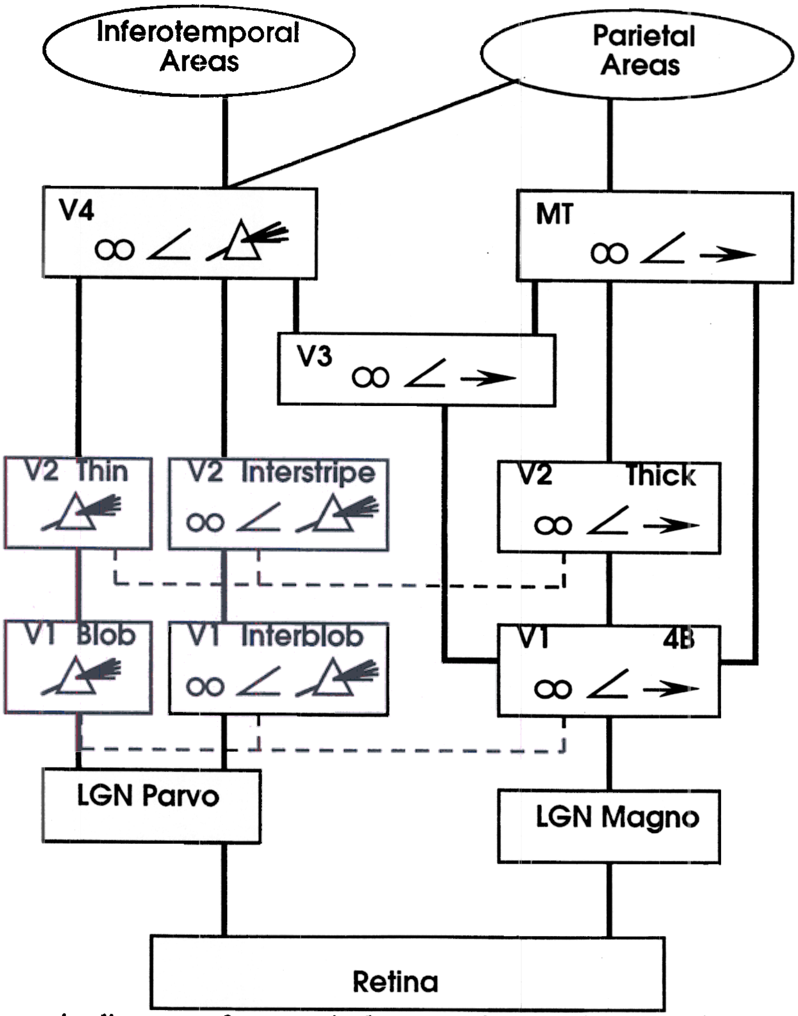


Figure 1. Schematic diagram of anatomical connections and neuronal selectivities of early visual areas in the macaque monkey brain. LGN = lateral geniculate nucleus (parvocellular

[parvo] and magnocellular [magno] divisions. Divisions of cortical visual area V1: blob = cytochrome oxidase blob regions, interblob = cytochrome oxidase-poor regions surrounding the blobs, 4B = layer 4B. Divisions of cortical visual area V2: thin = thin (narrow) cytochrome oxidase stripes, interstripe = cytochrome oxidase-poor regions between the thin and thick stripes, thick = thick (wide) cytochrome oxidase stripes. V3 = cortical visual area 3. V4 = cortical visual area(s) 4. MT = cortical 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 indicate the response selectivities of cells at each processing stage: rainbow = wavelength selectivity, angle symbol = orientation selectivity, spectacles = binocular selectivity, and right-pointing arrow = selectivity to motion in a prescribed direction. [Adapted with permission from E.A. DeYoe and D.C. van Essen. (1988). Concurrent processing streams in monkey visual cortex. *Trends in Neurosciences*, **11**, 219-226).]

The existence of such streams certainly supports the idea that brain processing is specialized, but it does not, in itself, imply that these streams are independent modules that are able to fully compute their particular processes on their own. In fact, much perceptual data argue against the existence of independent modules, because strong interactions are known to occur between perceptual qualities. For example, changes in the perceived form or color of an object can cause changes in its perceived motion, and vice versa, while changes in the perceived brightness of an object can cause changes in its perceived depth, and vice versa (Egusa, 1983; Faubert and von Grunau, 1995; Kanizsa, 1974; Pessoa, Beck and Mingolla, 1996; Smallman and McKee, 1995). The existence of such interactions suggests that the mechanisms whereby we perceive the geometry of the world do not obey the classical geometrical axioms on which a lot of mathematics is based. How and why do these qualities interact? What is the geometry by which we really see the world? An answer to these questions is needed to determine the functional and computational units that govern behavior as we know it.

A great deal of theoretical and experimental evidence suggests that the brain's processing streams compute *complementary* properties. Each stream's properties are related to those of a complementary stream much as a lock fits its key, or two pieces of a puzzle fit together. We are all familiar with complementarity principles in physics, such as the famous Heisenberg Uncertainty Principle of quantum mechanics which notes that precise measurement a particle's position forces uncertainty in measuring its momentum, and vice versa. As in physics, the mechanisms that enable each stream in the brain to compute one set of properties prevent it from computing a complementary set of properties. Due to the complementarity of the brain's processing streams, each stream exhibits complementary strengths and weaknesses. How, then, do these complementary properties get synthesized into a consistent behavioral experience? It is proposed that *interactions* between these processing streams overcome their complementary deficiencies and generate behavioral properties that realize the unity of conscious experiences. In this sense, *pairs* of complementary streams are the functional units because only through their interactions can key behavioral properties be competently computed. Said in another way, one needs to study how pairs of complementary streams interact together in order to understand how the brain computes unambiguous information about various aspects of the world. These interactions may be used to explain many of the ways in which perceptual qualities are known to influence each other. Thus, although analogies like a key fitting its lock, or puzzle pieces fitting together, are suggestive, they do not fully capture the dynamism of what complementarity means in the brain.

It is also well-known that each stream can possess multiple processing stages. For example, in Figure 1, there are distinct processing stages in the lateral geniculate nucleus (LGN) followed by the cortical areas V1, then V2, and then V4 on their way to the inferotemporal and parietal cortices. Why is this so? Accumulating evidence suggests that these stages realize a process of *hierarchical resolution of uncertainty*. 'Uncertainty' here means that computing one set of properties at a given stage can suppress information about a different set of properties at that stage. Uncertainty principles are also familiar in physics, such as the Heisenberg Uncertainty Principle. In the brain, these uncertainties are proposed to be overcome by using more than one processing stage to form a stream. Overcoming informational uncertainty utilizes both hierarchical interactions within the stream and the parallel interactions between streams that overcome their complementary deficiencies. The computational unit is thus not a single processing stage; it is, rather, an ensemble of processing stages that interact within and between complementary processing streams.

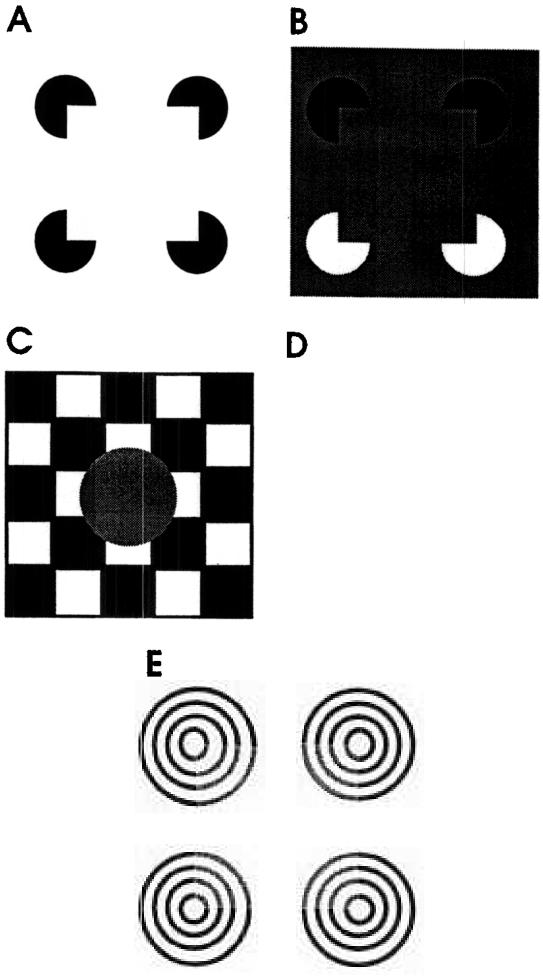
According to this view, the organization of the brain obeys principles of uncertainty and complementarity, as does the physical world with which brains interact, and of which they form a part. These principles reflect each brain's role as a self-organizing measuring device *in* the world, and *of* the world, and may better explain the brain's functional organization than the simpler view of computationally independent modules. How filling-in is controlled in the brain provides an excellent example of such complementary computing.

All Boundaries Are Invisible

To begin, let us recall that visual processing utilizes parallel processing streams (Figure 1). What evidence is there to suggest that these streams compute complementary properties, and how is this done? A neural theory, called FACADE (Form-And-Color-And-DEpth) theory (e.g., Grossberg, 1994, 1997), proposes that perceptual *boundaries* are formed in the LGN-Interblob-Interstripe-V4 stream, while perceptual *surfaces* are formed in the LGN-Blob-Thin Stripe-V4 stream. Many experiments have supported this prediction (e.g., Elder and Zucker, 1998; Lamme, Rodriguez-Rodriguez and Spekreijse, 1999; Rogers-Ramachandran and Ramachandran, 1998).

FACADE theory suggests how and why perceptual boundaries and perceptual surfaces compute complementary properties. Filling-in is proposed to occur within the surface processing stream. Due to the proposed complementarity of the boundary and surface streams, one needs to analyze both streams to fully understand the way in which either stream normally functions. One also needs to analyze how the streams interact to understand properties of the filling-in process per se. Figures 2a and 2b illustrates three pairs of complementary properties using visual illusions that are induced by variants of a Kanizsa square. For example, in response to viewing Figure 2a, our brains construct a percept of a square even though the image contains only four black pac-man, or pie-shaped, figures on a white background. As noted below, this percept is due to an interaction between the processing streams that form perceptual boundaries and surfaces.

You might immediately wonder why our brains construct a square where there is none in the image. There are several functional reasons for this. One is that there is a *blind spot* in our retinas; namely, a region where no light-sensitive photoreceptors exist. This region is blind because of the way in which the pathways from retinal photoreceptors are collected together to form the optic nerve that carries them from the retina to the LGN in Figure 1. We are not usually aware of this blind spot because our brains complete boundary and surface information across it. The actively completed parts of these percepts are visual illusions, because they are not derived directly from visual signals on our retinas. Thus many of the percepts that we believe to be "real" are visual illusions whose boundary and surface representations just happen to look real. I suggest that what we call a visual illusion is just an unfamiliar combination of boundary and surface information. This hypothesis is illustrated by the percepts generated in our brains from the images in Figure 2.



BOUNDARY COMPLETION	SURFACE FILLING-IN
oriented	unoriented
inward	outward
insensitive to contrast polarity	sensitive to contrast polarity

Figure 2. Visual boundary and surface interactions: (a) The emergent Kanizsa square can be seen and recognized because of the enhanced illusory brightness within the illusory square relative to the background brightness outside the square. (b) The reverse-contrast Kanizsa square can be recognized but not seen: We are aware of the square boundary even though the gray color inside and outside the square is approximately the same. (c) The boundary of the gray disk can form around its entire circumference, even though the relative contrast between the disk and the white and black background squares reverses periodically along the circumference. (d) The vertical illusory contour that forms at the ends of the horizontal lines can be consciously recognized even though it cannot be seen by virtue of any contrast difference between it and the background. (e) In this example of neon color spreading, the color in the gray contours spreads in all directions until it fills the square illusory contour. This percept illustrates the three complementary properties of boundary completion and surface filling-in that are summarized below the figure: The lines in the square boundary are completed using a mixed cooperative-competitive process whereby boundaries can form *inwardly* and in an *oriented* manner between pairs or greater numbers of image inducers. The output of this boundary system is also *insensitive*

to contrast polarity because it pools signals from opposite contrasts at each position, as illustrated by Figures (2b) and (2c). The gray surface color fills-in the square *outwardly* and in an *unoriented* fashion by a diffusive mechanism. It is *sensitive* to contrast polarity because it creates visible percepts of brightness and color. Boundaries are predicted to form within the interblob stream, whereas surfaces are predicted to form within the blob stream; see Figure 1.

In response to the images in Figures 2a and 2b, illusory contours form *inwardly* between cooperating pairs of colinear edges of the four pac man, or pie shaped, inducers in the image. Four such contours form the boundary of the perceived Kanizsa square. (If boundaries formed outwardly from a single inducer, then any speck of dirt in an image could crowd all our percepts with an outwardly growing web of boundaries.) This boundary completion process is *oriented* to form only between like-oriented and (almost) colinear inducers. Both of these properties are useful to complete edges in a scene which are not fully detected at the retina due to the blind spot. The square boundary in Figure 2a can be both seen and recognized because of the enhanced illusory brightness of the Kanizsa square relative to its background; see below for an explanation. In contrast, the square boundary in Figure 2b can be recognized even though it is not visible; that is, there is no brightness or color difference on either side of the boundary. Figure 2b shows that *some* boundaries can be recognized even though they are perceptually unseen, or invisible. FACADE theory predicts that *all boundaries are invisible* within the boundary stream, which is proposed to be the interblob cortical processing stream (Figure 1).

Why are all boundaries invisible? The invisible boundary in Figure 2b can be traced to the fact that its vertical boundaries form between black and white inducers that possess opposite contrast polarity with respect to the gray background; that is, the black inducers have a black-to-gray, or dark-to-light, polarity with respect to the background, whereas the white inducers have a white-to-gray, or light-to-dark, polarity with respect to the background. The same is true of the boundary around the gray circular disk in Figure 2c. In this figure, the gray disk lies in front of a black and white textured background whose contrasts with respect to the disk reverse across space. In order to build a boundary around the entire disk, despite these contrast reversals, the boundary system pools, or adds, signals from pairs of *simple cells* that are sensitive to the same orientation and position, but to opposite contrast polarities. This pooling process occurs in the V1 interblob stream at the *complex cells.* This is how the square boundary in response to Figure 2b, and the circular boundary in response to Figure 2c, start to form in our brains. This pooling process renders the boundary system output *insensitive* to contrast polarity. The boundary system hereby loses its ability to represent visible colors or brightnesses, since its output cannot signal the difference between dark and light. It is in this sense that "all boundaries are invisible". The *inward* and *oriented* boundary completion process that forms the illusory square is activated by these pooled signals in the V2 interstripe area (Von der Heydt, Peterhans, and Baumgartner, 1984; Peterhans and Von der Heydt, 1989). These three properties of boundary completion are summarized at the bottom of Figure 2. Figure 2d illustrates another invisible boundary that can be consciously recognized.

Such a boundary formation process in the brain is a key mechanism whereby we perceive geometrical objects such as lines, curves, and textured objects. Rather than being defined in terms of such classical units as points and lines, these boundaries arise as a coherent pattern of excitatory and inhibitory signals across a mixed cooperative-competitive feedback network that is defined by a nonlinear dynamical system which describes the cellular interactions from the retina through LGN and the V1 interblob and V2 interstripe areas (Gove, Grossberg, and Mingolla, 1995; Grossberg, 1999b; Grossberg and Raizada, 2000; Grossberg and Williamson, 2000). In such a network, spatially long-range excitatory, or cooperative, interactions try to build the boundaries across space, while interacting with shorter-range inhibitory, or competitive, interactions that suppress incorrect boundary groupings. These interactions select the best boundary grouping from among many possible interpretations of a scene. The winning grouping is represented either by an equilibrium point or a synchronous oscillation of the system, depending upon how system parameters are chosen. Classical geometry is hereby replaced by nonlinear neural networks that do a type of on-line statistical inference to select and complete the statistically most favored boundary groupings of a scene, while suppressing noise and incorrect groupings. The emerging patterns of boundary excitation obey the three boundary completion properties (inward, oriented, insensitive) that are summarized above. Our model for how such perceptual boundaries are formed has been called the Boundary Contour System, or BCS.

Surfaces Are For Seeing

If boundaries are invisible, then how do we see anything? FACADE theory predicts that visible properties of a scene are represented by a surface processing stream, which is predicted to occur within the Blob cortical stream (Figure 1). A key step in representing a visible surface is the filling-in process. What is filling-in and why and how does it occur? An early stage of surface processing compensates for variable illumination, or *discounts the illuminant.* Otherwise, illuminant variations, which can change from moment to moment, could seriously distort 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. Neural models have proposed how later stages of surface formation fill in the attenuated regions with these relatively uncontaminated color and brightness signals (Cohen and Grossberg, 1984; Gove, Grossberg, and Mingolla, 1995; Grossberg and Todorovic´, 1988; Grossberg and Kelly, 1999; Pessoa, Mingolla, and Neumann, 1995). Remarkably, the same process can also allocate brightness and color signals to their perceived depths on a 3-D surface, through a process called *surface capture*, whereby the boundaries formed within the V2 interstripes interact with the V2 thin stripes and area V4 (see Figure 1) to trigger depth-selective filling-in processes there (Grossberg, 1994, 1997; Grossberg and McLoughlin, 1997; Grossberg and Pessoa, 1998; Kelly and Grossberg, 2000). This multi-stage filling-in process is an example of hierarchical resolution of uncertainty, because the later filling-in stage overcomes uncertainties about brightness and color that were caused by discounting the illuminant at an earlier processing stage. How surface capture may occur in the brain is summarized below.

Before discussing depthful surface capture, we first need to understand a more basic property: How do the illuminant-discounted signals fill-in an entire region? Filling-in behaves like a diffusion of brightness across space. For an example, consider the percept of *neon color spreading* that is elicited by Figure 2e (Redies and Spillmann, 1981). This figure consists of circular annuli, part of which are black and part gray. In response to this figure, we can see an illusory square filled with a gray color. FACADE theory suggests that this percept is due to an interaction between the boundary and surface systems. In particular, the black boundaries cause small breaks in the gray boundaries where they join; see Grossberg and Mingolla (1985) and Grossberg (1994, 1999a) for further discussion of how this happens. The gray color can hereby spread through these breaks from the annuli into the illusory square. In this percept, filling-in spreads *outwardly* from the individual gray inducers in all directions. Its spread is thus *unoriented.* How is this spread of activation contained? FACADE theory predicts that signals from the boundary stream to the surface stream define the regions within which filling-in is restricted. These boundaries surround the annuli (except for their small breaks) and also form the square illusory contour. Thus, filling-in is a form of anisotropic diffusion in which boundary signals nonlinearly gate, or inhibit, the diffusive flow of signal. Without these boundary signals, filling-in would dissipate across space, and no surface percept could form. Invisible boundaries hereby indirectly assure their own visibility through their interactions with the surface stream, within which all visible percepts are predicted to form.

With these comments in mind, we can better understand finer aspects of the other percepts that form in response to the images in Figure 2. In Figure 2a, the square boundary is induced by four black pac-men that are all less luminant than the white background. In the surface stream, discounting the illuminant causes these pac-men to induce local brightness enhancements adjacent to the pac-men, just within the boundary of the square. At a subsequent processing stage, these enhanced brightness signals diffuse within the square boundary, thereby causing the entire interior of the square to look brighter. The filled-in square is visible because the filled-in activity level within the square is higher than the filled-in activity of the surrounding region. Filling-in can hereby lead to visible percepts because it is *sensitive* to contrast polarity. These three properties of surface filling-in (outward, unoriented, sensitive) are summarized at the bottom of Figure 2. They are easily seen to be complementary to the corresponding properties of boundary completion.

In Figure 2b, the opposite polarities of the two pairs of pac men with respect to the gray background lead to approximately equal filled-in activities inside and outside the square, so the boundary can be recognized but not seen. In Figure 2d, the white background can fill-in uniformly on both sides of the vertical boundary, by diffusing around the horizontal black lines, so no visible contrast difference is seen.

In addition to explaining percepts such as those arising from Figure 2, filling-in also clarifies how our brains can fill-in perceived brightnesses and colors within the boundaries that span retinal imperfections like the blind spot. Thus the same mechanisms can complete surface representations across those spatial gaps in retinal signaling that are caused at the retina itself by the blind spot, as well as across spatial gaps in retinal signaling that are caused by higher levels which actively suppress spurious retinal signals. Similar considerations help to explain such basic percepts as the color blue (Grossberg, 1987a, Section 31, which is caused by a spatially very sparse distribution of blue cones on the retina (Boynton, Eskew, and Olson, 1985; Tansley and Boynton, 1976, 1978).

These remarks just begin to illustrate the importance of filling-in, and how it seems to be organized in the brain. Even in the seemingly simple case of the Kanizsa square, one often perceives a square hovering in front of four partially occluded circular disks, which seem to be completed behind the square, even though they are invisible there. FACADE theory predicts how surface filling-in is organized to help such figure-ground percepts to occur, in response to both two-dimensional pictures and three-dimensional scenes; see Grossberg (1994, 1997), Grossberg and McLoughlin (1997), and Kelly and Grossberg (2000) for examples.

In summary, boundary and surface formation illustrate two key principles of brain organization: hierarchical resolution of uncertainty, and complementary interstream interactions. Figure 2 summarizes three pairs of complementary properties of the boundary and surface streams. Hierarchical resolution of uncertainty is illustrated by surface filling-in: Discounting the illuminant creates uncertainty by suppressing surface color and brightness signals except near surface discontinuities. Higher stages of filling-in complete the surface representation using properties that are complementary to those whereby boundaries are formed, guided by signals from these boundaries. Our model for how surfaces are formed is called the Feature Contour System, or FCS, because it clarifies how the "features" which we consciously see get processed into visible three-dimensional surface percepts. This happens through filling-in operations that are activated by the "feature contours" which are extracted when the illuminant is discounted. FACADE theory attempts to characterize how the BCS and FCS are internally organized and how they interact together to overcome their complementary deficiencies.

Boundary-gated surface filling-in provides a radically different view of how a surface is formed than the classical geometrical view whereby surfaces are defined in terms of surface normals or differential forms. The mathematical analysis of this type of anisotropic diffusion has hardly begun, even though its remarkable properties are already been successfully used in processing complex imagery in technology (Waxman et al, 1995). Another important problem on which a great deal of work remains to be done concerns the origin of the complementarity of boundaries and surfaces. I predict that this property arises through a process of global symmetry-breaking as the embryonic brain bifurcates into its parallel cortical processing streams.

From Brightness Constancy, Contrast, and Assimilation to Figure-Ground Separation, Texture Perception, and the McCollough Effect

There has been a great deal of discussion and controversy about whether or not a physical filling-in interaction exists; e.g., Dennett (1991) and Pessoa, Thompson, and Noë (1998). Such a question can only be answered empirically, by which I mean by direct experimental testing and by showing how neural models that include filling-in can explain many data that models which do not contain it. In this regard, it is important to note that, in the Dennett critique of the physical existence of filling-in, no explanations of the parametric properties of the percepts that have been used to support the filling-in concept were attempted. This is true despite the fact that various modeling articles had already explained and simulated quite a few perceptual data by making critical use of a neural filling-in process; e.g., Cohen and Grossberg (1984), Grossberg and Mingolla (1985), Grossberg (1987a, 1987b), Grossberg and Todorovic´ (1988). Viewpoints or models with a manifestly inferior explanatory and predictive range are simply not competitive. Data which directly support a filling-in process by trying to characterize its temporal dynamics have also been reported (Paradiso and Nakayama, 1991) and have been quantitatively simulated by Arrington (1994) using the brightness perception model of Grossberg and Todorovic´ (1988).

Since that time, many other data have been explained and simulated by FACADE theory with the help of filling-in. These include data about 3-D figure-ground perception (Grossberg, 1994, 1997; Grossberg and McLoughlin, 1997; Kelly and Grossberg, 2000), texture perception (Grossberg and Pessoa, 1998), brightness perception (Gove, Grossberg, and Mingolla, 1995; Grossberg and Kelly, 1999), and aftereffects (Francis and Grossberg, 1996), including the long-term McCollough effect (Grossberg, Hwang, and Mingolla, 2000; McCollough, 1965). Most of these data have no other mechanistic explanation. Any vision theory that purports to do without filling-in now needs to explain these data in order to be competitive. In particular, any such theory needs to provide principled explanations of how basic phenomena like discounting the illuminant and filling-in across the blind spot can occur.

One of the lessons from these modeling studies is that filling-in cannot adequately be studied outside the context of a more comprehensive vision model, if only because of the complementarity of boundary and surface computations. Another lesson is that different combinations of mechanisms may be rate-limiting in giving rise to the different percepts which depend in part on filling-in. For example, Grossberg and Todorovic´ (1988) showed that the following simple mechanisms are sufficient to explain quite a few data about brightness perception, but not all such data:

(1) an on-center off-surround network of cells that obey shunting, or membrane, equations. Such a network can discount the illuminant, compute Weber-law modulated estimates of image reflectances that are sensitive to the local context of luminance signals, and normalize image intensities;
(2) a boundary detection and completion network;
(3) a network for filling-in the discounted pattern computed by (1) within the boundaries computed by (2).

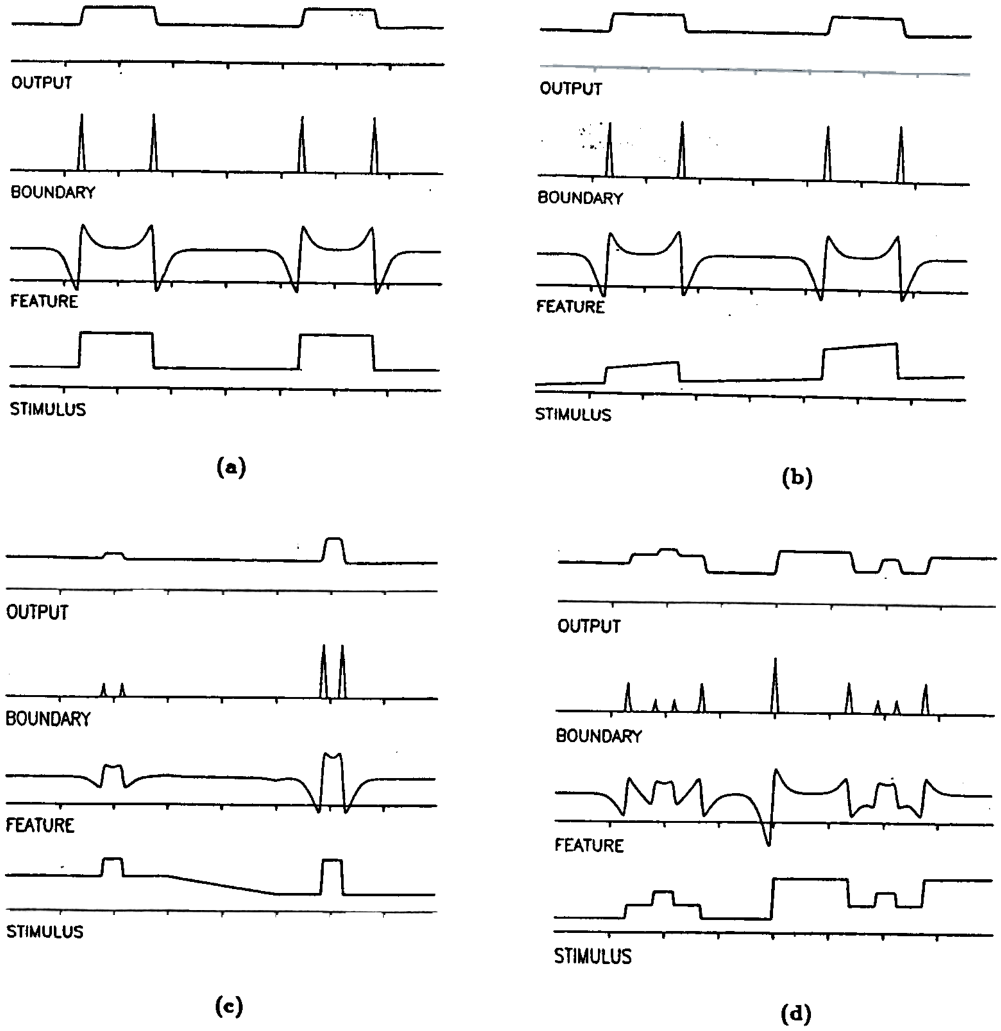


Figure 3. How filling-in can explain examples of brightness constancy (Figures 3a and 3b), brightness contrast (Figure 3c), and brightness assimilation (Figure 3d) using mechanisms that discount the illuminant (FEATURE) from a pattern of image luminances (STIMULUS) and use the discounted activity pattern to compute a BOUNDARY representation within which the FEATURE pattern fills-in to generate an OUTPUT brightness pattern. See text for details. [Adapted with permission from Grossberg and Todorovic´ (1988).]

Figure 3 gives four examples of how such a network can work. The lowest row of each panel in Figure 3 shows a one-dimensional cross-section of image luminance. The next-lowest row shows how a shunting on-center off-surround network of cells can transform these image intensities. Comparing (a) and (b) shows that such a network can compensate for a gradient of illumination; see the patterns labeled FEATURE in the figure. On the other hand, in so doing, it can also distort the true pattern of image reflectances by generating cusps and dips in the profile of cell activities across space. One of these distortions is the attenuation of image reflectances away from object boundaries or other rapidly changing luminance gradients across space. This is the key mechanism whereby the illuminant is discounted. Boundary and surface interactions help to compensate for these distortions by exploiting the information that survives the discounting process. The boundaries create a frame within which the illuminant-discounted signals can fill-in within the surface processing stream; see the patterns labeled BOUNDARY in the figure. Thus, in Figures 3a and 3b, boundaries form at the luminance discontinuities of the image because the boundary system is sensitive to discontinuities in the activity profile of discounted signals. The pattern of these discounted signals is topographically mapped into Filling-In Domains, or FIDOs, within the surface stream, or FCS. Here the discounted signals can begin to spread across space. This spreading process has many of the properties of diffusion. The signal spread is contained within boundary signals that are topographically mapped from the BCS into the FIDOs. The result is given in the top row of each panel; namely, the patterns labeled OUTPUT.

Figures 3a and 3b show how these simple mechanisms can discount the illuminant and recover the original pattern of image reflectances under some circumstances. However, due to the discounting process, image reflectances are not always veridically recovered. For example, the STIMULUS in Figure 3c contains two steps of equal luminance on a background that varies so gradually between them that no boundary is detected. In the OUTPUT profile, brightness contrast obtains; namely, the right step is more active than the left step in the OUTPUT activity profile. This is due to the sensitivity of the on-center off-surround network to image contrasts; see the FEATURE pattern. Remarkably, however, the luminance gradient that caused the brightness contrast is not visible in the final percept. The background has uniform brightness in the OUTPUT because no boundary exists whereby to restrict the filling-in process between the two luminance steps, as can also occurs *in vivo* under such conditions. In addition to showing how brightness contrast can occur due to the discounting process, this is also a philosophically interesting example because it demonstrates a "visible effect of an invisible cause".

Figure 3d shows that the same mechanisms can also cause the opposite of brightness contrast; namely, brightness assimilation (Helson, 1963). This figure simulates an effect that was reported by Shapley and Reid (1986). The luminance profile here is derived from a standard brightness contrast profile by the introduction of two additional test regions. These test luminance steps are the same and are placed on equally but less luminant backgrounds. A simple brightness contrast explanation would suggest that the two steps should have the same brightness. However, humans report that the left step looks brighter than the right one, as also occurs in the OUTPUT activity profile of the model. In some way, the perceived brightness of the background has been "assimilated" into the brightness of the steps. How this happens in the model can be directly inferred from Figure 3d, which shows that a complicated pattern of activity cusps and dips is caused by the discounting process. These cusps and dips are broader than the boundaries that they induce. When this FEATURE profile fills-in within its narrower boundaries, the reported assimilative effect obtains in the OUTPUT as an emergent property of network interactions.

The same model can explain many other brightness data in a unified way, including variants of the Craik-O'brien-Cornsweet effect, the Koffka-Benussi ring, Kanizsa-Minguzzi anomalous brightness differentiation, the Hermann grid, a Land Modrian viewed under constant and gradient illumination that cannot be explained by Retinex theory, impossible staircases, bull's eyes, and various nested combinations of luminance profiles. That such a simple combination of discounting, boundary, and surface interactions can explain such a large body of brightness data, with a fixed set of parameters, is a challenge to all other models of filling-in and brightness perception.

3-D Figure-Ground Separation

Although the mechanisms that are illustrated in Figure 3 may be necessary for explaining how filling-in works within the brain, they are certainly not sufficient. In particular, the mechanisms in Figure 3 are not sufficient to explain how two eyes work together to generate three-dimensional percepts of surfaces in depth, notably how percepts of occluding and occluded objects are generated in depth. The struggle to understand the large and challenging data bases about such figure-ground phenomena has been a key motivation for the further development of FACADE theory.

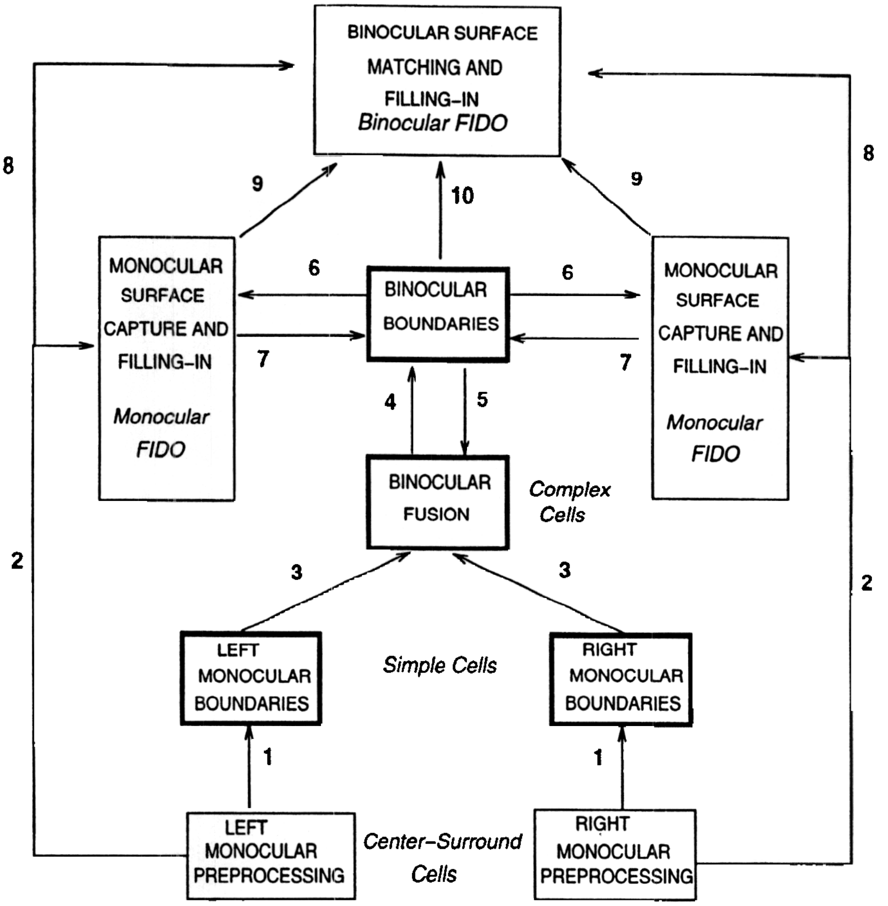


Figure 4. FACADE macrocircuit showing interactions of the Boundary Contour System (BCS) and Feature Contour System (FCS). See text for details. [Reprinted with permission from Kelly and Grossberg (2000).]

Figure 4 is a macrocircuit of FACADE theory in its present form. Because the interactions posited by the theory have explained and simulated so many data about 3-D vision, its main operations will be summarized here to clarify some of the perceptual issues that are handled by the theory, and to illustrate how surface filling-in processes may be intimately intertwined with boundary processes. Monocular processing of left-eye and right-eye inputs by the retina and lateral geniculate nucleus (LGN) discounts the illuminant and generates parallel signals to the BCS and FCS. These signals go to model cortical simple cells via pathways 1 in Figure 4, and to monocular filling-in domains (FIDOs) via pathways 2. Model simple cells have oriented receptive fields and come in multiple sizes. Simple cell outputs are binocularly combined at complex and complex end-stopped (or hypercomplex) cells via pathways 3. Complex cells with larger receptive fields can binocularly fuse a broader range of disparities than can cells with smaller receptive fields (see Smallman and MacLeod (1994) for a review). Competition across disparity at each position and among cells of a given size scale sharpens complex cell disparity tuning (Fahle and Westheimer, 1995). Spatial competition (end-stopping) and orientational competition convert complex cell responses into spatially and orientationally sharper responses at hypercomplex cells.

How are these responses from multiple receptive field *sizes* combined to generate positionally accurate representations of relative *depths* from the observer? FACADE theory proposes that hypercomplex cells activate bipole cells via pathway 4. These bipole cells carry out long-range grouping and boundary completion, and are proposed to occur in the cortical area V2 Interstripes. The bipole grouping process collects together the outputs from all hypercomplex cells, of all sizes, that are sensitive to a given depth range. All of these outputs activate a shared set of bipole cells. The bipole cells, in turn, send excitatory feedback signals via pathways 5 back to all hypercomplex cells that represent the same position and orientation, and inhibitory feedback signals to hypercomplex cells at the same and nearby positions and orientations. This feedback process binds together, or groups, cells of multiple *sizes* into a BCS representation, or copy, that is sensitive to a prescribed range of *depths*. In this way, each BCS copy completes boundaries only within a given depth range, using all the information that is available from the multiple receptive field sizes. Multiple BCS copies are formed, each corresponding to different (but possibly overlapping) depth ranges.

This grouping process is also proposed to play a key role in figure-ground separation. The main fact for present purposes is that each bipole cell has an oriented receptive field with two parts (Figure 5). Each part receives inputs from a range of almost colinear orientations and positions. When the bipole cell does not receive direct bottom-up activation of its cell body, it can only fire if both parts of its receptive field are simultaneously active. This assures that the cells do not complete boundaries beyond a line end unless there is another line end which provides evidence for such a linkage. The bipole cell thus behaves like a statistical AND gate. Such cells were first used by Cohen and Grossberg (1984) and Grossberg and Mingolla (1985) to model data about perceptual grouping and filling-in. Cells with similar properties in cortical area V2 were first reported by von der Heydt, Peterhans and Baumgartner (1984). Their properties are consistent with many psychophysical data; e.g., Field et al.(1993) and Shipley and Kellman (1992).

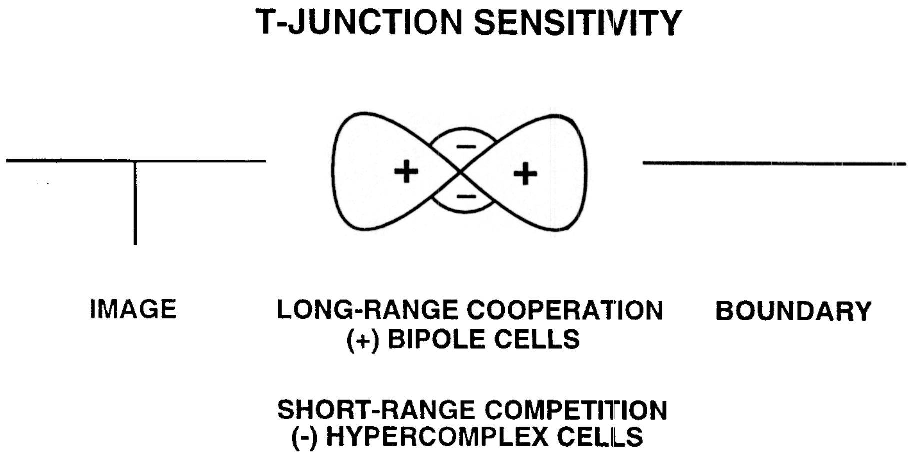


Figure 5. T-junction sensitivity in the BCS: (a) T-junction in an image. (b) Bipole cells provide long-range cooperation (+), whereas hypercomplex cells provide shorter-ranger competition (-). (c) An edn-gap in the vertical boundary arises due to this combination of cooperation and competition. [Reprinted with permission from Grossberg (1997).]

How does the grouping process contribute to figure-ground separation? As noted above, the feedback from bipole cells to hypercomplex cells combines long-range excitatory feedback with shorter-range inhibitory feedback (Figure 5). Together, these feedback processes make the system sensitive to T-junctions in an image, without the use of explicit T-junction operators. This is because excitatory bipole feedback strengthens the boundary along the top of a T while inhibiting nearby boundary positions where the stem of the T joins its top. This can be understood by considering horizontally-oriented cells that are located where the top of the T joins its stem. Such cells receive excitatory support from both branches of the top. On the other hand, vertically-oriented cells that process the stem of the T where it joins the top receive excitatory support only from one branch of their receptive field; namely, where it is activated by the stem. The inhibition of the stem by the top causes a gap in the boundary (see Figure 5), termed an *end-gap*. During filling-in, boundaries contain the filling-in process. Where end-gaps occur, brightness or color can flow out of a figural region would otherwise have been contained within the region defined by the T edges. FACADE theory predicts that this escape of color or brightness via the filling-in process is one of the key steps that initiates figure-ground separation; see Grossberg (1994, 1997), Grossberg and McLoughlin (1997), and Kelly and Grossberg (2000) for examples of how this can occur.

How are the multiple depth-selective BCS copies used to capture brightness and color signals within the corresponding depth-selective FCS surface representations? There are at least two stages in this surface filling-in process. The first stage is called *monocular filling-in domains*, or monocular FIDOs, which are presently thought to exist within the Thin Stripes of cortical area V2. Monocular FIDOs receive brightness and color signals from a single eye. A pair of monocular FIDOs, one for each eye, corresponds to each binocular BCS copy. Several BCS copies, that represent nearby depth ranges, may send convergent signals, albeit with possibly different weights, to each monocular FIDO, thereby generating a continuous change in perceived depth across a finite set of FIDOs.

The *surface capture* process is controlled by interacting BCS signals and illuminant-discounted FCS signals. Pathways 2 in Figure 4 input their discounted monocular FCS signals to *all* of the monocular FIDOs. The surface capture process then determines which of these FIDOs will succeed in selectively filling-in these signals, and thereby lifting the monocular FIDO signals into depth-selective surface representations for purposes of filling-in. The boundary signals along pathways 6 in Figure 4 determine which FIDOs will fill-in. These boundary signals selectively capture those FCS inputs that are spatially coincident and orientationally aligned with the BCS boundaries. Other FCS inputs are suppressed by this BCS-FCS interaction. These properties naturally arise when double-opponent cells process boundary-gated signals in the monocular FIDOs. How this happens, and how this interaction can explain data about binocular fusion and rivalry, among other percepts, are discussed in Grossberg (1987b).

The captured FCS inputs, and only these, can trigger diffusive filling-in of a surface representation within the selected FIDOs. Because these filled-in surfaces are activated by depth-selective BCS boundaries, they inherit the same depths as these boundaries. This property helps to explain how 3-D surface representations may represent both the depths and the qualia, such as color and brightness, that occur in our percepts of 3-D objects. This intimate linkage between depth and brightness helps to explain, for example, data about proximity-luminance covariation, or why brighter surfaces tend to look closer; e.g., Egusa (1983).

Not every such filling-in event can generate a surface representation. Because activity spreads until it hits a boundary, only surfaces that are surrounded by a connected BCS boundary, or fine web of such boundaries, are effectively filled-in. The diffusion of activity dissipates across the FIDO otherwise. This property helps to explain many data, ranging from data about neon color spreading to data about 3-D figure-ground perception; see, for example, Grossberg (1994) for further discussion.

An analysis of how the BCS and FCS react to 3-D images shows that too many boundary and surface fragments are formed as a result of the size-disparity correlation (Julesz and Schumer, 1981; Kulikowski, 1978; Richards and Kaye, 1974; Schor et al, 1984; Tyler, 1975). In particular, large scales can fuse a larger range of disparities than can small scales. How are the surface depths that we actually perceive selected from this range of possibilities across all scales? The proposed answer to this question clarifies how a unified percept of boundary and surface is achieved, despite the fact, as noted above, that the boundary and surface systems compute complementary properties. The key issue is thus: How is perceptual *consistency* derived from boundary-surface *complementarity*? FACADE theory predicts how this may be achieved by feedback between the boundary and surface streams, that is predicted to occur no later than cortical area V2. This mutual feedback helps to clarify many confusing properties of visual perception and visual neuroscience, ranging from figure-ground properties (see below) to why the blob and interblob streams seem to share so many receptive field properties even though they carry out such different tasks. In particular, this feedback interaction clarifies how boundary cells, which tend to summate inputs from both contrast polarities, can also be modulated by surface cells, which are sensitive to just one contrast polarity.

Boundary-surface consistency is achieved in FACADE theory by a contrast-sensitive process that detects the contours of successfully filled-in regions within the monocular FIDOs. Only successfully-filled in regions *can* activate such a contour-sensitive process, because other regions either do not fill-in at all, or their filling-in dissipates across space. The filled-in contours activate FCS-to-BCS feedback signals (pathways 7 in Figure 4). These feedback signals further excite the BCS boundaries corresponding to their own positions and depths. The boundaries that activated the successfully filled-in surfaces in the first place are hereby strengthened. The feedback signals also inhibit redundant boundaries at their own positions and farther depths. This inhibition from near-to-far is called *boundary pruning*. It illustrates a perceptual principle that I call the *asymmetry between near and far*. This principle shows itself in many perceptual data, including data about 3-D neon color spreading (Nakayama, Shimojo, and Ramachandran, 1990); see Grossberg (1994, 1999a) for a discussion of how to explain such data.

How does boundary pruning contribute to figure-ground separation? Boundary pruning spares the closest surface representation that successfully fills-in a given set of positions. Boundary pruning also inhibits redundant copies of the boundaries of occluding objects that would otherwise form at farther depths. When the competition from these redundant occluding boundaries is removed, the boundaries of partially occluded objects can be completed behind them on BCS copies that represent these farther depths. Moreover, when the redundant occluding boundaries collapse, the redundant surfaces that they momentarily supported at the monocular FIDOs collapse. Occluding surfaces are hereby seen to lie in front of occluded surfaces. The boundary pruning process helps to explain many paradoxical data about interactions between depth and brightness, such as: Why do brighter Kanizsa squares look closer (Bradley and Dumais, 1984; Kanizsa, 1955, 1974; Purghé and Coren, 1992)? Why is boundary pruning relevant to this phenomenon? The brightness of a Kanizsa square is an emergent property; it can only be determined after *all* the brightness and darkness inducers fill in within the Kanizsa square. Somehow this emergent brightness within the FIDOs then influences the perceived depth of the square. Within FACADE theory, this means that the brightness within the FIDO needs to influence the depth-selective BCS copies that control relative depth. FACADE theory shows how this can naturally occur via the BCS-to-FCS feedback signals that ensure boundary-surface consistency (Grossberg, 1997, Section 22).

Visible brightness percepts are not, however, represented within the monocular FIDOs. Indeed, all model representations in V2, both of binocular boundaries and monocular filled-in surfaces, are predicted to be *amodal*, or perceptually invisible. These representations are predicted to be used directly by object recognition mechanisms in inferotemporal cortex and beyond, since they accurately represent occluding and occluded objects. In particular, the boundary pruning process enables the boundaries of occluded objects to be completed within the BCS, which makes them much easier to recognize. The surface representations within the monocular FIDOs cannot, therefore, distinguish between which parts of a surface are occluded, and which are not. These surface representations fill-in an occluded object within the completed object boundaries, even behind an opaque occluding object. Thus, if only this representation of the world existed, then every occluding object would appear transparent.

This fact raises the following basic question: How does the visual cortex generate representations of occluding and occluded objects that can be easily recognized, yet also generate representations of occluding and occluded objects that allow us to consciously see, and reach for, only the unoccluded parts of objects? FACADE theory proposes that the latter goal is realized at the binocular FIDOs using a different combination of boundary and surface representations of occluded objects than is found at the monocular FIDOs. How is happens will now be summarized.

The surface representations that are generated at the monocular FIDOs are depth-selective, but they do not combine brightness and color signals from both eyes. Binocular combination of brightness and color signals takes place at the binocular FIDOs, which are predicted to exist in cortical area V4. It is here that *modal*, or visible, surface representations are predicted to occur, and to represent only the visible parts of occluded objects, except in cases where transparent percepts are selectively generated by configural scenic properties.

Thus it is in the binocular FIDOs that monocular FCS signals from both eyes (pathways 8 in Figure 4) are predicted to be binocularly matched. An analysis of the surviving matched signals shows that they are redundantly represented on multiple FIDOs at the same positions. Which signals are redundant can only be tested by assessing which monocular FIDOs can successfully fill-in. Then the corresponding binocular FIDO can be allowed to fill in, and all farther FIDOs at those positions can be inhibited. These redundant binocularly matched signals are pruned by inhibitory contrast-sensitive signals from the monocular FIDOs (pathways 9 in Figure 4). The pruning signals from the monocular FIDOs to the binocular FIDOs inhibit the FCS signals at their own positions and farther depths. As a result, occluding objects cannot redundantly fill-in surface representations at multiple depths. This is another example of the asymmetry between near and far. It is called *surface pruning*. Contrast-sensitive output signals from successfully filled-in regions within the monocular FIDOs are hereby predicted to carry out two types of pruning: they prune redundant boundaries in cortical area V2, and redundant surface elements in cortical area V4.

As in the case of the monocular FIDOs, the FCS signals to the binocular FIDOs can initiate filling-in only where they are spatially coincident and orientationally aligned with BCS boundaries. BCS-to-FCS pathways 10 in Figure 4 carry out depth-selective surface capture of the binocularly matched FCS signals that survive surface pruning. In all, the binocular FIDOs fill in FCS signals that: (a) survive within-depth binocular FCS matching and across-depth FCS inhibition; (b) are spatially coincident and orientationally aligned with the BCS boundaries; and (c) are surrounded by a connected boundary or fine web of such boundaries.

One further property is needed to complete this summary: At the binocular FIDOs, the BCS adds the boundaries that are computed at nearer depths to those that represent farther depths. This instance of the asymmetry between near and far is called *boundary enrichment*. The enriched boundaries prevent occluding objects from looking transparent by blocking filling-in of occluded objects behind them. The total filled-in surface representation across all binocular FIDOs represents the visible percept. It is called a FACADE representation because it combines together, or multiplexes, properties of Form-And-Color-And-Depth. It is this culminating interaction that gives FACADE theory its name.

Although the FACADE macrocircuit is perhaps the most complicated vision model yet proposed, all of its operations have supportive psychophysical and neural data, and it provides a unified explanation of many perceptual data, such as the Weisstein effect, 3-D neon color spreading, 3-D Kanizsa-Varin percepts, Bregman-Kanizsa figure-ground separation, Kanizsa stratification, daVinci stereopsis (Grossberg, 1994; Grossberg and McLoughlin, 1997), and various monocular and binocular percepts of brightness and lightness, including Fechner's paradox and the Munker-White, Benary cross, and checkerboard percepts (Grossberg, 1994, 1997; Grossberg and Kelly, 1999; Kelly and Grossberg, 2000).

Perceptual Learning, Aftereffects, and the McCollough Effect

FACADE theory also points to issues that are quite invisible without its framework as a guide. For example, how do binocular boundaries successfully interact with monocular FIDOs? It is well known that binocular fusion can positionally displace the perceived location of a binocularly fused boundary relative to the locations of its monocular inputs to the two eyes (von Tschermak-Seysenegg, 1952). How, then, do the displaced binocular boundaries get positionally aligned with the monocular FCS feature contour signals that they need to contain? Grossberg (1987b) suggested that this occurs through learning that is based upon interactions between the BCS and the FCS. Grossberg (1987b) outlined how this type of learning could qualitatively explain many properties of the McCollough effect (McCollough, 1965), which is an orientationally-specific long-term chromatic aftereffect. More recently, Grossberg, Hwang, and Mingolla (2000) have developed this suggestion into a rigorous computational study which shows how this type of learning may contribute to a quantitative simulation of thirteen different McCollough effect experiments. In addition to these learned alignments, one also needs to incorporate mechanisms for dynamically resetting cortical representations. These reset mechanisms can influence explanations of filling-in by showing how certain perceptual afterimages can occur (Francis and Grossberg, 1996). Thus, once one has a principled theory like FACADE theory as a tool, one can begin to explain, and to see unexpected mechanistic relationships between, data that would otherwise seem to be mysterious and disconnected. That is why, in the final analysis, we build models of how the brain sees. It is also why one cannot fully understand filling-in outside the context of such a comprehensive analysis.

References

Arrington, K. F. (1994). The temporal dynamics of brightness filling-in. *Vision Research*, **34**, 3371-3387.

Bradley, D.R. and Dumais, S.T. (1984). The effects of illumination level and retinal size on the depth stratification of subjective contour figures. *Perception*, **13**, 155-164.

Dennett, D. (1991). Consciousness explained. Boston: Little Brown.

Boynton, R.M., Eskew, R.T. Jr. and Olson, C.X. (1985). Research note: Blue cones contribute to border distinctness. *Vision Research*, **25**, 1349-1352.

Cohen, M.A. and Grossberg, S. (1984). Neural dynamics of brightness perception: Features, boundaries, diffusion, and resonance. *Perception & Psychophysics*, **36**, 428-456.

Egusa, H. (1983). Effects of brightness, hue, and saturation on perceived depth between adjacent regions in the visual fields. *Perception*, **12**, 167-175.

Elder, J.H. and Zucker, S.W. (1998). Evidence for boundary-specific grouping. *Vision Research*, **38**, 143-152.

Fahle, M. and Westheimer, G. (1995). On the time-course of inhibition in the stereoscopic perception of rows of dots. *Vision Research*, **35**, 1393-1399.

Faubert, J. and von Grünau, M. (1995). The influence of two spatially distinct primers and attribute priming on motion induction. *Vision Research*, **36**, 149-173.

Field, D.J., Hayes, A. and Hess, R.F. (1993). Contour integration by the human visual system: evidence for a local "association field". *Vision Research*, **33**, 173-193.

Francis, G. and Grossberg, S. (1996). Cortical dynamics of boundary segmentation and reset: Persistence, afterimages, and residual traces. *Perception*, **25**, 543-567.

Gove, A., Grossberg, S. and Mingolla, E. (1995). Brightness perception, illusory contours, and cortiogeniculate feedback. *Visual Neuroscience*, **12**, 1027-1052.

Grossberg, S. (1987a). Cortical dynamics of three-dimensional form, color, and brightness perception: I. Monocular theory. *Perception & Psychophysics*, **41**, 87-116.

Grossberg, S. (1987b). Cortical dynamics of three-dimensional form, color, and brightness perception: II. Binocular theory. *Perception & Psychophysics*, **41**,117-141.

Grossberg, S. (1994). 3-D vision and figure-ground separation by visual cortex. *Perception & Psychophysics*, **55**, 48-120.

Grossberg, S. (1999a). A comment on "Assimilation of achromatic color cannot explain the brightness effects of the achromatic neon effect" by Marc K Albert. *Perception*, **28**, 1291-1302.

Grossberg, S. (1999b). How does the cerebral cortex work? Learning, attention, and grouping by the laminar circuits of visual cortex. *Spatial Vision*, **12**, 163-186.

Grossberg, S., Hwang, S. and Mingolla, E. (2000). Thalamocortical dynamics of the McCollough effect: Boundary-surface alignment through perceptual learning. In preparation.

Grossberg, S. and Kelly, F. (1999). Neural dynamics of binocular brightness perception. *Vision Research*, **39**, 3796-3816.

Grossberg, S. and McLoughlin, N. (1997). Cortical dynamics of 3-D surface perception: Binocular and half-occluded scenic images. *Neural Networks*, **10**, 1583-1605.

Grossberg, S. and Mingolla, E. (1985). Neural dynamics of form perception: Boundary completion, illusory figures, and neon color spreading. *Psychological Review*, **92**, 173-211.

Grossberg, S. and Pessoa, L. (1998). Texture segregation, surface representation, and figure-ground separation. *Vision Research*, **38**, 2657-2684.

Grossberg, S. and Raizada, R.D.S. (2000). Contrast-sensitive perceptual grouping and object-based attention in the laminar circuits of primary visual cortex. *Vision Research*, **40**, 1413-1432.

Grossberg. S. and Todorovic´, D. (1988). Neural dynamics of 1-D and 2-D brightness perception: A unified model of classical and recent phenomena. *Perception & Psychophysics*, **43**, 241-277.

Grossberg. S. and Williamson, J.R. (2000). A neural model of how horizontal and interlaminar connections of visual cortex develop into adult circuits that carry out perceptual grouping and learning. *Cerebral Cortex*, in press.

Helson, H. (1963). Studies of anomalous contrast and assimilation. *Journal of the Optical Society of America*, **53**, 179-184.

Julesz, B. and Schumer, R.A. (1981). Early visual perception. *Annual Review of Psychology*, **32**, 572-627.

Kanizsa, G. (1955). Margini quasi-percettivi in campi con stimolazione omogenea. *Revista di Psicologia*, **49**, 7-30.

Kanizsa, G. (1974). Contours without gradients or cognitive contours. *Italian Journal of Psychology*, **1**, 93-113.

Kelly, F. and Grossberg, S. (2000). Neural dynamics of 3-D surface perception: Figure-ground separation and lightness perception. *Perception & Psychophysics*, in press.

Kulikowski, J.J. (1978). Limit of single vision in stereopsis depends on contour sharpness. *Nature*, **275**, 126-127.

Lamme, V.A.F., Rodriguez-Rodriguez, V. and Spekreijse, H. (1999). Separate processing dynamics for texture elements, boundaries, and surfaces in primary visual cortex of the macaque monkey. *Cerebral Cortex*, **9**, 406-413.

McCollough, C. (1965). Color adaptation of edge-detectors in the human visual system. *Science*, **149**, 1115-1116.

Nakayama, K, Shimojo, S. and Ramachandran, V.S.(1990). Transparency: Relation to depth, subjective contours, luminance, and neon color spreading. *Perception*, **19**, 497-513.

Paradiso, M.A. and Nakayama, K. (1991). Brightness perception and filling-in. *Vision Research*, **31**, 1221-1236.

Pessoa, L, Beck, J. and Mingolla, E. (1996). Perceived texture segregation in chromatic element-arrangement patterns: high luminance interference. *Vision Research*, **36**, 1745-1761.

Pessoa, L., Mingolla, E. and Neumann, H. (1995). A contrast- and luminance-driven multi-scale network model of brightness perception. *Vision Research*, **35**, 2201-2223.

Pessoa, L., Thompson, E. and Noë, A. (1998). Finding out about filling in: A guide to perceptual completion for visual science and the philosophy of perception. *Behavioral and Brain Sciences*, **21**, 723-802.

Purghé, F. and Coren, S. (1992). Amodal completion, depth stratification, and illusory figures: A test of Kanizsa's explanation. *Perception*, **21**, 325-335.

Redies, C. and Spillmann, L. (1981). The neon color effect in the Ehrenstein illusion. *Perception*, **10**, 667-681.

Richards, W.A. and Kaye, M.G. (1974). Local versus global stereopsis: Two mechanisms. *Vision Research*, **14**, 1345-1347.

Rogers-Ramachandran, D.C. and Ramachandran, V.S. (1998). Psychophysical evidence for boundary and surface systems in human vision. *Vision Research*, **38**, 71-77.

Schor, C.M., Wood, I. And Ogawa, J. (1984). Binocular sensory fusion is limited by spatial resolution. *Vision Research*, **24**, 661-665.

Shapley, R. and Reid, R.C. (1986). Contrast and assimilation in the perception of brightness. *Proceedings of the National Academy of Sciences USA*, **82**, 5983-5986.

Smallman, H.S. and MacLeod, D.I.A. (1994). Size-disparity correlation in stereopsis at contrast threshold. *Journal of the Optical Society of America A*, **11**, 2169-2183.

Smallman, H.S. and McKee, S.P. (1995). A contrast ratio constraint on stereo matching. *Proceedings of the Royal Society of London B*, **260**, 265-271.

Tyler, C.S. (1975). Spatial organization of binocular disparity sensitivity. *Vision Research*, **15**, 583-590

Von der Heydt, R., Peterhans, E. and Baumgartner, G. (1984). Illusory contours and cortical neuron responses. *Science*, **224**, 1260-1262.

Peterhans, E. and Von der Heydt, R. (1989). Mechanisms of contour perception in monkey visual cortex, II: contours bridging gaps. *Journal of Neuroscience*, **9**, 1749-1763.

Shipley, T.F. and Kellman, P.J. (1992). Perception of partly occluded objects and illusory figures: Evidence for an identify hypothesis. *Journal of Experimental Psychology: Human Perception & Performance*, **18**, 106-120.

Tansley, B.W. and Boynton, R.N. (1976). A line, not a space, represents visual distinctness of borders formed by different colors. Science, 191, 954-957.

Tansley, B.W. and Boynton, R.N. (1978). Chromatic border perception: The role of the red- and green-sensitivity cones. *Vision Research*, **18**, 683-697.

Von Tschermak-Seysenegg, A. (1952). *Introduction to physiological optics* (P. Boeder, Trans.). Springfield, IL: Thomas.

Waxman, A.M., Seibert, M.C., Gove, A., Fay, D.A., Bernardon, A.M., Lazott,C., Steele, W.R. and Cunningham, R.K. (1995). Neural processing of targets in visible, multispectral IR and SAR imagery. *Neural Networks*, **8**, 1029-1051.