Article
Neural Facades: Visual Representations of Static and Moving Form-And-Color-And-Depth

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1. Introduction: The Inadequacy of Visual Modules

This article discusses some implications for understanding vision of recent theoretical results concerning the neural architectures that subserve visual perception in humans and other mammals (Cohen and Grossberg 1984; Grossberg 1984, 1987a, 1987b, 1988; Grossberg and Marshall 1989; Grossberg and Mingolla 1985a, 1985b, 1987; Grossberg, Mingolla, and Todorović 1989; Grossberg and Rudd 1989; Grossberg and Todorović 1988). In addition, a new result is stated concerning differences between the neural mechanisms for perception of static visual forms and moving visual forms, indeed why both types of mechanisms exist.

These results contribute to the development of a neural theory of preattentive vision, called FACADE Theory. FACADE Theory clarifies that, whereas specialization of function surely exists during visual perception, it is not the type of specialization that may adequately be described by separate neural modules for the processing (say) of edges, textures, shading, stereo, and color information. In particular, the present theory provides an explanation of many data that do not support the modular approach described by Marr (1982).

A basic conceptual problem faced by a modular approach may be described as follows. Suppose that specialized modules capable of processing edges, or textures, or shading, *etc.* are available. Typically each of these modules is described using different mathematical rules that are not easily combined into a unified theory. Correspondingly, the modules do not respond well to visual data other than the type of data which they were designed to process. In order to function well, either the visual world which such a module is

allowed to process must be restricted, whence the module could not be used to process realistic scenes; or a smart preprocessor is needed to sort scenes into parts according to the type of data that each module can process well, and to expose a module only to that part of a scene for which it was designed. Such a smart preprocessor would, however, embody a more powerful vision model than the modules themselves; hence would render the modules obsolete. In either case, modular algorithms do not provide a viable approach to the study of real-world vision.

The task of such a smart preprocessor is, in any case, more difficult than one of sorting scenes into parts which contain only one type of visual information. This is because each part of a visual scene often contains locally ambiguous information about edges, textures, shading, stereo, motion, and color, all overlaid together. Humans are capable of using these multiple types of visual information cooperatively to generate an unambiguous 3=dimensional representation of Form-And-Color-And-DEpth; hence the term FACADE representation. The hyphens in 'Form-And-Color-And-DEpth' emphasize the well-known fact that changes in perceived color can cause changes in perceived depth and form, changes in perceived depth can cause changes in perceived brightness and form, and so on. Every stage of visual processing *multiplexes* together several key properties of the scenic representation. It is a central task of biological vision theories to understand how the organization of visual information processing regulates which properties are multiplexed together at each processing stage, and how the stages interact to generate these properties.

2. Hierarchical Resolution of Uncertainty Using Interactions Between Complementary Systems

FACADE Theory became possible through the discovery of several new uncertainty principles; that is, principles which show what combinations of visual properties cannot, in principle, be computed at a single processing stage (Grossberg 1987a; Grossberg and Mingolla 1985b). The theory describes how to design parallel and hierarchical interactions that can resolve these uncertainties using several processing stages. These interactions occur within and between two subsystems whose properties are computationally complementary. These complementary subsystems are called the Boundary Contour System (BCS) and the Feature Contour System (FCS).

Issues concerning uncertainty principles and complementarity lie at the foundations of quantum mechanics. Mammalian vision systems are also quantum systems in the sense that they can generate visual percepts in response to just a few light quanta. How the types of uncertainty and complementarity that are resolved by biological vision systems for purposes of macroscopic perception may be related to concepts of uncertainty and complementary in quantum mechanics is a theme of considerable importance for future research.

For present purposes, the themes of uncertainty and complementarity show the inadequacy of the modular approach from a deeper information theoretic perspective. Although the BCS, FCS, and their individual processing stages are computationally specialized, their *interactions* overcome computational uncertainties and complementary deficiences to generate useful visual representations, rather than properties that may be computed by independent processing modules.

Such an interactive theory also precludes the sharp separation between formal algorithm and mechanistic realization that Marr (1982) proposed. How computational uncertainties can be overcome, how particular combinations of multiplexed properties can be achieved, and how complementary processing properties can be interactively synthesized, are properties of particular classes of mechanistic realizations. Many workers in the field of neural networks summarize this state of affairs by saying that 'the architecture is the algorithm'.

3. Generating Invariant Boundary Structures and Surface Colors

FACADE Theory clarifies how our visual systems are designed to detect relatively invariant surface colors under variable illumination conditions, to detect relatively invariant object boundary structures amid noise caused by the eyes' own optics or occluding objects, and to recognize familiar objects or events in the environment. These three principle functions are performed by the Feature Contour System (FCS), the Boundary Contour System (BCS) and by an Object Recognition System (ORS), respectively, as indicated in the macrocircuit of Figure 1.

The computational demands placed on a system that is designed to detect invariant surface colors are, in many respects, complementary to the demands placed on a system that is designed to detect invariant boundary structures. That is why the FCS and BCS in Figure 1 process the signals from each monocular preprocessing (MP) stage in parallel. The FCS and BCS are not, however, independent modules. Figure 2 depicts in greater detail how levels of the FCS and BCS interact through multiple feedforward and feedback pathways to generate a FACADE representation at the final level of the FCS.

In addition to the complementary relationship between the FCS and the BCS, there also exist informational uncertainties at processing levels within each of these systems. In particular, the filtering computations within the FCS which reduce uncertainty due to variable illumination conditions create new uncertainties about surface brightnesses and colors that are resolved at a higher FCS level by a process of featural filling-in. The filtering computations within the BCS which reduce uncertainty about boundary orientation create new uncertainties about boundary position that are resolved at a higher BCS level by a process of boundary completion.

The division of labor between BCS and FCS is not simply a partitioning for simplicity or convenience. Rather, BCS dynamics require oriented
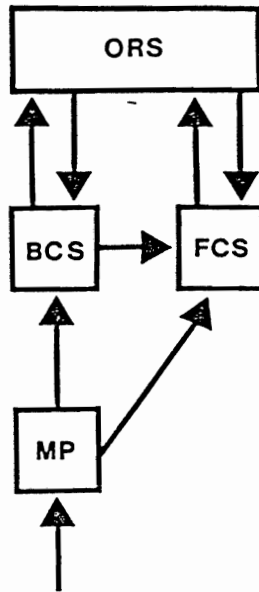
Figure 1 A macrocircuit of processing stages: Monocular preprocessed signals (MP) are sent independently to both the Boundary Contour System (BCS) and the Feature Contour System (FCS). The BCS preattentively generates coherent boundary structures from these MP signals. These structures send outputs to both the FCS and the Object Recognition System (ORS). The ORS, in turn, rapidly sends top-down learned template signals, or expectations, to the BCS. These template signals can modify the preattentively completed boundary structures using learned, attentive information. The BCS passes these modifications along to the FCS. The signals from the BCS organize the FCS into perceptual regions wherein filling-in of visible brightnesses and colors can occur. This filling-in process is activated by signals from the MP stage. The completed FCS representation, in turn, also interacts with the ORS.

filtering operations followed by oriented cooperative-competitive feedback interactions, because such an architecture can rapidly and in a context-sensitive manner perform the requisite boundary segmentations that the FCS itself needs in order to pool, or fill-in, its estimates of surface color among regions belonging to the same perceived objects. That pooling is a type of unoriented spatial averaging performed by a diffusion process. Were a diffusion of signals employed within the BCS itself, however, it could blur the very boundaries that it seeks to sharpen and thereby defeat
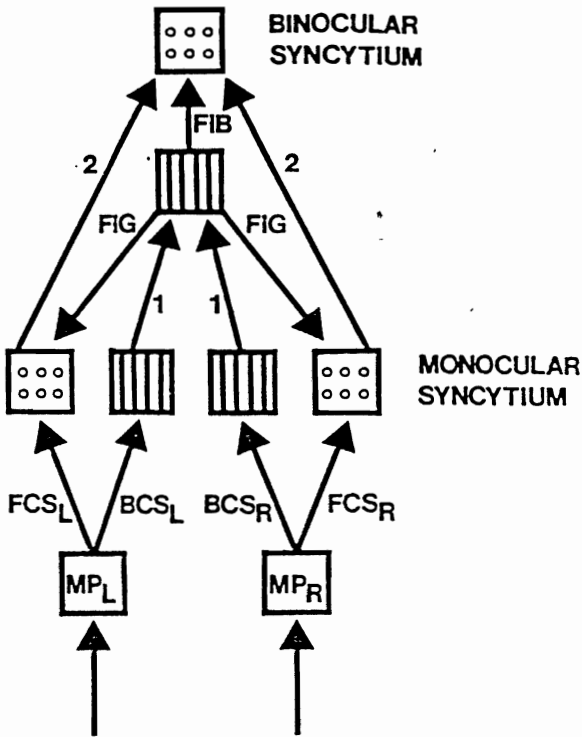
Figure 2 Macrocircuit of monocular and binocular interactions within the Boundary Contour System (BCS) and the Feature Contour System (FCS): Left and right monocular preprocessing stages (MP_L and MP_R) send parallel monocular inputs to the BCS (boxes with vertical lines) and the FCS (boxes with three pairs of circles). The monocular BCS_L and BCS_R interact via bottom-up pathways labelled 1 to generate a coherent binocular boundary segmentation. This segmentation generates output signals called filling-in generators (FIGs) and filling-in barriers (FIBs). The FIGs input to the monocular filling-in domains, or syncytia, of the FCS. The FIBs input to the binocular filling-in domains, or syncytia, of the FCS. Inputs from the MP stages interact with FIGs at the monocular syncytia where they select those monocular FC signals that are binocularly consistent. The selected FC signals are carried by the pathways labelled 2 to the binocular syncytia, where they interact with FIB signals from the BCS to generate a multiple scale representation of form-and-color-and-depth within the binocular syncytia. The present article describes some monocular properties of the interactions from an MP stage through the first few BCS and FCS stages, namely those symbolized by the pathways labelled 1 and FIG.

both the BCS and FCS system goals. Accordingly, as shown in Figure 1, the BCS processes occur separately of, and in parallel with, FCS processes, but send topographically matched signals to the FCS to organize the spatial structuring of the FCS filling-in process.

4. Preattentive Visual Processing by the Boundary Contour System and Feature Contour System

The theory's general-purpose capabilities depend upon its decomposition into BCS, FCS, and ORS subsystems. Both the BCS and FCS operate pre-attentively and automatically upon all images, whether or not these images have been experienced before. The BCS is a general-purpose device in the sense that it can generate an emergent 3-D boundary segmentation in response to a wide variety of image properties. For example, it is capable of detecting, sharpening, and completing image edges; of grouping textures; of generating a boundary web of boundary compartments that conform to the shape of smoothly shaded regions; and of carrying out a disparity-sensitive and scale-sensitive binocular matching process that generates fused binocular structures from disparate pairs of monocular images. The outcome of this 3-D boundary segmentation process is perceptually invisible within the BCS. Visible percepts are a property of the FCS.

A completed segmentation within the BCS elicits topographically organized output signals to the FCS. These completed BC Signals regulate the hierarchical processing of color and brightness signals by the FCS (Figure 2). Notable among FCS processes are the automatic extraction from many different types of images of color and brightness signals that are relatively uncontaminated by changes in illumination conditions—again a general-purpose property. These Feature Contour signals interact within the FCS with the output signals from the BCS to control featural filling-in processes. These filling-in processes lead to visible percepts of form-and-color-and-depth at the final stage of the FCS, which is called the Binocular Syncytium (Figure 2).

Such a theoretical decomposition of the vision process conforms to, and has in fact predicted, properties of a similar decomposition that governs the design of the mammalian visual cortex. For example, in the theory's analyses and predictions of neurobiological data, the Monocular Prepro-cessor Stage (MP_L, MP_R) of Figures 1 and 2 is compared with opponent cells of the lateral geniculate nucleus, the first stage of the BCS is compared with simple cells of the hypercolumns in area V1 of striate cortex, the first stage of the FCS is compared with cells of the cytochrome oxydase staining blobs of area V1 of striate cortex, the Binocular Syncytium is compared with cells of area V4 of the prestriate cortex, and the intervening BCS and FCS stages are compared with complex, hypercomplex, double opponent, and related cell types in areas V1, V2, and V4 of striate and prestriate cortex (Grossberg 1987a; Grossberg and Mingolla 1985a).

5. Interactions Between Preattentive Vision and Attentive Learned Object Recognition

The processes summarized in Figures 1 and 2 are preattentive and automatic. These preattentive processes may, however, influence and be influenced by attentive, learned object recognition processes. The macrocircuit depicted in Figure 1 suggests, for example, that a preattentively completed boundary segmentation within the BCS can directly activate an Object Recognition System (ORS), whether or not this segmentation supports visible contrast differences within the FCS. In the Glass pattern of Figure 3, for example, the circular groupings can be recognized by the ORS even though they do not support visible contrast differences within the FCS.

Figure 3 A Glass pattern: The emergent circular pattern is 'recognized', although it is not 'seen', as a pattern of differing contrasts. The text suggests how this happens.

The ORS can, in turn, read-out attentive learned priming, or expectation, signals to the BCS. Why the ORS needs to read-out learned top-down attentive feedback signals is clarified elsewhere by results from Adaptive Resonance Theory, which has demonstrated that learned top-down expectations help to stabilize the self-organization of object recognition codes in response to complex and unpredictable input environments (Carpenter and Grossberg 1987a, 1987b, 1988). Learned top-down expectations seem to be a computational universal in all self-organizing cognitive systems, including systems for speech and language processing (Cohen and Grossberg 1986, 1987; Cohen, Grossberg, and Stork 1988; Dell 1986;

Grossberg 1978; 1980, 1982, 1986, 1987c; Grossberg and Stone 1986;
McClelland and Rumelhart 1981; Ratcliff and McKoon 1988; Rumelhart
and McClelland 1982).

In response to familiar objects in a scene, the final 3-D boundary
segmentation within the BCS may thus be *doubly* completed, first by
automatic preattentive segmentation processes and then by attentive
learned expectation processes. This doubly completed segmentation
regulates the featural filling-in processes within the FCS that lead to a
percept of visible form. The FCS also interacts with the ORS in order to
generate recognitions of color and surface properties.

The feedback interactions between the preattentive BCS and FCS and
the attentive, adaptive ORS emphasize that these subsystems are not
independent modules, and clarify why the distinction between preattentive
and attentive visual processing has been so controversial and elusive in
the vision literature. Indeed, while seminal workers such as Jacob Beck
and Bela Julesz have probed the preattentive aspects of textural grouping,
other scientists have emphasized the attentive and cognitive aspects of
vision, as in the 'unconscious inferences' of Helmholtz and the 'cognitive
contours' of Richard Gregory. The possibility that emergent segmentations
within the BCS can be doubly completed, both by preattentive emergent
segmentations and attentive learned expectations, helps to unify these
parallel lines of inquiry, and cautions against ignoring the influence of
attentive feedback upon the 'preattentive' BCS and FCS. The rules whereby
such parallel inputs from the BCS and the FCS are combined within the
ORS have recently been the subject of active experimental investigation,
especially due to the excitement surrounding the discovery of 'illusory
conjunctions' (Treisman and Schmidt 1982), whereby form and color
information may be improperly joined under suitable experimental
conditions.

The functional distinction between the attentive learned ORS and the
'preattentive' BCS and FCS also has a neural analog in the functional
architecture of mammalian neo-cortex. Whereas the BCS and FCS are
neurally interpreted in terms of data about areas V1, V2, and V4 of visual
cortex (Desimone, Schein, Moran, and Ungerleider 1985; Zeki 1983a,
1983b), the ORS is interpreted in terms of data concerning inferotemporal
cortex and related brain regions (Mishkin 1982; Mishkin and Appenzeller
1987; Schwartz, Desimone, Albright, and Gross 1983).

The complementarity that exists between BCS and FCS computations is
illustrated by example in the next two sections.

6. Discounting the Illuminant and Filling-In

One form of uncertainty with which the nervous system deals is due to
the fact that the visual world is viewed under variable lighting conditions.
When an object reflects light to an observer's eyes, the amount of light

energy within a given wavelength that reaches the eye from each object location is determined by a product of two factors. One factor is a fixed ratio, or reflectance, which determines the fraction of incident light that is reflected by that object location to the eye. The other factor is the variable intensity of the light which illuminates the object location. Two object locations with equal reflectances can reflect different amounts of light to the eye if they are illuminated by different light intensities. Spatial gradients of light across a scene are the rule, rather than the exception, during perception, and wavelengths of light that illuminate a scene can vary widely during a single day. If the nervous system directly coded into percepts the light energies which it received, it would compute false measures of object colors and brightnesses, as well as false measures of object shapes.

Land (1977) and his colleagues have sharpened contemporary understanding of this issue by carrying out a series of remarkable experiments. In these experiments, a picture constructed from overlapping patches of colored paper, called a McCann Mondrian, is viewed under different lighting conditions. If red, green, and blue lights simultaneously illuminate the picture, then an observer perceives surprisingly little color change as the intensities of illumination are chosen to vary within wide limits. The stability of perceived colors obtains despite the fact that the intensity of light at each wavelength that is reflected to the eye varies linearly with the incident illumination intensity at that wavelength. This property of color stability indicates that the nervous system 'discounts the illuminant', or suppresses the 'extra' amount of light in each wavelength, in order to extract a color percept that is invariant under many lighting conditions.

In another experiment, inhomogeneous lighting conditions were devised such that spectrophotometric readings from positions within the interiors of two color patches were the same, yet the two patches appeared to have different colors. The perceived colors were, moreover, close to the colors that would be perceived when viewed in a homogeneous source of white light.

These results show that the signals from within the interiors of the colored patches are significantly attenuated in order to discount the illuminant. This property makes ecological sense, since even a gradual change in illumination level could cause a large cumulative distortion in perceived color or brightness if it were allowed to influence the percept of a large scenic region. In contrast, illuminant intensities typically do not vary much across a scenic edge. Thus the ratio of light signals reflected from the two sides of a scenic edge can provide an accurate local estimate of the relative reflectances of the scene at the corresponding positions. We have called the color and brightness signals which remain unattenuated near scenic edges FC signals.

The neural mechanisms which 'discount the illuminant' overcome a

scenic edges, then why do not we see just a world of colored edges? How are these local FC signals used by later processing stages to synthesize global percepts of continuous color fields and of smoothly varying surfaces?

FC signals activate a process of lateral spreading, or filling-in, of color and brightness signals within the FCS. This filling-in process is contained by topographically organized output signals from the BCS to the FCS (Figure 2).Where no BC signals obstruct the filling-in process, its strength is attenuated with distance, since it is governed by a nonlinear diffusion process.

Many examples of featural filling-in and its containment by BC signals can be cited. A classical example of this phenomenon is described in Figure 4. The image in Figure 4 was used by Yarbus (1967) in a stabilized image experiment. Normally the eye jitters rapidly in its orbit, and thereby is in continual relative motion with respect to a scene. In a stabilized image experiment, prescribed regions in an image are kept stabilized, or do not move with respect to the retina. Stabilization is accomplished by the use of a contact lens or an electronic feedback circuit. Stabilizing an image with respect to the retina can cause the perception of the image to fade. The adaptive utility of this property can be partially understood by noting that, in humans, light passes through retinal veins before it reaches the photosensitive retina. The veins form stabilized images with respect to the retina, hence are fortunately not visible under ordinary viewing conditions.

In the Yarbus display shown in Figure 4, the large circular edge and the vertical edge are stabilized with respect to the retina. As these edge percepts fade, the red color outside the large circle is perceived to flow over and envelop the black and white hemi-discs until it reaches the small red circles whose edges are not stabilized. This percept illustrates how FC signals can spread across, or fill-in, a scenic percept until they hit perceptually significant boundaries. Our neural network model of this process explains how filling-in occurs within the black and white regions, and why the left red disk appears lighter and the right red disk appears darker than the surrounding red region that envelops the remainder of the percept. The model has in addition been used to simulate a wide range of classical and recent phenomena concerning brightness perception which have not heretofore been explained by a single theory (Cohen and Grossberg 1984; Grossberg and Todorović 1988).

The Yarbus percept illustrates three properties of the FCS that are complementary to properties of the BCS (Figure 5); namely, filling-in is an *outward* flowing process that is *unoriented*, and FCS computations are *sensitive to direction-of-contrast*, or contrast polarity, since otherwise the FCS could not represent different brightnesses or colors.

In summary, the uncertainty of variable lighting conditions is resolved by discounting the illuminant and extracting contour-sensitive FC signals. The uncertainty created within the discounted regions is resolved at a later processing stage via a featural filling-in process that is activated by the FC signals and contained within boundaries defined by BC signals.
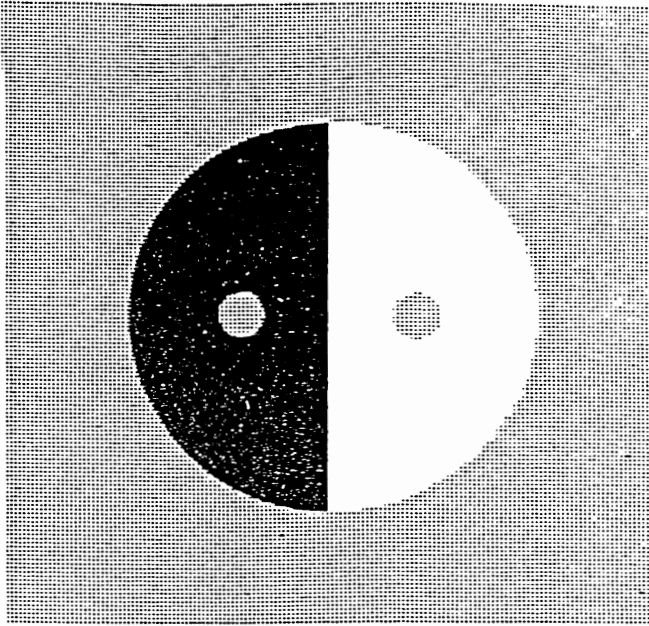
Figure 4 A classical example of featural filling-in: When the edges of the large circle and the vertical line are stabilized on the retina, the red color (dots) outside the large circle envelopes the black and white hemidisks except within the small red circles whose edges are not stabilized. The red inside the left circle looks brighter and the red inside the right circle looks darker than the enveloping red.

7. Oriented Boundary Filtering and Emergent Segmentation: BCS/FCS Complementarity

The corresponding complementary properties of the BCS may be seen by inspecting a reverse-contrast Kanizsa square in Figure 6. The photographic reproduction process may have weakened the percept of this 'illusory' square. The critical percept is that of the square's vertical boundaries. The black-grey vertical edge of the top-left pac-man figure is a dark-light vertical edge. The white-grey vertical edge of the bottom-left pac-man figure is a light-dark vertical edge. These two vertical edges possess the same orientation but opposite directions-of-contrast. The percept of the vertical boundary that spans these opposite direction-of-contrast edges shows that the BCS is sensitive to boundary orientation but is indifferent to direction-of-contrast. Moreover, the horizontal boundaries of the square, which connect edges of like direction-of-contrast, group together with the
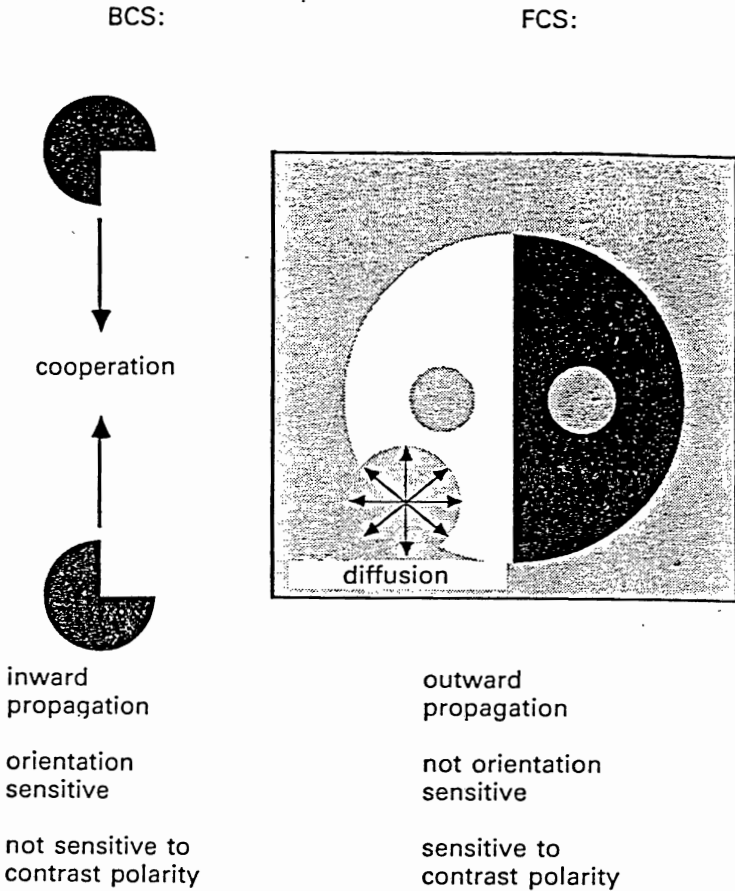
BCS: FCS:

cooperation

inward   outward
propagation   propagation

orientation   not orientation
sensitive   sensitive

not sensitive to   sensitive to
contrast polarity   contrast polarity

Figure 5 Computationally complementary properties of the BCS and FCS:
The outcome of a BCS interaction is independent of direction-of-contrast,
oriented and induced by pairs, or larger numbers, of oriented inducers.
The outcome of an FCS interaction is dependent upon direction-of-contrast,
unoriented, and generated by individual inducers.

vertical boundaries to generate a unitary percept of a square. Opposite
direction-of-contrast and same direction-of-contrast boundaries both input
to the same BCS in order to achieve broad-band boundary detection. In
contrast, the FCS maintains its sensitivity to direction-of-contrast and
elaborates it into a double-opponent color and brightness perception
system.

Figure 6 A reverse-contrast Kanizsa square: An illusory square is induced by two black and two white pac-man figures on a grey background. Illusory contours can thus join edges with opposite directions-of-contrast. (This effect may be weakened by the photographic reproduction process.)

The BCS and the FCS differ in their spatial interaction rules in addition to their rules of contrast. Indeed, their spatial interaction rules exhibit complementary properties. For example, in Figure 6, a vertical illusory boundary forms between the Boundary Contours generated by a pair of vertically-oriented and spatially aligned pac-man edges. Thus the process of boundary completion is due to an *inwardly* directed and *oriented* interaction whereby *pairs* of inducing BC signals can trigger the formation of an intervening boundary of similar orientation. In contrast, in the filling-in reactions of Figure 4, featural quality can flow from each FC signal in all directions until it hits a Boundary Contour or is attenuated by its own spatial spread. Thus featural filling-in is an *outwardly* directed and *unoriented* interaction that is triggered by *individual* FC signals. These complementary properties of the BCS and FCS interaction rules are summarized in Figure 5.

8. Cognitive Impenetrability of Neural Computations

An analysis of how the BCS implements the types of properties summarized in Figure 5 illustrates the cognitive impenetrability of neural computations.

In other words, we are designed so that our neural mechanisms and the organizational principles that govern their design are hidden from the direct introspective evidence of daily experience. The behavioral level can thus concern itself with percepts, feelings, ideas, and plans rather than with neurons, ions, and chemical transmitters.

In particular, early stages of BCS design include a circuit that contains formal analogs of cortical simple cells, complex cells, and hypercomplex cells, but the computational constraints that are predicted to govern this circuit's neural design are not obvious on the behavioral level. This fact may be highlighted by a personal anecdote. I did not notice the, now obvious, neurophysiological interpretation of the model hypercomplex cells until at least two years after the circuit was derived from perceptual considerations.

One of the hardest things to understand about neural modelling is how a modeller can discover a behavioral analysis from which neural mechanisms can be derived, despite the fact that these neural mechanisms are not obvious from our daily experiences, and the behavioral significance of the neural mechanisms may not at first be clear from direct neural measurements. In the present instance, at least two stumbling blocks to understanding can be identified: (1) The activities of BCS cells do not themselves become perceptually visible; they control properties of visibility that develop within the FCS. (2) The output stage (the hypercomplex cells) of the circuit in question is designed to overcome a computational uncertainty that is created at the input stage (the simple cells). Thus the circuit hides its perceptual function, except during perceptual anomalies, such as visual illusions.

In particular, the model simple cells, complex cells, and hypercomplex cells are predicted to be part of a circuit module that overcomes, through its hierarchical intercellular interactions, a computational uncertainty in processing image line ends and corners that is due to simple cells' oriented receptive fields. This compensatory process also generates properties of hyperacuity, that have since been psychophysically reported (Badcock and Westheimer 1985a, 1985b). Thus the perceptual analysis of the computational limitations of oriented receptive fields predicts why simple cells, complex cells, and hypercomplex cells exist and, as an additional surprise, suggests a new understanding of hyperacuity. Some of these considerations will next be discussed.

9. Oriented Receptive Fields Imply Positional Uncertainty at Line Ends and Corners

In order to effectively build up boundaries, the BCS must be able to determine the orienfation of a boundary at every position. To accomplish this, the cells at the first stage of the BCS possess orientationally tuned receptive fields, or oriented masks. Such a cell, or cell population, is

selectively responsive to orientations that activate a prescribed small region of the retina, and whose orientations lie within a prescribed band of orientations with respect to the retina. A collection of such orientationally tuned cells is assumed to exist at every network position, such that each cell type is sensitive to a different band of oriented contrasts within its prescribed small region of the scene, as in the hypercolumn model, which was developed to explain the responses of simple cells in area V1 of the striate cortex (Hubel and Wiesel 1977).

These oriented receptive fields are oriented *local contrast* detectors, rather than edge detectors. This property enables them to fire in response to a wide variety of spatially nonuniform image contrasts including edges, spatially nonuniform densities of unoriented textural elements, and spatially nonuniform densities of surface gradients. Thus by sacrificing a certain amount of spatial resolution in order to detect oriented local contrasts, these masks achieve a general detection characteristic which can respond to edges, textures, and surfaces.

The fact that the receptive fields of the BCS are *oriented* greatly reduces the number of possible groupings into which their target cells can enter. On the other hand, in order to detect oriented local contrasts, the receptive fields must be elongated along their preferred axis of symmetry. Then the cells can preferentially detect differences of average contrast across this axis of symmetry, yet can remain silent in response to differences of average contrast that are perpendicular to the axis of symmetry. Such receptive field elongation creates greater positional uncertainty about the exact locations within the receptive field of the image contrasts which fire the cell. This positional uncertainty becomes acute during the processing of image line ends and corners.

Oriented receptive fields cannot easily detect the ends of thin scenic lines (Grossberg and Mingolla 1985b) whose widths fall within a certain range: wider than lines which generate a continuous band of vertically oriented receptive field responses, and narrower than lines which generate a band of horizontally oriented receptive field responses throughout their lowest extremity. Such a choice of lines always exists if the receptive field is elongated by a sufficient amount in a preferred orientation. This property illustrates a basic uncertainty principle which says: Orientational 'certainty' implies positional 'uncertainty' at the ends of scenic lines whose widths are neither too small nor too large with respect to the dimensions of the oriented receptive field. If no BC signals are elicited at the ends of lines, however, then in the absence of further processing within the BCS, Boundary Contours will not be synthesized to prevent featural quality from flowing out of line ends within the FCS. Many percepts would hereby become badly degraded by featural flow.

Thus basic constraints upon visual processing seem to be at odds with each other. The need to discount the illuminant leads to the need for featural filling-in. The need for featural filling-in leads to the need to synthesize boundaries capable of restricting featural filling-in to

appropriate perceptual domains. The need to synthesize boundaries leads to the need for orientation-sensitive receptive fields. Such receptive fields are, however, unable to restrict featural filling-in at scenic line ends or sharp corners. Thus, orientational certainty implies a type of positional uncertainty, which is unacceptable from the perspective of featural filling-in requirements.

Later processing stages are needed to recover both the positional and orientational information that are lost in this way. We have called the process which completes the boundary at a line end an *end cut*. End cuts actively reconstruct the line end at a processing stage higher than the oriented receptive field much as they do to form an Ehrenstein figure (Figure 7). In order to emphasize the paradoxical nature of this process, we say that *all line ends are illusory*.
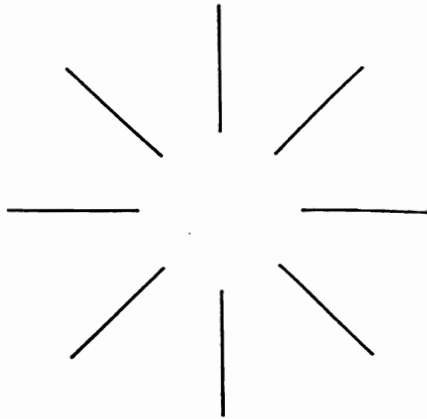

Figure 7 An Ehrenstein figure: A bright circular disk is perceived even though all white areas are equally luminant. The text suggests how this happens.

10. The OC Filter: Simple, Complex, and Hypercomplex Cells

The processing stages that are hypothesized to generate end cuts are summarized in Figure 8. First, oriented simple cell receptive fields of like position and orientation, but opposite direction-of-contrast, generate rectified output signals. These output signals summate at the next processing stage to activate complex cells whose receptive fields are sensitive to the same position and orientation as themselves, but are insensitive to direction-of-contrast. These complex cells are sensitive to *amount* of oriented contrast, but not to the *direction* of this oriented

contrast, as in our explanation of Figure 6. They pool inputs from receptive fields with opposite directions-of-contrast in order to generate boundary detectors which can detect the broadest possible range of luminance or chromatic contrasts (De Valois, Albrecht, and Thorell 1982; Spitzer and Hochstein 1985).

The rectified output from the complex cells activates a second filter which is composed of two successive stages of spatially short-range competitive interaction whose net effect is to generate end cuts (Figure 8). First, a cell of prescribed orientation excites like-oriented cells corresponding to its location and inhibits like-oriented cells corresponding to nearby locations at the next processing stage. In other words, an on-center off-surround organization of like-oriented cell interactions exists around each perceptual location. This mechanism is analogous to the neurophysiological process of *end stopping*, whereby hypercomplex cell receptive fields are fashioned from interactions of complex cell output signals (Hubel and Wiesel 1965; Orban, Kato, and Bishop 1979). The outputs from this competitive mechanism interact with the second competitive mechanism. Here, cells compete that represent different orientations, notably perpendicular orientations, at the same perceptual location. This competition defines a push-pull opponent process. If a given orientation is excited, then its perpendicular orientation is inhibited. If a given orientation is inhibited, then its perpendicular orientation is excited via disinhibition.

The combined effect of these two competitive interactions generates end cuts as follows. The strong vertical activations along the edges of a scenic line inhibit the weak vertical activations near the line end. These inhibited vertical activations, in turn, disinhibit horizontal activations near the line end. Thus the positional uncertainty generated by orientational certainty is eliminated at a subsequent processing level by the interaction of two spatially short-range competitive mechanisms which convert complex cells into two distinct populations of hypercomplex cells.

The properties of these competitive mechanisms have successfully predicted and helped to explain a variety of neural and perceptual data. For example, the prediction of the theory summarized in Figure 8 anticipated the report by von der Heydt, Baumgartner, and Peterhans (1984) that cells in prestriate visual cortex respond to perpendicular line ends, whereas cells in striate visual cortex do not. These cells properties also help to explain why color is sometimes perceived to spread across a scene, as in the phenomenon of neon color spreading (Grossberg 1987a; Grossberg and Mingolla 1985a; Redies and Spillmann 1981) by showing how some BC signals are inhibited by Boundary Contour processes. The end cut process also exhibits properties of hyperacuity which have been used (Grossberg 1987a) to explain psychophysical data about spatial localization and hyperacuity (Badcock and Westheimer 1985a, 1985b; Watt and Campbell 1985). A version of the double filter in Figure 8 was also derived from data about texture segregation (Graham and Beck 1988) in a
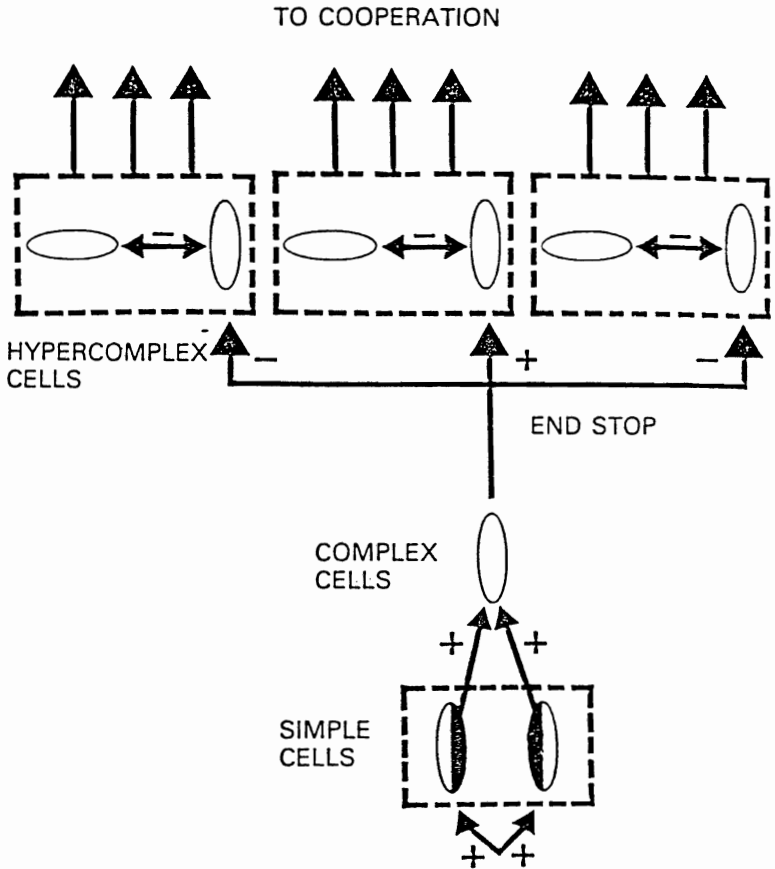
Figure 8 *Early stages of Boundary Contour processing: At each position exist cells with elongated receptive fields (simple cells) of various sizes which are sensitive to orientation, amount-of-contrast, and direction-of-contrast. Pairs of such cells sensitive to like orientation but opposite directions-of-contrast (lower dashed box) input to cells (complex cells) that are sensitive to orientation and amount-of-contrast but not to direction-of-contrast (white ellipses). These cells, in turn, excite like-oriented cells (hypercomplex cells) corresponding to the same position and inhibit like-oriented cells corresponding to nearby positions at the first competitive stage. At the second competitive stage, cells corresponding to the same position but different orientations (higher-order hypercomplex cells) inhibit each other via a push-pull competitive interaction.*

way that supports the texture analyses of Grossberg and Mingolla (1985b). These analyses also utilize the cooperative-competitive feedback interactions, indicated in Figure 9, to generate emergent boundary segmentations, such as the circular groupings generated in response to the Glass pattern in Figure 3 and the Kanizsa square generated in response to the four pac-man figures in Figure 6. These feedback interactions between bipole cells and hypercomplex cells have properties akin to those discovered experimentally in visual cortex by von der Heydt, Peterhans, and Baumgartner (1984) and Peterhans and von der Heydt (1989) during the formation of illusory contours, and by Eckhorn *et al.* (1988) and Gray, König, Engel, and Singer (1989) during long-range cooperative linking operations among assemblies of similarly coded visual features. The process of emergent boundary segmentation will not be further discussed herein. Instead, I will indicate how further analysis of this hierarchical network leads to explanations of data about motion perception.

11. Why is a Motion Boundary Contour System Needed?

It is well known that some regions of visual cortex are specialized for motion processing, notably region MT (Albright, Desimone, and Gross 1984; Maunsell and van Essen 1983; Newsome, Gizzi, and Movshon 1983; Zeki 1974a, 1974b). On the other hand, even the earliest stages of visual cortex processing, such as the simple cells in $V1$ (Figure 8), require stimuli that change through time for their maximal activation and are direction-sensitive (De Valois, Albrecht, and Thorell 1982;. Heggelund 1981; Hubel and Wiesel 1962, 1968, 1977; Tanaka, Lee, and Creutzfeldt 1983). Why has evolution gone to the trouble to generate regions such as MT, when even $V1$ is change-sensitive and direction-sensitive? What computational properties are achieved by MT that are not already available in $V1$?

As indicated above, the monocular BCS theory of Grossberg and Mingolla (1985a, 1985b), schematized in Figure 9, and its binocular generalization (Grossberg 1987b; Grossberg and Marshall 1989), has successfully modelled many boundary segmentation properties of $V1$ and its prestriate projections. This BCS model has thusfar been used to analyse data generated in response to static visual images. Henceforth we therefore call such a BCS a static BCS model. The cells of the static BCS model can easily be gated by cells sensitive to image transients, such as Y cells (Enroth-Cugell and Robson 1966; Hoffmann 1973; Sekuler 1975; Stone 1972; Stone and Dreher 1973; Tolhurst 1973), to generate receptive fields sensitive to image transients. How does a motion BCS differ from a static BCS whose cells are sensitive to image transients? The answer to this question that is suggested by Grossberg and Rudd (1989) illustrates once again the importance of BCS/FCS complementary in understanding preattentive vision, and the inadequacy of a modelling approach based on independent processing modules.
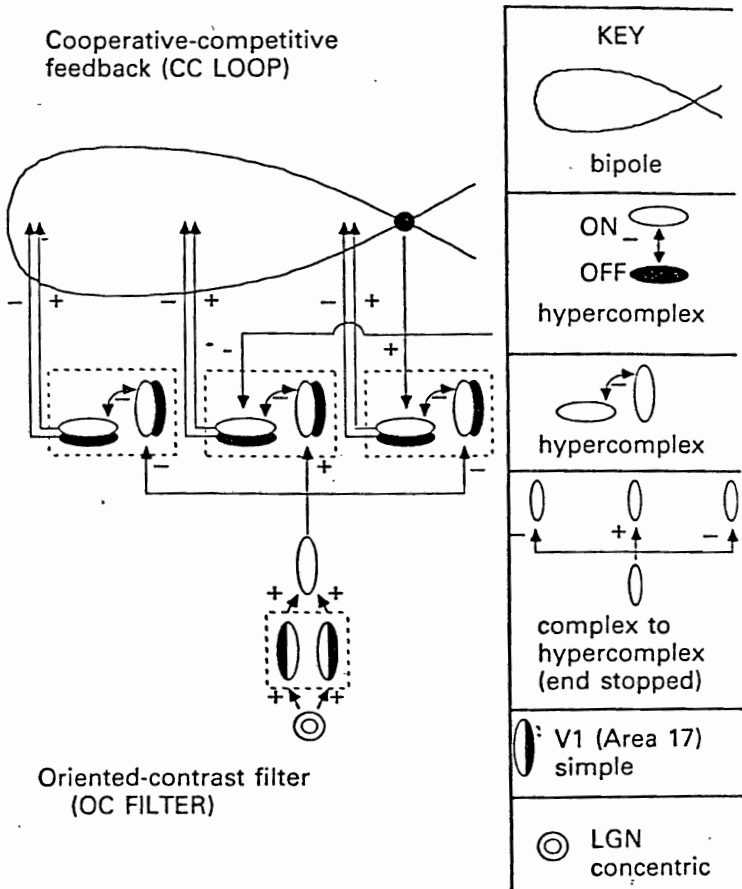
Figure 9 The static Boundary Contour circuit described by Grossberg and Mingolla (1985b). The circuit is divided into an oriented contrast-sensitive filter (OC Filter) followed by a cooperative-competitive feedback network (CC Loop). Multiple copies of this circuit are used, one corresponding to each receptive field size of the OC Filter. The depicted circuit has been used to analyse data about monocular vision. A binocular generalization of the circuit has also been described (Grossberg 1987b; Grossberg and Marshall 1989).

12. *Joining Sensitivity to Direction-of-Motion with Insensitivity to Direction-of-Contrast*

As shown in Figure 8, although the simple cells of the BCS are sensitive to direction-of-contrast, or contrast polarity, the complex cells of the BCS are rendered insensitive to direction-of-contrast by receiving inputs from pairs of simple cells with opposite direction-of-contrast. Such a property is also true of the simple cells and complex cells in area V1 (De Valois, Albrecht, and Thorell 1982; Poggio, Motter, Squatrito, and Trotter 1985; Thorell, De Valois, and Albrecht 1984).

This property is useful for extracting boundaries along contrast reversals in the image. As a result, however, the output of the OC Filter is unable to differentiate direction-of-motion. For example, the complex cell in Figure 8 can respond to a vertical light-dark contrast moving to the right, and to a vertical dark-light contrast moving to the left. Because the complex cell can respond to image contrasts that move in opposite directions, it is insensitive to direction-of-motion. A key property of the motion BCS model of Grossberg and Rudd (1989) is that it possesses a modified OC Filter that multiplexes the property of insensitivity to direction-of-contrast, which is equally useful for the processing of static and moving forms, with sensitivity to direction-of-motion. The properties of this Motion OC Filter, or MOC Filter, mirror many properties of motion perception, including percepts of apparent motion. When the MOC Filter is connected to a CC Loop, as in Figure 9, a much larger body of data, including coherent global motion percepts such as induced motion and motion capture, can also be analysed.

This model suggests that a fundamental computational property achieved by a motion segmentation system, such as MT, is to generate output signals that maintain insensitivity to direction-of-contrast without sacrificing sensitivity to direction-of-motion. The fact that such a modest change of the static OC Filter enables us to define a motion BCS that is useful to analyse a large body of data concerning motion segmentation provides additional support for both the static BCS model and the motion BCS model by showing that both models may be considered variations on a single neural architectural theme.

The property of insensitivity to direction-of-contrast in the static BCS reflects one of the fundamental new insights of the FACADE theory of preattentive vision. Insensitivity to direction-of-contrast is possible within the BCS because all boundary segmentations within the BCS are perceptually invisible. Visibility is a property of the complementary FCS, whose computations are sensitive to direction-of-contrast. Thus a vision theory built up from independent processing modules could not articulate the heuristics of the motion BCS because it could not understand BCS/FCS complementarity.

Once the MOC filter was defined, its properties clarified a new set of issues that also argue against the existence of independent modules. One

issue concerns why parallel systems exist for the processing of static visual forms and moving visual forms. Why is not a motion system sufficient, given that objects typically move with respect to an observer's eye movements in a natural environment? We link the existence of these parallel systems to a symmetry principle that is predicted to govern the development of visual cortex (Section 15), with the static and motion systems as two interdependent parts of its overall design. A second issue concerns how orientational tuning in the static form system is replaced by directional tuning in the motion form system (Section 17), with the same direction-of-motion being computed from more than one orientation of a moving figure. As we will see in the next section, both short-range and long-range spatial interactions are needed to define a MOC Filter whose output signals are insensitive to direction-of-contrast but sensitive to direction-of-motion. The extra degree of freedom provided by the long-range interaction permits merging of many static orientations in the service of a single direction-of-motion.

13. Design of a MOC Filter

A MOC Filter is mathematically defined in Grossberg and Rudd (1989). Its five processing stages are qualitatively summarized in Figure 10 and described below.

Level 1: Preprocess Input Pattern

The image is preprocessed before activating the filter. For example, it is passed through a shunting on-center off-surround net to compensate for variable illumination, or to 'discount the illuminant' (Grossberg and Todorović 1988).

Level 2: Sustained Cell Short-Range Filter

Four operations occur here:

(1) **Space-Average**: Inputs are processed by individual oriented receptive fields, or simple cells.
(2) **Rectify**: The output signal from a simple cell grows with its activity above a signal threshold.
(3) **Short-Range Spatial Filter**: A spatially aligned array of simple cells with like direction-of-contrast pool their output signals to activate the next cell level. This spatial pooling plays the role of the short-range motion limit D_{max} (Braddick 1974). The breadth of spatial pooling scales with the size of the simple cell receptive fields. Thus 'D_{max}' is not independent of the spatial frequency content of the image (Anderson and Burr 1987; Burr, Ross, and
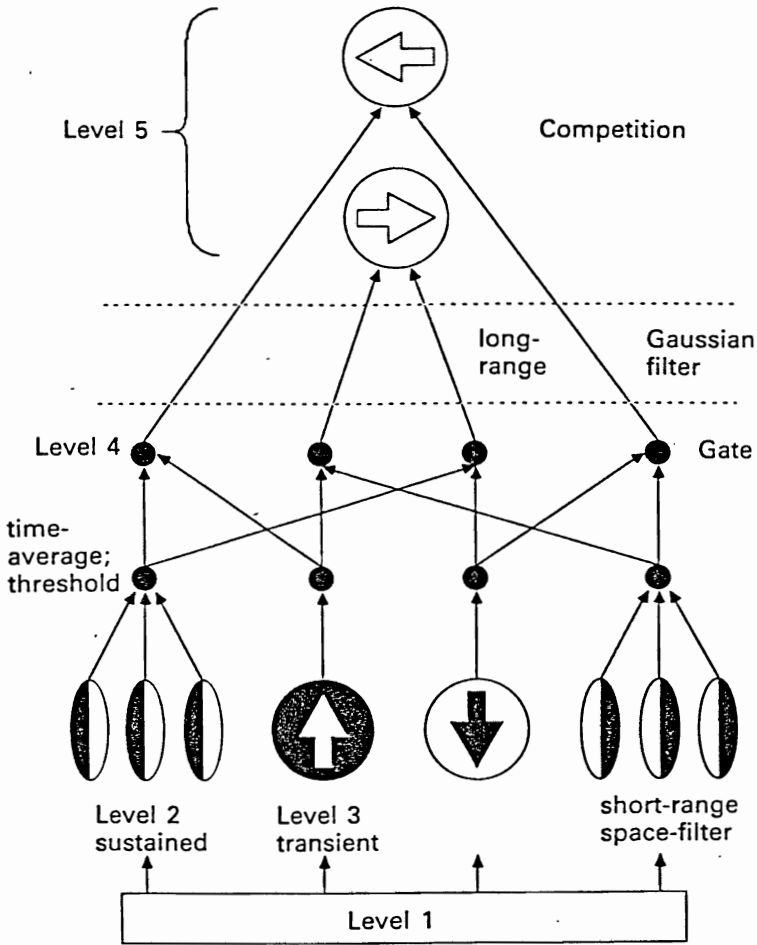
Figure 10 The motion OC Filter: Level 1 registers the input pattern. Level 2 consists of sustained response cells with oriented receptive fields that are sensitive to direction-of-contrast. Level 3 consists of transient response cells with unoriented receptive fields that are sensitive to direction-of-change in the total cell input. Level 4 cells combine sustained cell and transient cell signals to become sensitive to direction-of-motion and sensitive to direction-of-contrast. Level 5 cells combine Level 4 cells to become sensitive to direction-of-motion and insensitive to direction-of-contrast.

Morrone 1986; Nakayama and Silverman 1984, 1985), and is not a universal constant.

The direction of spatial pooling may not be perpendicular to the oriented axis of the simple cell receptive field (Grossberg and Mingolla 1990). The target cells are thus sensitive to a movement *direction* that may not be perpendicular to the simple cell's preferred orientation.

(4)   **Time-Average:** The target cell time-averages the directionally-sensitive inputs that it receives from the short-range spatial filter. This operation has properties akin to the 'visual inertia' during apparent motion that was reported by Anstis and Ramachandran (1987).

Level 3: Transient Cell Filter

In parallel with the sustained cell filter, a transient cell filter reacts to input increments (on-cells) and decrements (off-cells) with positive outputs. This filter uses four operations too:

(1)   **Space-Average:** This is accomplished by a receptive field that sums inputs over its entire range.

(2)   **Time-Average:** This sum is time-averaged to generate a gradual growth and decay of total activation.

(3)   **Transient Detector:** The on-cells are activated when the time-average increases. The off-cells are activated when the time-average decreases. This may be accomplished using a combination of feedforward inhibitory interneurons (Grossberg 1970) and a gated dipole opponent organization of on-cells and off-cells (Grossberg 1976).

Level 4: Sustained-Transient Gating Yields Direction-of-Motion Sensitivity and Direction-of-Contrast Sensitivity

Maximal activation of a Level 2 sustained cell filter is caused by image contrasts moving in either of two directions that differ by 180°. Multiplicative gating of each Level 2 sustained cell output with a Level 3 transient cell on-cell or off-cell removes this ambiguity. For example, consider a sustained cell output from vertically oriented light-dark simple cell receptive fields that are joined together in the horizontal direction by the short-range spatial filter. Such a sustained cell output is maximized by a light-dark image contrast moving to the right or to the left. Multiplying this Level 2 output with a Level 3 transient on-cell output generates a Level 4 cell that responds maximally to motion to the right. Multiplying it with a Level 3 off-cell output generates a Level 4 cell that responds

maximally to motion to the left. Multiplying a sustained cell with a transient cell is the main operation of the Marr and Ullman (1981) motion detector. Despite this point of similarity, Grossberg and Rudd (1989) described six basic differences between the MOC Filter and the Marr-Ullman model. For example, none of the operations such as short-range spatial filtering, time-averaging and rectification occurs in the Marr-Ullman model. In addition, the rationale of the MOC Filter—to design a filter that is sensitive to direction-of-motion and insensitive to direction-of-contrast—is not part of the Marr-Ullman model. This difference is fundamental. The Marr-Ullman model is a product of the 'independent modules' perspective. The MOC Filter's insensitivity to direction-of-contrast can only be formulated within the framework of BCS/FCS complementarity: One cannot understand why a boundary filter's output needs to be insensitive to direction-of-contrast unless there exists a complementary 'seeing' system that is sensitive to direction-of-contrast.

The cell outputs from Level 4 are sensitive to direction-of-contrast. Level 5 consists of cells that pool outputs from Level 4 cells which are sensitive to the same direction-of-motion but to opposite directions-of-contrast.

Level 5: Long-Range Spatial Filter and Competition

Outputs from Level 4 cells sensitive to the same direction-of-motion but opposite directions-of-contrast activate individual Level 5 cells via a long-range spatial filter that is Gaussianly distributed across space. In particular, this long-range filter groups together Level 4 cell outputs from Level 3 short-range filters with the same directional preference but different simple cell orientations. Thus the long-range filter provides the extra degree of freedom that enables Level 5 cells to function as 'direction' cells, rather than 'orientation' cells.

The long-range spatial filter broadcasts each Level 4 signal over a wide spatial range in Level 5. Competitive, or lateral inhibitory, interactions within Level 5 contrast-enhance this input pattern to generate spatially sharp Level 5 responses. A winner-take-all competitive network (Grossberg 1973, 1982) can transform even a very broad input pattern into a focal activation at the position that receives the maximal input. A contrast-enhancing competitive interaction has also been modelled at the complex cell level of the SOC Filter (Grossberg 1987b; Grossberg and Marshall 1989). The Level 5 cells of the MOC Filter are, in other respects too, computationally homologous to the SOC Filter complex cells. The winner-take-all assumption is a limiting case of how competition can restore positional localization. More generally, we suggest that this competitive process partially contrast-enhances its input patttern to generate a motion signal whose breadth across space increases with the breadth of its inducing pattern.

## 14. Continuous Motion Paths from Spatially Stationary Flashes: An Emergent Property

MOC Filter properties suggest an answer to long-standing questions in the vision literature concerning why individual flashes do not produce a percept of long-range motion, yet long-range interaction between spatially discrete pairs of flashes can produce a spatially sharp percept of continuous motion. Such apparent motion phenomena are a particularly useful probe of motion mechanisms because they describe controllable experimental situations in which nothing moves, yet a compelling percept of motion is generated. They also provide a simple example of a perceptual *emergent property*; namely, a property that is generated by system interactions operating in real-time, and thus that cannot be explained as a consequence of independently computed quantities, or a list of algorithmic statements.

For example, two brief flashes of light, separated in both time and space, create an illusion of movement from the location of the first flash to that of the second when the spatiotemporal parameters of the display are within the correct range (Figure 11a). Variants of apparent motion include *phi motion*, or the *phi phenomenon*, whereby a 'figureless' or 'objectless' motion signal propagates from one flash to the other, analogous to the rapid motion of an object so quickly that its form cannot be clearly identified; *beta motion*, whereby a well-defined form seems to move smoothly and continuously from one flash to the other; and *gamma motion*, the apparent expansion at onset and contraction at offset of a single flash of light (Bartley 1941; Kolers 1972).

Outstanding theoretical issues concerning apparent motion include the resolution of a trade-off that exists between the long-range spatial interaction that is needed to generate the motion percept, and the localization of the perceived motion signal that smoothly interpolates the inducing flashes. If a long-range interaction between the flashes must exist in order to generate the motion percept, then why is it not perceived when only a single light is flashed? Why are not outward waves of motion-carrying signals induced by a single flash? What kind of long-range influence is generated by each flash, yet only triggers a perceived motion signal when at least two flashes are activated? What kind of long-range influence from individual flashes can generate a smooth motion signal between flashes placed at variable distances from one another? How does the motion signal speed up to smoothly interpolate flashes that occur at larger distances but the same time lag (Kolers 1972)? How does the motion signal speed up to smoothly interpolate flashes when they occur at the same distance but shorter time lags (Kolers 1972)?

A well-known apparent motion display, originally due to Ternus (1926/1950), illustrates the fact that not only the existence of a motion percept, but also its figural identity, may depend on subtle aspects of the display, such as the interstimulus interval, or *ISI*, between the offset of the first flash and the onset of the second flash (Figure 11b). In the Ternus
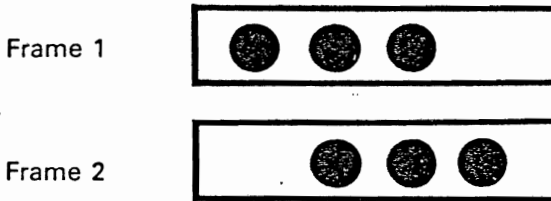
TWO FLASH DISPLAY
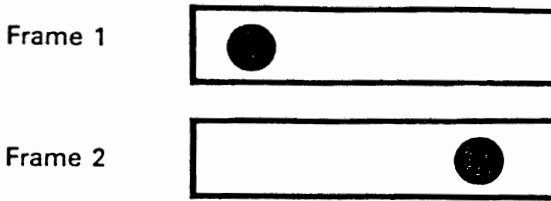
Small ISI: Stationarity
Intermediate ISI: Motion
Large ISI: Motion

(a)

TERNUS DISPLAY

Small ISI: Stationarity
Intermediate ISI: Element Motion
Large ISI: Group Motion

(b)

Figure 11 Two types of apparent motion displays in which the two frames outline the same region in space into which the dots are flashed at successive times: In (a) , a single dot is flashed, followed by an interstimulus interval (ISI), followed by a second_dot. At small ISIs, the two dots appear to flicker in place. At longer ISIs, motion from the position of the first dot to that of the second is perceived. (b) In the Ternus display, three dots are presented in each frame such that two of the dots in each frame occupy the same positions. At short ISIs, all the dots appear to be stationary. At longer ISIs the dots at the shared positions appear to be stationary, while apparent motion occurs from the left dot in Frame 1 to the right dot in Frame 2. At still longer ISIs, the three dots appear to move from Frame 1 to Frame 2 as a group.

display, a cyclic alternation of two stimulus frames gives rise to competing visual movement percepts. In Frame 1, three black elements are arranged in a horizontal row on a white background. (The contrast may be reversed without consequence to the discussion which follows.) In Frame 2, the elements are shifted to the right in such a way that the positions of the two leftwardmost elements in Frame 2 are identical to those of the two rightwardmost elements in Frame 1. Depending on the stimulus conditions, the observer will see either of two bistable motion percepts. Either the elements will appear to move to the right as a group between Frames 1 and 2 and then back again during the second half of a cycle of the display or, alternatively, the leftwardmost element in Frame 1 will appear to move to the location of the rightwardmost element in Frame 2, jumping across two intermediate elements which appear to remain stationary. We will refer to the first percept as 'group' motion; and the second percept as 'element' motion. At short *ISIs* there is a tendency to observe element motion. At longer *ISIs*, there is a tendency to observe group motion.

Formal analogs of these phenomena occur at Level 5 of the MOC Filter in response to sequences of flashes presented to Level 1. Intuitively, a signal for motion will arise when a spatially continuous flow of activation crosses the network through time. Each activation represents the peak, or maximal activity, of a broad spatial pattern of activation across the network. The broad activation pattern (Figure 12b) is generated by the long-range spatial filter in response to a spatially localized flash to Level 1 (Figure 12a). The sharply localized response function, denoted by $x_i^{(R)}$ in Figure 12c, is due to the contrast-enhancing action of the competitive network within Level 5. A stationary localized $x_i^{(R)}$ response will be generated in response to a single flashing input every time it occurs.

Apparent motion can emerge when two input flashes occur with the following spatial and temporal separations. Let the positions of the flashes be $i = 1$ and $i = N$. Let the activity $r_1(t)$ caused by the first flash start to decay as the activity $r_N(t)$ caused by the second flash starts to grow. Suppose, moreover, that the flashes are close enough that the spatial patterns $r_1 G_{1i}$ and $r_N G_{Ni}$ overlap that are caused by broadcasting r_1 through the long-range filter G_{1i} and r_N through G_{Ni} to all Level 5 positions i. Then the total input

$$R_i = r_1 G_{1i} + r_N G_{Ni}$$

to the ith cell in Level 5 can change in such a way that the maximum value of the spatial pattern $R_i(t)$ through time, namely $x_i^{(R)}(t)$, first occurs at $i = 1$, then $i = 2$, then $i = 3$, and so on until $i = N$. A percept of continuous motion from the position of the first flash to that of the second will result. In other words, two properly positioned and timed flashes can cause a travelling wave of activation across Level 5.

This basic property of the MOC Filter is illustrated by the computer simulations from Grossberg and Rudd (1989) that are schematized in Figures 13–15. Figure 13 depicts the temporal response to a single flash at

SPATIAL RESPONSE TO A
SINGLE FLASH

x_{IR}

SPACE   i

(a)

$R_i = \sum_j r_j G_{ji}$

SPACE   i

(b)

$x_i^{(R)}$
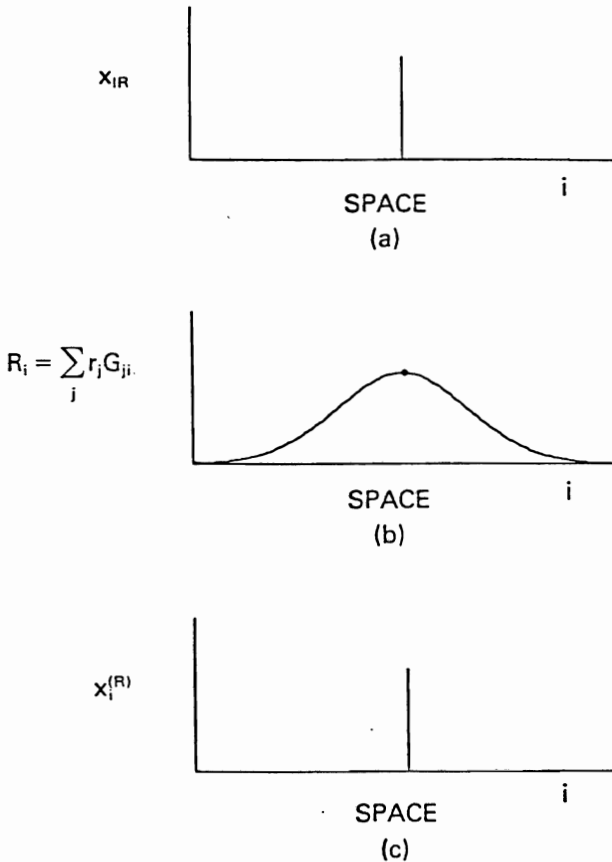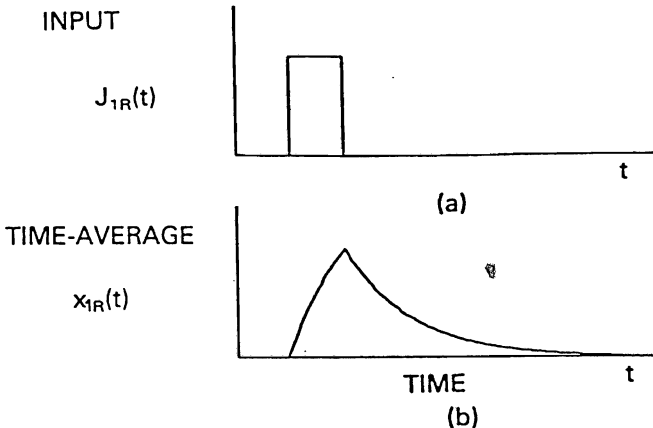
· SPACE   i

(c)

Figure 12 Spatial response of the Motion OC Filter to a point input.
(a) Sustained activity of a Level 2 cell. (b) Total input pattern to Level 5.
(c) Contrast-enhanced response at Level 5.

position 1 of Level 1. The sustained cell response at position 1 of Level 2
undergoes a gradual growth and decay of activation (Figure 13b), although
the position of maximal activation in the input to Level 5 does not change
through time (Figure 13c).

Figure 14 illustrates an important implication of the fact that the Level
2 cell activations persist after their Level 1 inputs shut off. If a flash at

TEMPORAL RESPONSE TO A
SINGLE FLASH

INPUT

$J_{1R}(t)$

(a)

TIME-AVERAGE

$x_{1R}(t)$

TIME   t

(b)

GROWTH OF ACTIVATION AS A
FUNCTION OF SPACE AND TIME

$$R_i = \sum_j r_j G_{ji}$$

t=4
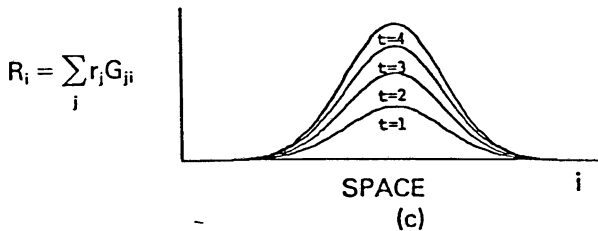t=3
t=2
t=1

SPACE   i

(c)

Figure 13 Temporal response of sustained response cells to a point input:
(a) The input is presented for a brief duration at location 1. (b) The activity
of the sustained response cell gradually builds up after input onset, then
decays after input offset. (c) Growth of the input pattern to Level 5
through time with transient cell activity held constant. The activity pattern
retains a Gaussian shape centered at the location of the input.

TEMPORAL RESPONSE TO
TW0 SUCCESSIVE FLASHES

INPUTS

$J_{1R}(t)$

$J_{NR}(t)$
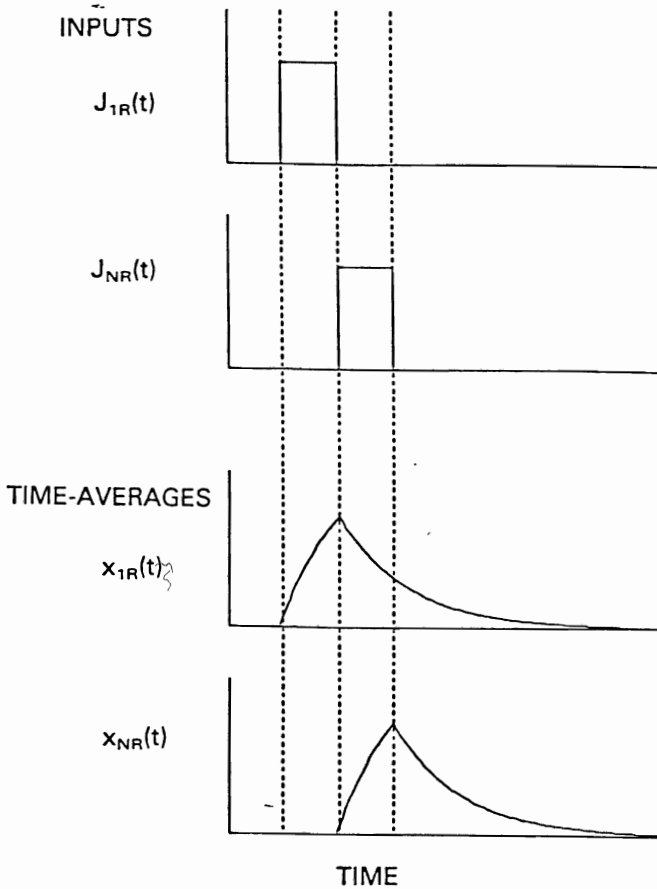
TIME-AVERAGES

$x_{1R}(t)$

$x_{NR}(t)$

TIME

Figure 14 Temporal response of the sustained response cells at Level 2 to two successive point inputs. One input is presented briefly at location 1, followed by a second input at location N. For an appropriately timed display, the decaying response at position 1 overlaps the rising response at position N.

position 1 is followed, after an appropriate delay, by a flash at position N, then the sustained response to the first flash [*e.g.* $x_{1R}(t)$] can decay while the response to the second flash [*e.g.* $x_{NR}(t)$] grows.

Assume for the moment that the transient signals computed at Level 3 are held constant and consider how the waxing and waning of sustained cell responses from Level 2 control the motion percept. Then the total input pattern R_i to Level 5 can change through time in the manner depicted in Figure 15. Each row of Figure 15a illustrates the total input to Level 5 caused, at a prescribed time t, by $x_{1R}(t)$ alone, by $x_{NR}(t)$ alone, and by both flashes together. Successive rows plot these functions at equally spaced later times. Note that as $x_{1R}(t)$ decays and $x_{NR}(t)$ grows, the maximum value of $R_i(t)$ moves continuously to the right. Figure 15b depicts the position $x_i^{(R)}(t)$ of the maximum value at the corresponding times.

In summary, the time-averaged and space-averaged responses to individual flashes do not change their position of maximal activation through time (Figure 13c). In this case, 'nothing moves'. On the other hand, properly phased multiple flashes can generate a temporally and spatially averaged total response whose maximum moves continuously between the positions of the flashes through time (Figure 15). In addition, by gating sustained cell responses by transient cell responses, the changeover occurs from element motion to group motion in response to the Ternus display as ISI is increased (Figure 11b). Grossberg and Rudd (1989) have analysed a wide variety of data about short-range and long-range motion using such properties of the MOC Filter.

15. Why are Both Static and Motion Boundary Contour Systems Needed?

As illustrated above, the motion BCS has begun to provide explanations of a large body of psychophysical and neurobiological data about the perception of moving form. Once the MOC Filter was defined, however, a new puzzle emerged. If Nature could design a MOC filter that is sensitive to direction-of-motion and insensitive to direction-of-contrast, then why did the SOC Filter evolve, in which insensitivity to direction-of-contrast comes only at the cost of a loss of sensitivity to direction-of-motion? This question is perplexing given the facts that animals' eyes are usually in relative motion with respect to their visual environment, and that simple cells in V1 are already sensitive to direction-of-motion.

I suggest an answer to this puzzle in which the static form and motion form systems are part of a larger design. In particular, the computation of static and motion properties are not realized by independent modules. This answer is suggested by reanalysing the SOC Filter in terms of how transient cells interact with the sustained cells depicted in Figures 8 and 9.

LONG-RANGE INTERACTION

$$R_i = \sum_j r_j G_{ji}$$

SHARP MOTION SIGNAL

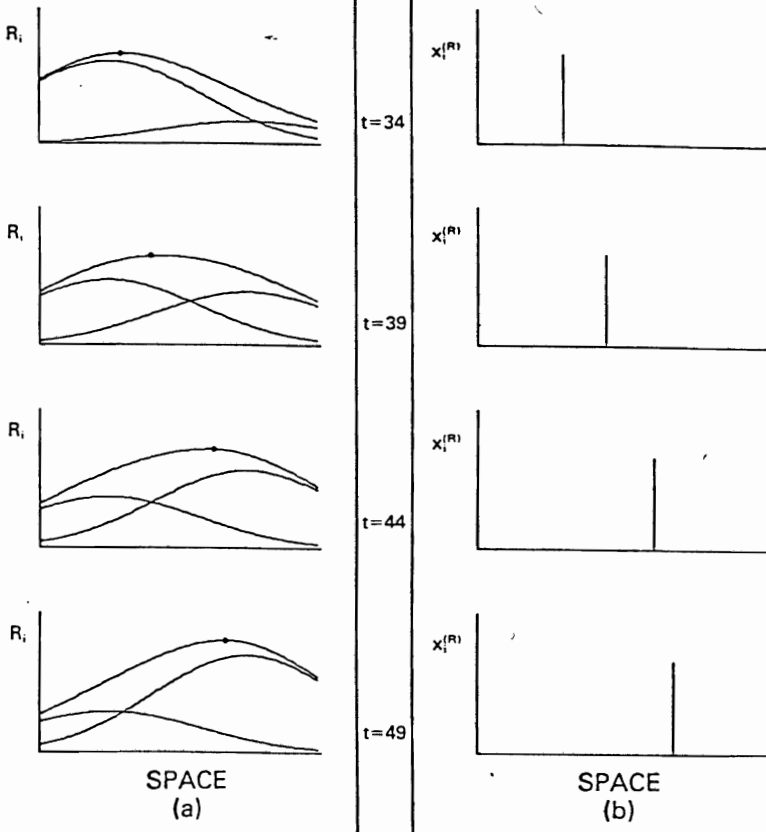$$x_i^{(R)} = \begin{cases} 1 & \text{if } R_i > R_j, j \neq i \\ 0 & \text{otherwise} \end{cases}$$

R_i $x_i^{(R)}$ t=34

R_i $x_i^{(R)}$ t=39

R_i $x_i^{(R)}$ t=44

R_i $x_i^{(R)}$ t=49

SPACE (a)   SPACE (b)

Figure 15 Motion OC Filter simulation in response to a two flash display. Successive rows correspond to increasing times: (a) The two lower curves in each row depict the total input to Level 5 caused by each of the two flashes. The input due to the left flash decreases while the input due to the right flash increases. The total input due to both flashes is a travelling wave whose maximum value moves from the location of the first flash to that of the second flash. (b) Position of the contrast-enhanced response at Level 5.
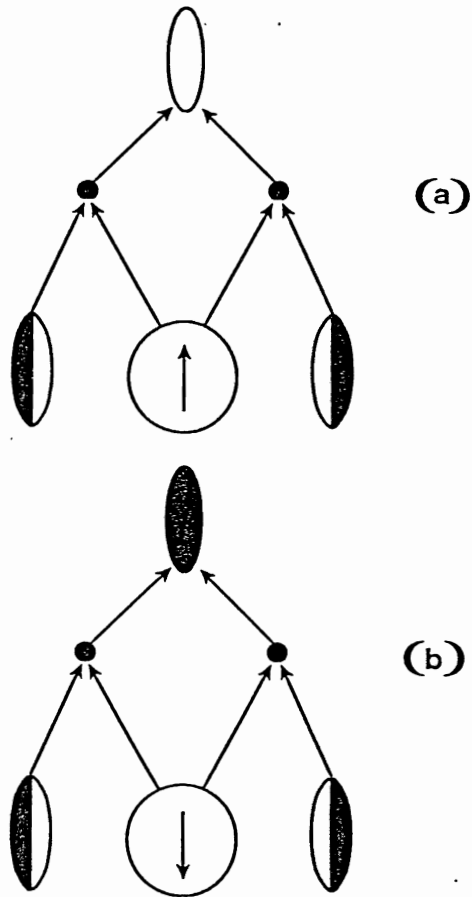
Figure 16 (a) A complex/orientation/on cell: Pairs of rectified sustained cells with opposite direction-of-contrast are gated by rectified transient on-cells before the gated responses are added. (b) A complex/orientation/off cell: Pairs of rectified sustained cells with opposite direction-of-contrast are gated by rectified transient off-cells before the gated responses are added.

16. The Symmetric Unfolding of Opponent Processes

Inspection of the CC Loop in Figure 9 provides an important clue. There, the hypercomplex cells are organized into opponent on-cells and off-cells,

. yet the SOC Filter explicitly depicts only pathways to the hypercomplex on-cells from the simple on-cells via complex on-cells. Moreover, all of these cells are of sustained cell type. Interactions with transient cells are not described. When interactions with transient cells are added, a role for parallel SOC Filter and MOC Filter designs is suggested.

Let simple on-cells be defined by gating each pair of like-oriented sustained cells in Figure 8 with a transient on-cell. Such a gated pair of on-cells is depicted in Figure 16a, where it gives rise to a complex on-cell. Likewise, a pair of simple off-cells can be defined by gating the pair of like-oriented sustained cells in Figure 3 with a transient off-cell. Such a gated pair of simple off-cells is depicted in Figure 16b, where it gives rise to a complex off-cell.

Let the complex on-cell in Figure 16a input to hypercomplex on-cells as in Figure 9. In a similar fashion, let the complex off-cell in Figure 16b input to hypercomplex off-cells in Figure 9. The process of gating sustained cells by transient cells in the static BCS thus makes the overall design of this architecture more symmetric by showing how simple and complex on-cells and off-cells fit into the scheme.

Symmetry considerations also clarify why a static BCS and a motion BCS both exist. This symmetry principle controls the simultaneous satisfaction of three constraints; namely,

(1) **Sustained-Transient Gating:** multiplicative interaction, or gating, of all combinations of sustained cell and transient cell output signals to form four sustained-transient cell types;

(2) **Opponent Pairs:** symmetric organization of these sustained-transient cell types into two pairs of opponent processes, such that

(3) **Independence of D.O.C.:** output signals from the opponent processes are independent of direction-of-contrast.

As shown above, multiplicative gating of sustained cells and transient cells generates receptive field properties of oriented on-cells and off-cells within the static BCS, and direction-sensitive cells within the motion BCS. Opponent processing is a fundamental organizational principle whose role in stabilizing the self-organization of cortical circuits has been analysed within Adaptive Resonance Theory (Grossberg 1980, 1982). The constraint that output signals be independent of direction-of-contrast enables both the static BCS and the motion BCS to generate emergent boundary segmentations along image contrast reversals.

Thus, the MOC Filter and SOC Filter realize all possible ways of symmetrically gating opponent pairs of sustained cells with transient cells to generate two opponent pairs of output signals that are insensitive to direction-of-contrast. One opponent pair of outcomes contains cell pairs that are insensitive to direction-of-motion, but sensitive to either the onset or the offset of an oriented contrast difference. These cells may be called complex/orientation/on cells (Figure 16a) and complex/orientation/off cells

(Figure 16b), respectively. They belong to the SOC Filter. The other opponent pair of outcomes contains the MOC Filter cell pairs that are sensitive to opposite directions-of-motion. These cells may be called (for example) complex/direction/left cells (Figure 17a) and complex/direction/right cells (Figure 17b). When both sets of pairs are combined into a single symmetric diagram, the result is shown in Figure 18, which summarizes how parallel, but interdependent, streams of static form and motion form processing are predicted to be organized in visual cortex.
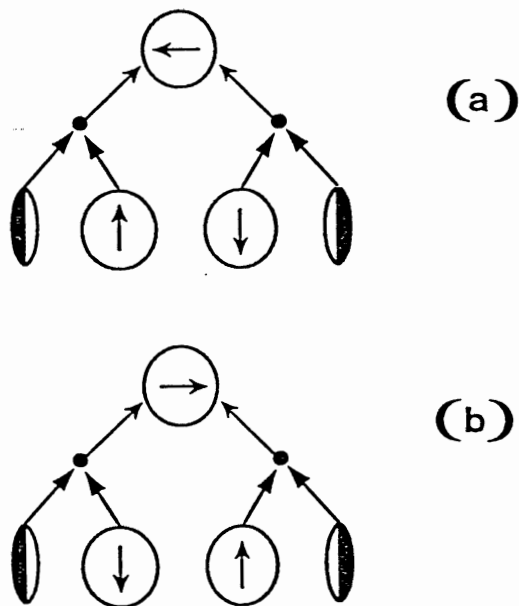

Figure 17 (a) A complex/direction/left cell: Pairs of rectified sustained cells with opposite direction-of-contrast are gated by pairs of rectified transient on-cells and off-cells, before the gated responses are added. (b) A complex/direction/right cell: Same as in (a) , except sustained cells are gated by the opposite transient cell.

17. 90% Orientations and 180% Directions: From V1 to V2 and from V1 to MT

An important consequence of the abstract symmetries described in Figures 16 and 17 is the familiar fact from daily life that opposite orientations are 90% apart, whereas opposite directions are 180% apart. In particular, the
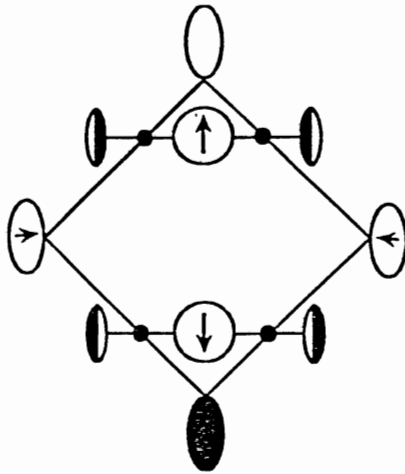
Figure 18 Symmetric unfolding of pairs of opponent orientation cells and opponent direction cells whose outputs are insensitive to direction-of-contrast: The gating combinations from Figures 16 and 17 are combined to emphasize their underlying symmetry.

opposite orientation of 'vertical' is 'horizontal', and the opposite direction of 'up' is 'down'. The symmetry implied by the former distinction is a 90% symmetry, whereas that implied by the latter distinction is 180% symmetry. How does this difference arise?

The 90% symmetry of opposite orientations is implied by the mechanisms for generating perpendicular end cuts at the hypercomplex cells of the static BCS, as sketched in Section 10 and analysed in Grossberg and Mingolla (1985b). This perpendicularity property is possible because the opponent feature of a complex/orientation/on cell is a complex/orientation/off cell (Figure 16). To illustrate this property, suppose that a vertical line end excites a complex/vertical/on cell in Figure 8. Suppose that the end stopped competition inhibits hypercomplex/vertical/on cells at positions beyond the line end. Hypercomplex/horizontal/on cells at these positions are thereby activated, and generate an end cut. As a result, a net excitatory input is generated from the horizontally oriented hypercomplex cells to the horizontally oriented bipole cells of the CC Loop at that position (Figure 9). These excitatory end cut inputs cooperate across positions to generate a horizontal emergent segmentation, that is perpendicular to the vertical line, along the entire line end.

In contrast, the opposite feature of a complex/direction cell is another complex/direction cell whose direction preference differs from it by 180° (Figure 17). When this latter property is organized into a network topogra-

phy, one finds the type of direction hypercolumns that were described in MT by Albright, Desimone, and Gross (1984). A pictorial indication of how direction hypercolumns in MT may be generated from the orientation
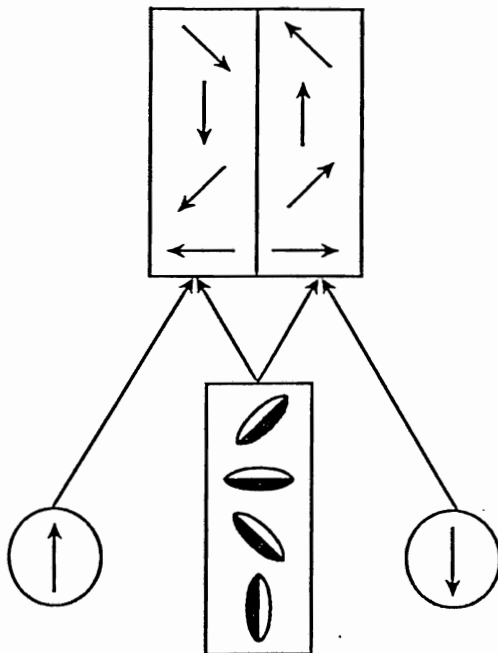

Figure 19 Orientation and direction hypercolumns: A single hypercolumn of orientation cells (say in V1) can give rise to a double hypercolumn of opponent direction cells (say MT) through gating with opponent pairs of transient cells.

hypercolumns of V1 is shown in Figure 19. This figure acknowledges that the pathways from V1 to MT combine signals from sustained cells and transient cells (Figure 17) in a different way than the pathways from V1 to V2 (Figure 16).

18. Opponent Rebounds: Rapid Reset Limits Smearing of Resonating Segmentations

A further example of perceptual complementarity may be understood by assuming that the opponent cell pairs shown in Figures 16 and 17 are capable of *antagonistic rebound*; that is, offset of one cell in the pair after

its sustained activation can trigger an antagonistic rebound that transiently activates the opponent cell in the pair (Figure 20). A neural model of such an opponent process is called a *gated dipole* (Grossberg 1972, 1982, 1988). Such an antagonistic rebound can rapidly reset a resonating boundary in response to rapid changes in the stimulus.

For example, consider a time interval when the horizontally oriented hypercomplex cells in Figure 9 are cooperating with horizontally oriented bipole cells to generate a horizontal boundary segmentation in the CC Loop. Suppose that the input pattern is then suddenly shut off. In the absence of opponent processing, the positive feedback signals between the active hypercomplex on-cells and bipole cells could maintain the boundary segmentation for a long time after input offset, thereby causing serious smearing of the visual percept in response to rapidly changing scenes. Due to opponent processing, however, offset of the horizontal complex on-cells can trigger an antagonistic rebound that activates the horizontal complex off-cells (Figure 20a). The horizontal hypercomplex off-cells are hereby activated, and they generate inhibitory signals to the horizontal bipole cells, as in Figure 9. These inhibitory signals shut off the resonating segmentation. Thus antagonistic rebound by off-cells which directly inhibit bipole cells in area V2 is predicted to be one of the inhibitory processes that control the amount of smear caused by a moving image in the experiments of Hogben and Di Lollo (1985).

19. Relating Rapid Reset to Spatial Impenetrability

This explanation of rapid reset of a resonating segmentation uses the fact that on-cells and off-cells of a given orientation generate excitatory inputs and inhibitory inputs, respectively, to bipole cells of like orientation (Figure 9). Grossberg and Mingolla (1985b) have shown that such a circuit design also generates the property of *spatial impenetrability*, whereby emergent segmentations are prevented from penetrating figures whose boundaries are built up from non-colinear orientations. In particular, in a cartoon drawing of a person standing in a grassy field, the horizontal contours where the ground touches the sky do not generate horizontal emergent boundaries that cut the person's vertical body in half. The present discussion predicts that sudden offset of a previously sustained figure that contains many vertically oriented lines may facilitate, rather than block, the propagation of horizontal emergent boundary segmentations between the horizontally oriented lines that surround the location of the figure on both sides.

20. MacKay Afterimages, the Waterfall Effect, and Long-Range MAE

The previous sections argued that some positive aftereffects may be partly due to a lingering resonance, and some negative aftereffects may be partly
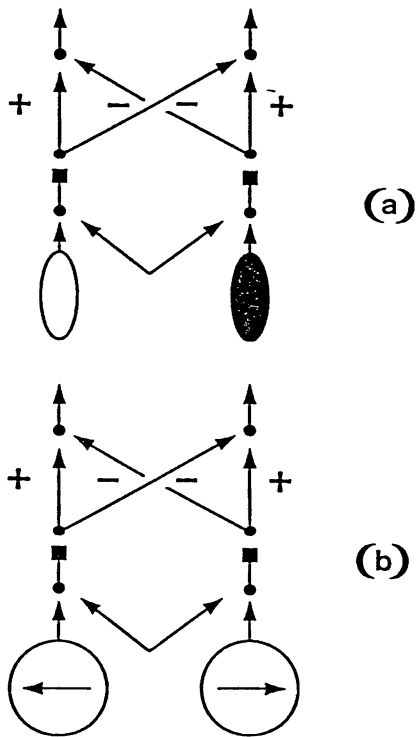
Figure 20 Opponent rebounds: When opponent cells are organized into gated dipole opponent circuits, as in (a) , offset of orientation on-cell can transiently activate like-oriented off-cells, as well as perpendicular on-cells (see text). Likewise, as in (b), offset of a direction cell can transiently activate cells tuned to the opposite direction.

due to an antagonistic rebound, in a CC Loop. Within the static BCS, negative aftereffects tend to activate perpendicular segmentations via the same 90° symmetry of the SOC Filter that generates perpendicular end cuts. Due to this symmetry, sustained inspection of a radial image can induce a circular aftereffect if a blank screen is subsequently attended (MacKay 1957). In a similar fashion, it follows from the 180° symmetry of the MOC Filter that sustained inspection of a waterfall can induce an upward-moving motion aftereffect (MAE) if a blank screen is subsequently attended (Sekuler 1975).

The assumption that a level of gated dipoles occurs subsequent to Level 5 of the MOC Filter also provides an explanation of how a long-range MAE

can occur between the locations of two flashes that previously generated apparent motion between themselves (von Grünau 1986).

Such data properties, and the coexistence of parallel systems for the analysis of static form and moving form, may now be traced to a developmental process within the visual cortex that is predicted to realize a symmetry principle: generate all possible sustained-transient BCS output signals that are independent of direction-of-contrast and organized into opponent dipoles.

21. The Visual Process as a Self-Organizing Quantum Sensitive System

In the preceding discussion, I have touched upon some of the design principles that seem to govern the neural architecture that subserves visual perception. These include principles of complementarity (Section 6), uncertainty (Sections 6 and 9), symmetry (Section 16), and resonance (Section 18). When asked what other theory is based upon these four types of principles, most of us would answer: quantum mechanics.

The visual system is also a quantum sensitive system. Our brains are tuned to be able to see even a few light quanta. FACADE Theory seems to be uncovering some of the neural designs whereby our minds achieve their competence to function perceptually in the quantized world of light.

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