PERGAMON

Neuroscience and Biobehavioral Reviews 25 (2001) 513–526

NEUROSCIENCE AND
BIOBEHAVIORAL
REVIEWS

www.elsevier.com/locate/neubiore

Review

Linking the laminar circuits of visual cortex to visual perception: Development, grouping, and attention

Stephen Grossberg*

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

Abstract

How do the laminar circuits of visual cortical areas V1 and V2 implement context-sensitive binding processes such as perceptual grouping and attention, and how do these circuits develop and learn in a stable way? Recent neural models clarify how preattentive and attentive perceptual mechanisms are intimately linked within the laminar circuits of visual cortex, notably how bottom-up, top-down, and horizontal cortical connections interact within the cortical layers. These laminar circuits allow the responses of visual cortical neurons to be influenced, not only by the stimuli within their classical receptive fields, but also by stimuli in the extra-classical surround. Such context-sensitive visual processing can greatly enhance the analysis of visual scenes, especially those containing targets that are low contrast, partially occluded, or crowded by distractors. Attentional enhancement can selectively propagate along groupings of both real and illusory contours, thereby showing how attention can selectively enhance object representations. Recent models explain how attention may have a stronger facilitatory effect on low contrast than on high contrast stimuli, and how pop-out from orientation contrast may occur. The specific functional roles which the model proposes for the cortical layers allow several testable neurophysiological predictions to be made. Model mechanisms clarify how intracortical and intercortical feedback help to stabilize cortical development and learning. Although feedback plays a key role, fast feedforward processing is possible in response to unambiguous information. Model circuits are capable of synchronizing quickly, but context-sensitive persistence of previous events can influence how synchrony develops. © 2001 Elsevier Science Ltd. All rights reserved.

Keywords: Visual cortex; Perceptual grouping; Cortical development; Attention; Neural network

Contents

---

* Tel.: +1-617-353-7858; fax: +1-617-353-7755.
E-mail address: steve@bu.edu (S. Grossberg).

PII: S0149-7634(01)00030-6

1. Introduction

The cerebral cortex is the seat of the highest forms of biological intelligence in all sensory and cognitive modalities. It also exhibits a characteristic organization into six distinct cortical layers [7,66]. Characteristics of these layers have been invaluable for classifying neocortex into more than 50 divisions, or areas, to which distinct functions have been attributed. Why the cortex has such a laminar organization for the control of behavior has, however, remained a mystery until recently. Succinctly put: How does laminar computing contribute to biological intelligence?

A number of cortical models have recently been proposed [19,62,89,90,94,99] to simulate aspects of cortical dynamics, but have not articulated explicitly why cortex has a laminar architecture. One neural model, called the LAMINART model, has recently proposed clear functional roles for these layers for purposes of visual perception [38,48,51]. These functional roles also appear to be generalizable to other forms of sensory and cognitive processing.

This model suggests how bottom-up, top-down, and horizontal interactions within the cortical layers generate adaptive behaviors. In particular, it proposes how these interactions help the visual cortex to realize: (1) the binding process whereby cortex groups distributed data into coherent object representations; (2) the attentional process whereby cortex selectively processes important events and (3) the developmental and learning processes whereby cortex shapes its circuits to match environmental constraints. One of the model's remarkable conclusions is that the mechanisms which achieve property (3) imply properties (1) and (2). That is, constraints which control stable cortical self-organization in the infant strongly constrain properties of learning, perception, and attention in the adult. A close study of the model also suggests that the mechanisms whereby horizontal connections develop and learn to perform perceptual groupings in visual cortex may, suitably specialized, be used to carry out a range of other associative learning tasks in different cortical areas.

2. Perceptual grouping and attention

During visual perception, the visual cortex can generate perceptual groupings and can focus attention upon objects of interest. *Perceptual grouping* is the process whereby the brain organizes image contrasts into emergent boundary structures that segregate objects and their backgrounds in response to texture, shading and depth cues in scenes and images. Perceptual grouping is a basic step in solving the 'binding problem', whereby spatially distributed features are bound into representations of objects and events in the world. Vivid perceptual groupings, such as illusory contours, can form over image positions that do not receive contrastive bottom-up inputs from an image or scene. Perceptual groupings can form *preattentively* and automatically, without requiring the conscious attention of a viewing subject [69].

Attention enables humans and other animals to selectively process information that is of interest to them. In contrast to perceptual grouping, top-down attention does not form visible percepts over positions that receive no bottom-up inputs. Attention can modulate, sensitize, or prime, an observer to expect an object to occur at a given location, or with particular stimulus properties [20,78]. But were attention, by itself, able to routinely generate fully formed perceptual representations at positions that did not receive bottom-up inputs, then we could not tell the difference between external reality and internal fantasy.

Despite the fact that perceptual grouping and attention make opposite requirements on bottom-up inputs, recent data have shown that both perceptual grouping and attention can simultaneously occur within the same circuits of the visual cortex, notably cortical areas V1 and V2. In fact, both processes act to enhance weak stimuli, but may have a neutral or even suppressive effect on stimuli that are already strong. Both processes also act to suppress rival stimuli. Finally, although groupings may arise preattentively, attentional task demands can influence which of several possible alternative groupings actually form. These groupings, in turn, can affect attentional phenomena such as illusory conjunctions or reaction times in visual search tasks. It has also been shown that attentional enhancement can propagate along both real and illusory contours; see Refs. [38,48] for reviews of these phenomena.

How is it possible for grouping and attention to be so intimately interact, yet to also obey such different constraints? In particular, how does cortical circuitry form perceptual groupings that *can* complete a boundary grouping over locations which receive no bottom-up visual inputs, whereas top-down attention *cannot* do so? Why *should* attention be deployed throughout the visual cortex, including cortical areas which previously were thought to accomplish purely preattentive processing? An answer can be found by exploring the link between attention and learning, and using this link to further constrain the model.

3. Attention and learning

Earlier modeling work has suggested that top-down attention is a key mechanism whereby the brain solves the *stability–plasticity* dilemma [39]. The stability–plasticity dilemma concerns that fact that our brains can rapidly learn throughout life, without just as rapidly forgetting what they already know. Brains are *plastic* and can rapidly learn new experiences, without losing the *stability* that prevents catastrophic forgetting. How are such attentive processes realized within neocortex in order to stabilize its learning through time?

An improper solution to this problem could easily lead to an infinite regress. This is true because perceptual groupings can form preattentively, and provide the substrate upon which higher-level attentional processes can act. How can the preattentive grouping mechanisms develop in a stable way, before higher-order attentional processes can develop with which to stabilize them? How does the brain prevent an infinite regress; namely, how can you use attentional top-down mechanisms to stabilize the formation of preattentive horizontal grouping circuits, if these attentional mechanisms cannot develop until the preattentive grouping mechanisms do? This is called the *attention–preattention interface problem* because the laminar cortical circuits enable preattentive grouping to use some of the same circuitry that attention uses, even before attentive mechanisms may come into play, in order to stabilize their own cortical development and learning.

The solution proposed herein to the attention–preattention interface problem builds upon earlier efforts to solve the stability–plasticity dilemma. Adaptive Resonance Theory, or ART, proposed a solution of how attention solves the stability–plasticity dilemma by modeling how bottom-up signals activate top-down expectations whose signals are matched against bottom-up data. Both the bottom-up and top-down pathways contain adaptive weights, or long-term memory traces, that may be modified by experience. The learned top-down expectations 'focus attention' upon information that matches them. They select, synchronize, and amplify the activities of cells within the attentional focus, while suppressing the activities of irrelevant cells, which could otherwise be incorporated into previously learned memories and thereby destabilize them. The cell activities which survive such top-down attentional focusing rapidly reactivate bottom-up pathways, thereby generating a type of feedback *resonance* between bottom-up and top-down signal exchanges. Such resonances rapidly bind and synchronize distributed information at multiple levels of brain processing into context-sensitive representations of objects and events. These resonances are proposed to support slower processes of learning; hence the name *adaptive* resonance. ART analyses have shown how learning in feedforward networks can easily lead to catastrophic forgetting in response to a changing world, and how learned top-down expectations that focus attention can stabilize learning if it satisfies four properties [13], which together are called the *ART Matching Rule.*

3.1. Bottom-up automatic activation

A cell, or cell population, can become active enough to generate output signals if it receives a large enough bottom-up input. Such an input can drive the cell to supraliminal levels of activation.

3.2. Top-down modulation

A cell becomes subliminally active if it receives only a large top-down expectation input. Such a top-down modulatory, or priming, signal can sensitize the cell, and thereby prepare it to react more quickly and vigorously to subsequent bottom-up inputs that match the top-down prime. But the top-down prime, by itself, cannot generate output signals from the cell.

3.3. Match

A cell's activity can be driven, and even amplified, by large convergent bottom-up and top-down inputs.

3.4. Mismatch

A cell's activity is suppressed, even if it receives a large bottom-up input, if it also receives only a small, or zero, top-down expectation input.

Recent data analyses suggested that variants of the simplest circuit, a top-down on-center off-surround network, realizes the ART Matching Rule in the brain [39] (Fig. 1). When only bottom-up signals are active in this circuit, all cells can fire that receive large enough inputs. When only top-down attention is active, cells that receive inhibition but no excitation can get strongly inhibited, while cells that receive a combination of excitation and inhibition can get at most subliminally activated due to the balance between excitation and inhibition. When bottom-up and top-down inputs match (pathway 2 in Fig. 1C), the two excitatory sources of excitation (bottom-up and top-down) that converge at the cell can overwhelm the one inhibitory source; it is a case of 'two-against-one'. When bottom-up and top-down inputs mismatch (pathway 1 in Fig. 1C), the top-down inhibition can neutralize the bottom-up excitation; it is a case of 'one-against-one'. One of the present model's accomplishments is to show how the ART Matching Rule is realized by known laminar cortical interactions.

4. Attention is modulatory

The ART Matching Rule predicted that top-down attention accomplishes modulatory *priming* and *matching.* By itself, it cannot supraliminally activate cells, thereby enabling them to generate output signals. Data compatible

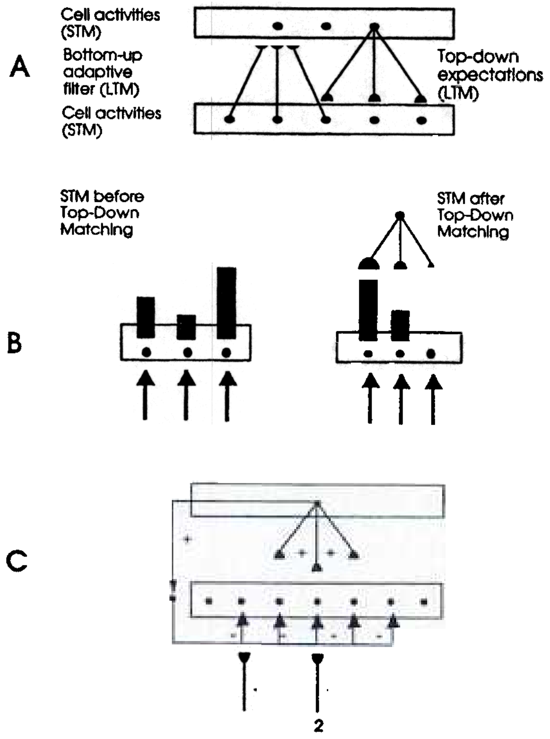

Fig. 1. (A) Patterns of activation, or short-term memory (STM), on a lower processing level send bottom-up signals to a higher processing level. These signals are multiplied by adaptive weights, or learned long-term memory (LTM) traces, which influence the activation of the cells at the higher processing level. These latter cells, in turn, activate top-town expectation signals that are also multiplied by learned LTM traces. These top-down expectations are matched against the STM pattern that is active at the lower level. (B) This matching processes confirms and amplifies STM activations that are supported by large LTM traces in an active top-down expectation, and suppresses STM activations that do not get top-down support. The size of the hemidisks at the end of the top-down pathways represents the strength of the learned LTM trace that is stored in that pathway. (C) The ART Matching Rule may be realized by a top-down on-center off-surround network, as discussed in the text. (Reprinted with permission from Grossberg [38]).

with this prediction have gradually been reported over the years. For example, Zeki and Shipp ([100] p. 316) wrote that 'backward connections seem not to excite cells in lower areas, but instead influence the way they respond to stimuli'. Likewise, the data of Sillito et al. ([88] pp. 479–482) on attentional feedback from V1 to LGN led them to conclude that "the cortico-thalamic input is only strong enough to exert an effect on those dLGN cells that are additionally polarized by their retinal input...the feedback circuit searches for correlations that support the 'hypothesis' represented by a particular pattern of cortical activity". Their experiments demonstrated all of the properties of the ART Matching Rule, since they found in addition that 'cortically induced correlation of relay cell activity produces coherent firing in those groups of relay cells with receptive-field alignments appropriate to signal the particular orientation of the moving contour to the cortex...this increases the gain of the input for feature-linked events detected by the cortex'. In other words, top-down priming, by itself, cannot fully activate LGN cells; it needs matched bottom-up retinal inputs to do so; and those LGN cells whose bottom-up signals support cortical activity get synchronized and amplified by this feedback. In addition, anatomical studies have shown that the top-down V1 to LGN pathway realizes a top-down on-center off-surround network. Data that more directly support the predicted cortical substrate of the ART Matching Rule will be summarized below as soon as the proposed circuit is identified.

5. How to stabilize cortical development and learning

The above discussion suggests that suitable top-down mechanisms should be present in *every* cortical area wherein self-stabilizing learning can occur, since without top-down learned expectations that focus attention via the ART Matching Rule, any such learned memories could easily be degraded due to catastrophic forgetting.

These analyses should, then, apply to the perceptual grouping process, because the cortical horizontal connections that support perceptual grouping in cortical areas like V1 develop through a learning process that is influenced by visual experience; e.g., Antonini and Stryker [2], Callaway and Katz [10], Löwel and Singer [63]. It is also known that many developmental and learning processes, including those that control horizontal cortical connections, are stabilized dynamically, and can be reactivated by lesions and other sources of cortical imbalance [17,30]. Moreover, adult learning often seems to use the same types of mechanisms as the infant developmental processes upon which it builds [55]. What cortical mechanisms ensure this type of dynamical stability?

This is a particularly challenging problem for perceptual groupings because they can generate suprathreshold responses over positions that do *not* receive bottom-up inputs. They therefore seem to violate the ART Matching Rule. How, then, can the horizontal connections that generate perceptual groupings maintain themselves in a stable way? Why are they not washed away whenever an illusory contour grouping forms over positions which do not receive a bottom-up input? The LAMINART model proposes an answer to this question that clarifies how attention, perceptual grouping, development, and perceptual learning are realized by the laminar circuits of visual cortex.

6. Preattentive mechanisms of perceptual grouping

Four circuit properties summarize this proposal of how the visual cortex, notably areas V1 and V2, uses its laminar design to generate coherent perceptual groupings that maintain their analog sensitivity to environmental inputs, the so-called property of *analog coherence*. Four additional circuit properties will then be summarized whereby ART

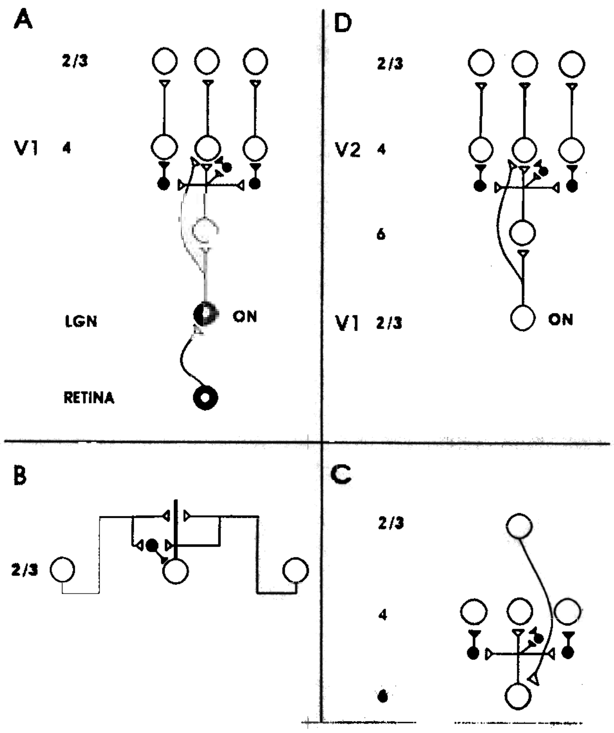

Fig. 2. A model circuit of retinal, lateral geniculate nucleus (LGN), and cortical V1 interactions: Open symbols indicate excitatory interactions and closed symbols inhibitory interactions. (A) Feedforward circuit from retina to LGN to cortical layers 4 and 6: Retina: Retinal ON cells have an on-center off-surround organization. Retinal OFF cells have an off-center on-surround organization. LGN: The LGN ON and OFF cells receive feedforward ON and OFF cell inputs from the retina. Layer 4: Layer 4 cells receive feedforward inputs from LGN and layer 6. LGN ON and OFF cell excitatory inputs to layer 4 directly establish oriented simple cell receptive fields. Layer 6 cells excite layer 4 cells with a narrow on-center and inhibit them using inhibitory interneurons that span a broader off-surround, which includes cells in the on-center (not shown). Like-oriented layer 4 simple cells with opposite contrast polarities compete (not shown) before generating half-wave rectified outputs that converge on layer 2/3 pyramidal (complex) cells. Layer 2/3: The converging simple cell outputs enable complex cells to respond to both polarities. They hereby full-wave rectify the image. (B) Horizontal grouping interactions in layer 2/3: After being activated by inputs from layer 4, layer 2/3 pyramidal (complex) cells excite each other monosynaptically via horizontal connections, primarily on their apical dendrites. They also inhibit one another via disynaptic inhibition that is mediated by model smooth stellate cells. Multiple horizontal connections share a common pool of stellate cells near each target pyramidal cell. This ensures that boundaries form inwardly between pairs or greater numbers of boundary inducers, but not outwardly from a single inducer. (C) Cortical feedback loop from Layer 2/3 to Layer 6: Layer 6 cells receive excitatory inputs from layer 2/3. The long-range cooperation hereby engages the feedforward layer 6-to-4 on-center off-surround network, which then reactivates layer 2/3 cells. This 'folded feedback' loop can select winning groupings without a loss of analog coherence. (D) Outputs from layer 2/3 to area V2 directly excite layer 4 cells and layer 6 cells, which indirectly influence layer 4 cells via an on-center off-surround network, as in area V1. [Reprinted with permission from Grossberg [38].]

principles of attention, development, and learning are integrated into this laminar design. Each of these design constraints is supported by neurophysiological, anatomical, and psychophysical data.

6.1. Analog sensitivity to bottom-up sensory inputs

Bottom-up inputs from the retina go through the Lateral Geniculate Nucleus (LGN) on their way to cortex. LGN outputs directly excite layer 4 [4,22]. LGN inputs also excite layer 6 [4], which then indirectly influences layer 4 via an on-center off-surround network of cells [1,9,67,91], as in Fig. 2A. The net effect of LGN inputs on layer 4 cells is thus via an on-center off-surround network. Such a feedforward on-center off-surround network of cells can preserve the analog sensitivity of, and normalize, the activities of target cells if these cells obey the membrane equations of neurophysiology [19,34]. This network preserves the analog sensitivity of layer 4 cells in response to LGN inputs that may vary greatly in intensity

6.2. Bipole boundary grouping

The active layer 4 cells input to pyramidal cells in layer 2/3 [11,25]. These cells initiate the formation of perceptual groupings. They generate excitatory signals among themselves using monsynaptic long-range horizontal connections, and inhibition using short-range disynaptic inhibitory connections, as in Fig. 2B. These interactions are predicted to support *inward* perceptual groupings between two or more boundary inducers, as in the case of illusory contours, but not *outward* groupings from a single inducer, which would fill the visual field with spurious groupings.

These grouping properties may be ensured as follows: when a single active pyramidal cell sends horizontal monosynaptic excitation to other pyramidal cells, it also generates a similar amount of disynaptic inhibition, thereby canceling its own excitation at other pyramidal cells; this is another case of 'one-against-one'. It has been shown in model simulations that such an approximate balance between excitation and inhibition is needed to stabilize the growth of developing horizontal connections [51]. A different result obtains when two or more pyramidal cells are activated at positions that are located at opposite sides of a target pyramidal cell, and all the cells are approximately collinear across space. Then the excitation from the active pyramidal cells summates at the target cell, thereby generating a larger total excitatory input than a single pyramidal cell could. These active cells also excite a single population of disynaptic inhibitory interneurons, which generates a saturating, or normalized, inhibitory output to the target cell. Thus excitation is bigger than inhibition in this case, so that grouping can occur; it is another case of 'two-against-one'. This combination of constraints is called the *bipole* property.Layer 2/3 pyramidal cells may hereby become active either due to direct inputs from layer 4, or due to bipole boundary groupings that form in response to other active layer 2/3 cells.

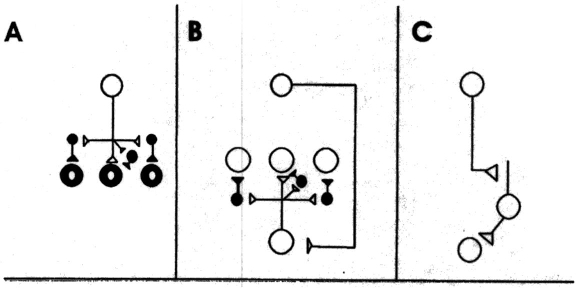

Fig. 3. (A) Top-down corticogeniculate feedback from Layer 6: LGN ON and OFF cells receive topographic excitatory feedback from layer 6 in V1, and more broadly distributed inhibitory feedback via LGN inhibitory interneurons that are excited by layer 6 signals. The feedback signals pool outputs over all cortical orientations and are delivered equally to ON and OFF cells. Cortiogeniculate feedback selects, gain-controls, and synchronizes LGN cells that are consistent with the cortical activation that they cause, thereby acting like a type of automatic attentional focus. (B) Attentional feedback from V2 to V1: Layer 6 in V2 activates layer 6 in V1, which then activates the layer 6-to-4 on-center off-surround network that attentionally primes layer 4 cells. (C) One feedback pathway arises from Layer 6 cells in V2 and activates apical dendrites in Layer 1 of V1. Cells in Layer 5 are activated through these apical dendrites and thereupon activate Layer 6 cells. Layer 6 in V2 can also modulate layer 2/3 of V1 by activating layer 1 dendrites of both excitatory and inhibitory cells in layer 2/3. [Reprinted with permission from Grossberg [38].]

6.3. Folded feedback and analog coherence

Active cells in layer 2/3 can form groupings on their own in response to unambiguous visual inputs. Thus some groupings can form quickly and in an approximately feedforward way; Thorpe, Fize, and Marlot [92]. In response to scenes wherein multiple groupings can form in layer 2/3, but only a few of them are correct, intracortical feedback helps to select the strongest grouping, and also binds its cells together in a coherent and synchronous way. This feedback is proposed to occur as follows: active layer 2/3 cells send excitatory feedback to layer 6 [5,58], say via layer 5, as in Fig. 2C. Layer 6 then activates the on-center off-surround network from layer 6–4. This feedback process is called *folded feedback*, because feedback signals from layer 2/3 to layer 6 get transmitted in a feedforward fashion back to layer 4. The feedback is hereby 'folded' back into the feedforward flow of bottom-up information within the laminar cortical circuits.

Folded feedback turns the cortex into a feedback network that binds the cells throughout layers 2/3, 4, and 6 into functional columns [71]. The on-center off-surround network now helps to select the strongest groupings that are formed in layer 2/3 and to inhibit weaker groupings, while preserving the analog values of the selected groupings. In particular, the on-center signals from layer 6-to-4 support the activities of those pyramidal cells in layer 2/3 that are part of the strongest horizontal groupings. The off-surround signals can inhibit inputs to layer 4 that were supporting less active groupings in layer 2/3. In this way, signals from layer 4 to the less active groupings in layer 2/3 are removed, and thus these groupings collapse.

6.4. Self-similar hierarchical boundary processing

Converging evidence suggests that area V2 replicates aspects of the structure of area V1, but at a larger spatial scale. Thus layer 2/3 in area V1 sends bottom-up inputs to layers 4 and 6 of area V2, much as LGN sends bottom-up inputs to layers 4 and 6 of area V1 [21,96], as in Fig. 2D. This input pattern from V1 to V2 can preserve the analog sensitivity of layer 4 cells in V2 for the same reason that the LGN inputs to V1 can preserve the analog sensitivity of layer 4 cells in V1. The shorter perceptual groupings in layer 2/3 of area V1 [33,81] are proposed to group together, and enhance the signal-to-noise ratio of, nearby V1 cells with similar orientation and disparity selectivity. The longer perceptual groupings in area V2 [75,97] are proposed to build long-range boundary segmentations that separate figure-from-background; generate 3-D groupings of the edges, textures, shading, and stereo information that go into object representations; and complete boundaries across gaps in bottom-up signals due to the retinal blind spot and veins [35,60].

7. Attention, development, and learning

The following four circuit properties are proposed to integrate top-down attention into the preattentive grouping process.

7.1. Top-down feedback from V1 to LGN

As noted above, layer 6 of area V1 sends a top-down on-center off-surround network to the LGN, as in Fig. 3A. This top-down pathway automatically 'focuses attention' on those LGN cells whose activities succeed in activating V1 cells. Data of Sillito et al. [88] are compatible with the hypothesis that this feedback obeys the ART Matching Rule, and thus can only subliminally activate, or modulate, LGN cells. Matched bottom-up inputs are needed to supraliminally activate LGN cells while top-down signals are active. This process is predicted to help stabilize the development of receptive fields in V1, including disparity-tuned complex cells, during the visual critical period.

7.2. Folded feedback from layer 6 of V2 to Layer 4 of V1

A similar top-down process seems to occur at all stages of visual cortex, and probably beyond. Layer 6 in a given cortical area, such as V2, generates top-down cortical signals to layer 6 of lower cortical areas, such as V1, where they activate the layer 6-to-4 folded feedback network in the lower area (Fig. 3B). One such known top-down pathway exits layer 6 in V2 and activates V1 via layer 1 [83], then layer 5, then layer 6 [29,65], as in Fig. 3C. Top-down feedback can hereby activate a top-down on-center

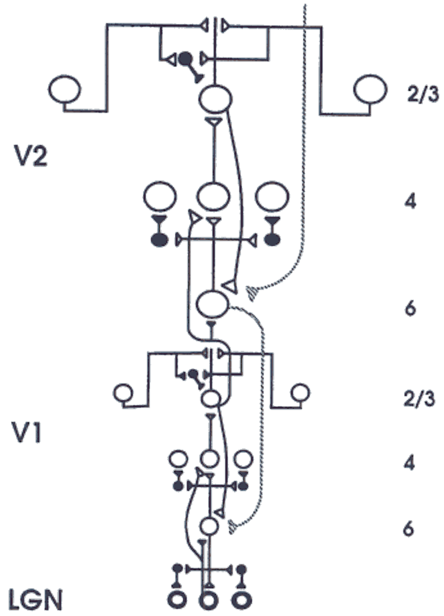

Fig. 4. A model synthesis of bottom-up, top-down, and horizontal interactions in LGN, V1, and V2. Cells and connections with open symbols denote preattentive excitatory mechanisms that are involved in perceptual grouping. Closed symbols denote inhibitory mechanisms. Gray denotes top-down attentional mechanisms. [Reprinted with permission from Grossberg [38].]

off-surround circuit, as required by the ART Matching Rule. Intercortical attention is hereby suggested to use outputs from layer 6 of a given cortical area to activate layer 4 of a lower cortical area via layer 6-to-4 folded feedback.

7.3. *Layer 6-to-4 signals are modulatory*

The ART Matching Rule predicts that this top-down pathway modulates, or subliminally activates, cells in layer 4. This modulatory property is predicted to be due to the fact that the excitatory and inhibitory signals within the on-center from layer 6-to-4 are approximately balanced, so that at most a weak excitatory effect occurs after activating the circuit via top-down feedback. Consistent data show that 'feedback connections from area V2 modulate but do not create center-surround interactions in V1 neurons' ([54] p. 1031) and that top-down connections have an on-center off-surround organization [8]. This prediction is also consistent with data showing that layer 4 EPSPs elicited by layer 6 stimulation are much weaker than those caused by stimulation of LGN axons or of neighboring layer 4 sites [91], and with data showing that binocular layer 6 neurons synapse onto monocular layer 4 cells of both eye types without reducing these cells' monocularity ([9] p. 56). Grossberg and Williamson [51] have modeled how such an approximate balance between excitation and inhibition can develop and that it is needed to achieve stable development of interlaminar 6-to-4 connections.

Although it is modulatory, this top-down circuit can have a major effect on cortical cell activations when the cortex is activated bottom-up by visual inputs: It can strongly inhibit activities of layer 4 cells whose layer 2/3 cell projections are not bound into strong groupings, and amplify the strongest groupings until they can resonate. In particular, higher-level influences such as figure–ground separation or even learned object prototypes from still higher cortical areas can hereby bias the cortex to select consistent groupings at lower cortical levels. In this way, automatic early vision filtering, 3-D boundary and surface processing, and higher-order knowledge constraints can mutually influence one another.

7.4. *Two bottom-up input sources to layer 4*

A simple functional explanation can now be given of a cortical design constraint which could otherwise seem quite mysterious; namely, why there are direct bottom-up inputs to layer 4, as well as indirect bottom-up inputs to layer 4 via layer 6 (Fig. 2A and D). Why are not these two separate input pathways redundant? In particular, why is not the indirect layer 6-to-4 pathway sufficient to fully activate layer 4 cells *and* to maintain their analog sensitivity using its on-center off-surround network? The proposed explanation is that the indirect layer 6-to-4 inputs need to be modulatory to preserve the stability of cortical development and learning. Direct inputs to layer 4 are therefore needed to supraliminally activate layer 4 cells.

Taken together, these eight cortical design principles lead to the circuit diagram in Fig. 4 for perceptual grouping, attention, and learning within and between areas LGN, V1, and V2. The generality of the grouping, attentional, developmental, and learning constraints which lead to this design poses the intriguing possibility that the same cortical circuits may explain data at multiple levels and modalities of neocortical sensory and cognitive processing.

8. The preattentive perceptual grouping is its own attentional prime

These circuit constraints suggest how the horizontal connections within cortical area V1 and V2 can develop and learn stably in response to visual inputs, thereby proposing the following solution to the attention–preattention interface problem: Both preattentive perceptual groupings within V1 and attentive feedback from V2 to V1 generate feedback signals to layer 6 of V1. Both types of feedback activate the folded feedback circuit from layer 6-to-4. Top-down attention uses this circuit to focus attention within V1 by inhibiting layer 4 cells that are not supported by excitatory 6-to-4 feedback. Perceptual groupings use it to select the correct grouping by inhibiting layer 4 cells that would otherwise form incorrect groupings. In both cases, folded feedback prevents the wrong combinations of cells in layers 4 and 2/3 from being active simultaneously. In the adult, this selection process defines perceptual grouping properties. In the infant, and also during adult perceptual learning, it is

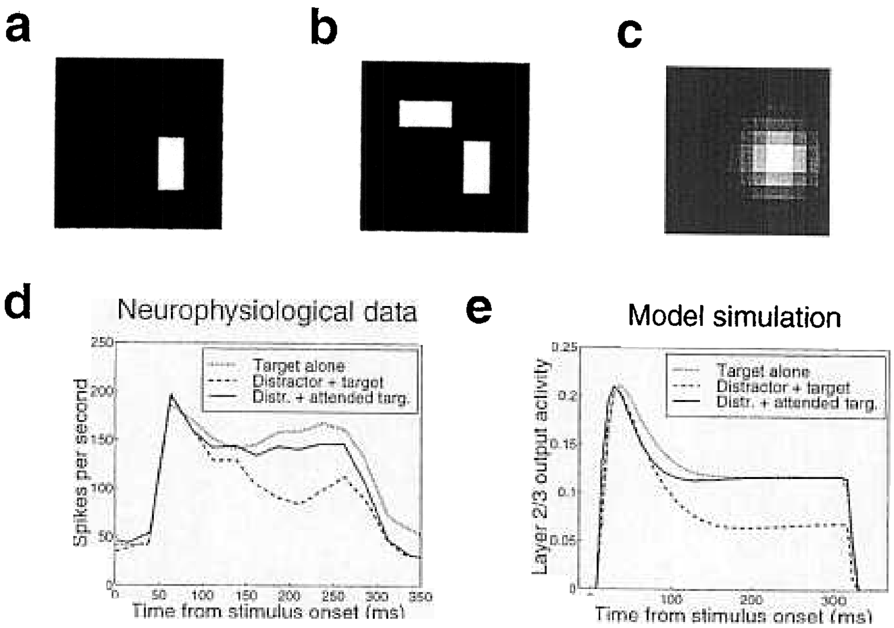

Fig. 5. The effect of attention on competition between visual stimuli. (a, b, c). Visual stimuli used in the experimental paradigm of Reynolds et al. [82]: (a) a target stimulus, presented on its own elicits strong neural activity. (b) When a second distractor stimulus is presented nearby, it competes against the target, and activity is reduced. (c) Directing spatial attention to the location of the target stimulus protects the target from this competition, and restores neural activity to the levels elicited by the target on its own. (d) Data adapted with permission from Reynolds et al. [82]. (e) Model simulation of the data, reproduced with permission from Grossberg and Raizada [48].

predicted to prevent incorrect horizontal connections from being learned, since 'cells that fire together wire together'.

The folded feedback circuit from layer 6-to-4 gets activated by perceptual grouping signals from layer 2/3 at *all* positions of the grouping, even positions that do not receive bottom-up inputs. The ART Matching Rule is thus satisfied at all positions, and the source of the 'top-down expectation' is the perceptual grouping itself. In summary, the *preattentive perceptual grouping is its own attentional prime* because it can use the modulatory 6-to-4 selection circuit to stabilize its own development using *intra* cortical feedback, even before attentional *inter* cortical feedback can develop.

This sharing of the layer 6-to-4 selection circuit by both grouping and attention clarifies how attention can bias the selection of which grouping will be perceived in an unambiguous situation. It can also explain macaque V1 data about how attention can propagate along a boundary grouping and thereby selectively prime an object representation [84], which the model simulated in Grossberg and Raizada [48].

9. A unified explanation of developmental, neurophysiological, and perceptual data

Using the intimate link between processes of development, grouping, and attention that the model proposes, it has been used to simulate several different types of developmental, neurophysiological, and perceptual data. For example, the developmental study of Grossberg and Williamson [51] simulated the projection range of pyramidal cells in cat striate cortex as a function of age [28] and the orientation bias in ferret striate cortex as a function of age [85]. After model development stabilized, it simulated the projection field of adult tree shrew striate cortex [24], the cortical point spread function in macaque V1 [32], and psychophysical data about the strength of illusory contours as a function of their support ratio [87] and density [61], as well as the detection thresholds for Gabor patches as a function of the distance between collinear flankers [77]. These results supported the hypothesis that the mechanisms which enable the cortex to develop in a stable way give rise to adult mechanisms of visual perception. In another study [44], the model was used to simulate how certain input patterns can cause illusory contours to form in both macaque V1 and V2 [33] while others, with more widely separated inducers, can cause illusory contours to form in V2 but not V1 [97]; how horizontal orientations can compete with a vertical grouping [56]; and how Gestalt grouping laws may arise.

Grossberg and Raizada [48] and Raizada and Grossberg [79] have simulated data about how attention can protect macaque neurons from masking by nearby stimuli [82], as in Fig. 5; how collinear flanking Gabor stimuli can enhance the response of a low-contrast Gabor patch while inhibiting the response of a high-contrast Gabor patch relative to a path with no flanking stimuli [76], as in Fig. 6; how attention can enhance responses along both real and illusory contours [70,84], as in Fig. 7; and how orientation contrast can occur in response to a surround with bars oriented

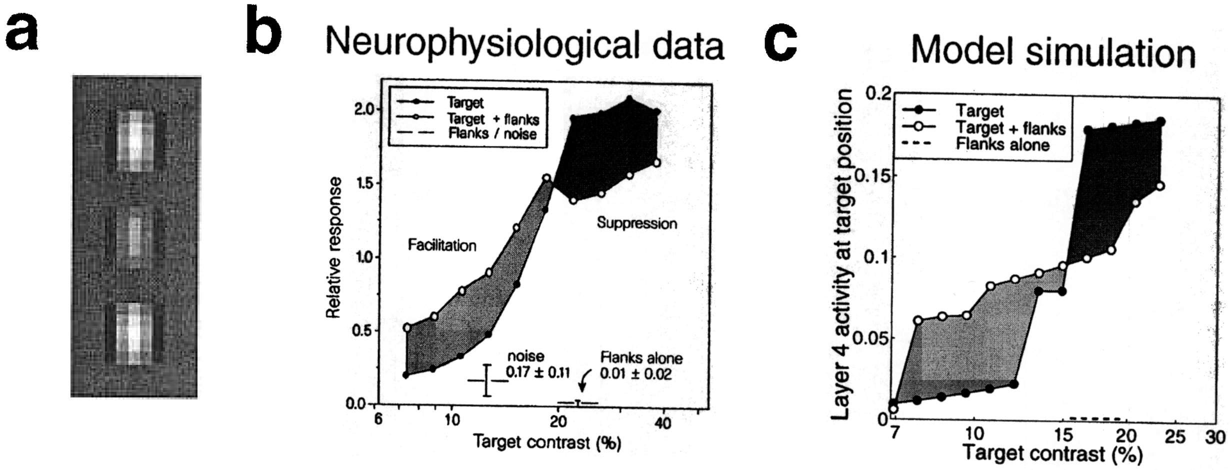

Fig. 6. Contrast-dependent perceptual grouping in primary visual cortex. (a) Illustrative visual stimuli. A variable-contrast oriented Gabor patch stimulates the classical receptive field with collinear flanking Gabors of fixed high-contrast outside of the classical field. (b) Neural responses recorded from cat V1. The collinear flankers have a net facilitatory effect on weak targets which are close to the cell's contrast-threshold, but they act to suppress responses to stronger, above-threshold targets. When the flankers are presented on their own, with no target present, the neural response stays at baseline levels. Reproduced with permission from Polat et al. [76]. (c) Model simulation of the Polat et al. [76] data. Reproduced with permission from Grossberg and Raizada [48].

perpendicular to a target bar [59], as in Fig. 8. Taken together, these simulations critically utilize all of the model mechanisms, and removing any one of them would prevent the model from simulating some of the data.

The model has not yet been developed to explain how the laminar cortical circuits are organized to perceive objects in depth, or figure–ground relations between multiple objects. Neural models have been developed to explain substantial

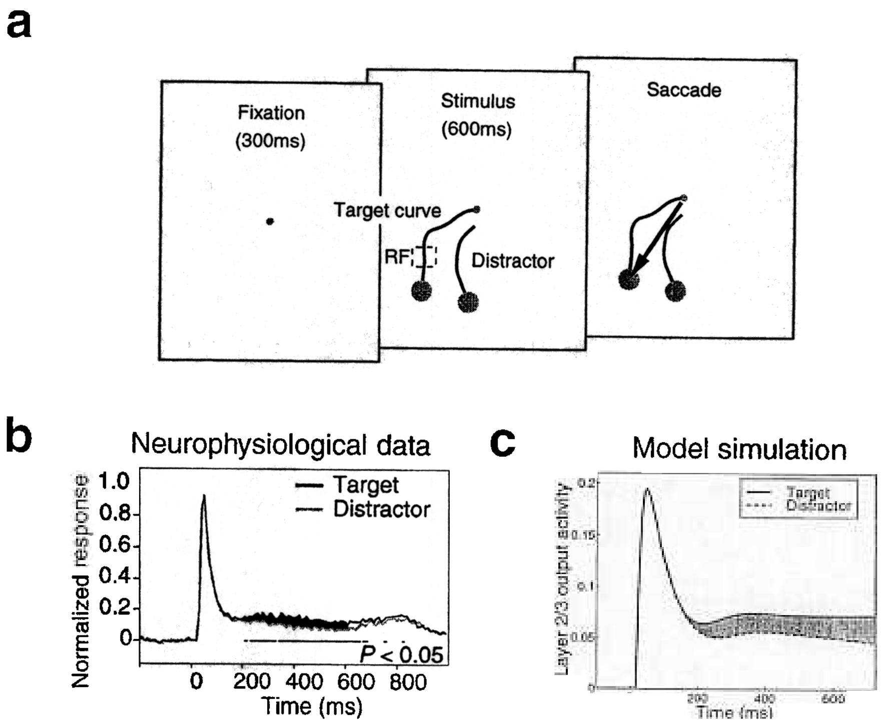

Fig. 7. Spread of visual attention along an object boundary grouping. (a) Experimental paradigm of Roelfsema et al. [84]. Macaque monkeys peformed a curve-tracing task, during which physiological recordings were made in V1. A fixation spot was presented for 300 ms, followed by a target curve and a distractor curve presented simultaneously. The target was connected at one end to the fixation point. While maintaining fixation, the monkeys had to trade the target curve, then, after 600 ms, make a saccade to its endpoint. (b) Neurophysiological data showing attentional enhancement of the firing of a neuron when its receptive field lay on the target curve, as opposed to the distractor. Enhancement occurs about 200 ms after the initial burst of activity. Further studies have indicated that the enhancement starts later in distal curve segments far from the fixation point, than it does in proximal segments closer to fixation (Pieter Roelfsema, personal communication.) This suggests that attentional signals propagate along the length of the target curve. Figures (a) and (b) adapted with permission from Roelfsema et al. [84]. (c) Model simulation of the data. Reproduced with permission from Grossberg and Raizada [48].

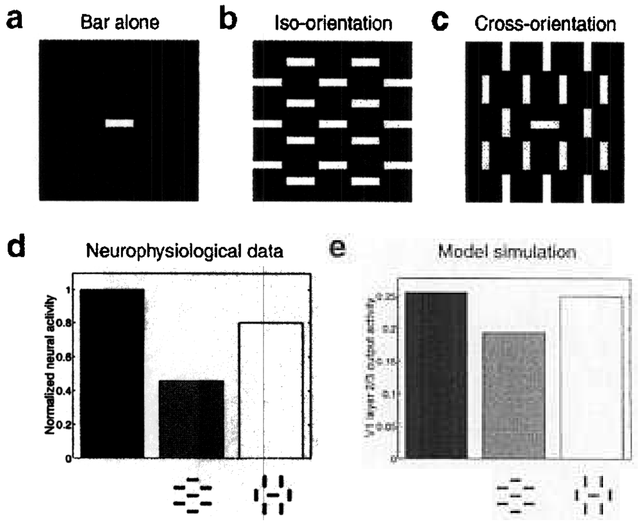

Fig. 8. Orientation contrast in V1. (a)–(c): Stimuli of the sort used by Knierim and Van Essen [59]. The neural responses elicited by an isolated bar are recorded, then compared with responses when the same bar is embedded either in an iso-orientation or cross-orientation texture surround. The images shown here are the actual stimuli that were presented to the model network. (d) Neurophysiological data from macaque V1, adapted with permission from Knierim and Van Essen [59]. The icons along the x-axis indicate that the stimuli presented were of the sorts shown in (a)–(c). Both sorts of texture surrounds have a suppressive effect on neural activity, compared to when the bar is presented on its own, but the orthogonal surround produces less suppression, thereby making the bar seem to 'pop out' from the orthogonal background but not from the iso-orientation surround. (e) Model simulation of the data. Reproduced with permission from Raizada and Grossberg [79].

data bases in these areas [35,36,42,43,47,57,68], but have not yet clarified what combinations of identified cells in prescribed cortical lamina support these perceptual processes. Research is now ongoing to answer these questions.

10. Discussion

The neural model presented here shows how visual cortex can implement several types of contextual processing at once, and also allow them to interact. The model proposes specific functional roles for known laminar circuits to carry out the contextual processing, and suggests how attention and perceptual grouping can interact within this laminar circuitry to solve the attention–preattention interface problem.

A number of other cortical models have been described in the literature, but none of them seems to meet the challenge of the attention–preattention interface problem by attempting to emulate cortex's ability to perform attention and perceptual grouping simultaneously. Whereas the functional importance of top-down attention is clear, the formation of illusory contours may at first sight appear to be an almost epiphenomenal consequence of the seemingly more fundamental process of collinear facilitation. However, illusory contours can perform a crucial task which mere facilitation cannot: They can actively close incomplete boundaries, a process that requires that cells with unstimulated cortical receptive fields can nonetheless become active. This boundary closure can guide surface reconstruction, complete boundaries over visual gaps caused by the blind-spot and retinal veins, and also provide enhanced information for the recognition of partially occluded objects [35].

Several other models of collinear grouping in V1 produce facilitation but not illusory contours, and hence are unable to capture this important aspect of cortical processing [62,89,90,99]. Those models which do implement illusory contours either leave out any consideration of top-down cortical feedback [53,98], fail to capture the on-center off-surround form of attention by treating top-down feedback as having a purely excitatory multiplicative effect [73], or treat 'reentrant' feedback signals from higher areas 'as if they were signals from real contours in the periphery entering via 4Cα' ([23] p. 3197), thereby creating the risk of perceptual hallucinations.

Conversely, many models of top-down feedback in visual processing do not implement perceptual grouping [52,72,74,80,93,95], therefore leaving untouched what we suggest are crucial design constraints which shape the functional laminar architecture of cortex.

LAMINART modeling results also clarify other properties of cortical coding. For example, in response to unambiguous visual information, a boundary grouping can start to form very rapidly in response to a feedforward sweep of signal from layer 4 to layer 2/3. Thus the existence of cortical feedback does not preclude fast cortical processing [92]. Intracortical feedback is predicted to become increasingly important when multiple groupings of the image or scene are possible. Even here, the model's selection of a final grouping can often converge within one or at most a few feedback cycles between layers 4-2/3-6-4. Intercortical feedback may be needed when attention must select some cue combinations over others, based on higher-order constraints. The model shows how very high-order constraints can, in principle, modulate even low-order feature detectors by propagating across multiple cortical regions via their layers 6, without ever fully activating their groupings in layer 2/3. An open experimental question concerns whether and how such a propagating priming effect is attenuated as a function of the number of cortical regions that are traversed. It has also been simulated how these grouping and attentional circuits may rapidly synchronize, and can generate fast synchronizing oscillations under some conditions [41,49].

All of these statements require qualification, however. For example, *visual persistence* is context-dependent, and may depend upon properties of stimulus contrast duration, and contextual interactions. Key experimental properties of persistence are simulated in the model of Francis, Grossberg, and Mingolla [26] and Francis and Grossberg [27]. Different amounts of persistence in different parts of a scene may interfere with the synchronous onset of subsequent groupings across the scene. Another factor worth considering is the fact that attention-induced increases in firing rate can propagate along perceptual groupings, thereby selectively enhancing object representations; see monkey data in Roelfsema et al. [84], simulations in Grossberg and Raizada [48], and Fig. 7. This result shows that synchronous activation of an object by attention is not necessary in all cases.

Finally, one needs to emphasize that the discussion above concerns only processing of visual boundaries within the interblob stream of visual cortex. It does not consider at all the processing of surface brightness and color within the blob stream. Boundary groupings within the interblob stream are predicted, in the absence of surface featural information, to be invisible, or *amodal*. Hence, all of the results summarized above are relevant only the salience of boundary groupings, not to the visible perception of the surfaces which these boundaries enclose. Visibility is predicted to be a property of surface representations within the blob stream, with these surfaces arising due to the filling-in of brightness and color within closed boundary groupings formed in the interblob stream [35]. Whereas contour salience and visibility often covary, this is not always the case: for example, Glass patterns [31] contain highly salient concentric contour groupings, but do not induce any brightness differences that would cause bright Ehrenstein-like circular surfaces to be visible.

Another limitation of the present model is that it does not describe how transient responses to changing or moving stimuli can rapidly attract visual attention. One major pathway for this mechanism is likely to be the Where dorsal cortical stream. Recent models of motion processing clarify the key role of these transient responses [3,15], and also how they can attract visual attention [37].

Because the present model assigns specific functional roles to many aspects of ortical laminar circuitry, many testable predictions can be derived from it. Several such predictions are summarized in Grossberg and Raizada [48]. A core prediction is that the layer 6-to-4 on-center should be subthreshold. In the strongest form of this prediction, intracellularly evoked layer 6 activity should modulate, but not drive, layer 4 spiny stellates and layer 2/3 pyramidals. A weaker form proposes that, if layer 6 can activate layer 4, then this activation cannot be sufficient to drive layer 2/3 pyramids. Failure to confirm this prediction would constitute serious evidence against the model. The model also predicts that attentional feedback into layer 6, possibly routed there from layer 1, passes into this modulatory 6-to-4 on-center to remain subthreshold in the absence of bottom-up visual input. Thus, it predicts that attentional elevation of a neuron's baseline firing rate when there is no stimulus in its receptive field, as observed by Luck et al. [64], should cause above-threshold activation in layer 6, but below-threshold activation of layer 4 spiny stellates. The intimate link between attention and grouping that the model proposes predicts that V2 groupings should feed back into V1 through the same pathway as attentional signals. For example, widely spaced collinear inducers (like the flankers in the study by Polat et al. [76], should cause illusory contour activation in V2 layer 2/3, but not V1 layer 2/3, with feedback from this V2 grouping supraliminally activating V1 layer 6 but not 4, just like attention to empty space.

A related testable prediction concerns the spread of attention along illusory as well as real contour groupings. The LAMINART model proposes that measurable neurophysiological correlates of such flow should exist particularly in layer 2/3 of V2, and possibly also of V1. This could be tested by replicating the Roelfsema et al. [84] study, but having the monkeys trace curves made of dashed instead of solid lines. V2 neurons lying along the empty parts of the dashed lines should fire as a result of collinear grouping [97], and we predict that attention to the traced curve should be able to enhance such firing, just as in the case where the complete contour is physically present. It also follows from the model that attentional enhancement should be more pronounced for low contrast stimuli, as in the simulation of the data of DeWeerd et al. [18] in Raizada and Grossberg [79]. Thus, using low contrast dashed lines should make it easier to observe the predicted attentional effect.

All sensory and cognitive neocortical areas share key laminar properties. For example, long-range horizontal connections are known to occur in many areas of neocortex, such as the auditory and language areas of the human temporal cortex [86]. It remains to be seen whether and how the above principles of how to achieve stable cortical development and learning, to bind together distributed cortical data through a combination of bottom-up adaptive filtering and horizontal association, and to modulate it with top-down attention will generalize to these other cortical areas. Neural models of visual object recognition [6,12,14,39,50], visual motion perception [15,16,45], and of auditory and speech perception [39,40,46], among other competences, have been developed in which ART mechanisms play a key role. It remains to be seen how such ART mechanisms are specialized within the laminar circuits of other cortical areas to realize a variety of intelligent behaviors.

Acknowledgements

This work was supported in part by the Defense Advanced Research Projects Agency and the Office of Naval Research (ONR N00014-95-1-0409), the National Science Foundation (NSF IRI-97-20333), and the Office of Naval Research (ONR N00014-95-1-0657). The author wishes to thank Robin Amos and Diana Meyers for their valuable assistance in the preparation of the manuscript.

References

[1] Ahmed B, Anderson JC, Martin KAC, Nelson JC. Map of the synapses onto layer 4 basket cells of the primary visual cortex of the cat. J Comp Neuro 1997;380:230–42.
[2] Antonini A, Stryker MP. Functional mapping of horizontal connections in developing ferret visual cortex: experiments and modeling. J Neurosci 1993;14:7291–305.
[3] Baloch AA, Grossberg S, Mingolla E, Nogueira CAM. Neural model of first-order and second-order motion perception and magnocellular dynamics. J Optical Soc America A 1999;15:953–78.
[4] Blasdel GG, Lund JS. Termination of afferent axons in macaque striate cortex. J Neurosci 1983;3:1389–413.
[5] Blasdel GG, Lund JS, Fitzpatrick D. Intrinsic connections of macaque striate cortex: axonal projections of cells outside lamina 4C. J Neurosci 1985;5:3350–69.
[6] Bradski G, Grossberg S, Fast-learning VIEWNET. architectures for recognizing three-dimensional objects from multiple two-dimensional views. Neural Net 1995;8:1053–80.
[7] Brodmann K. Vergleichende Lokalisationslehre der Grosshirnrinde in ihren Prinzipien dargestellt auf Grund des Zellenbaues. Leipzig: Barth, 1909.
[8] Bullier J, Hupé JM, James A, Girard P. Functional interactions between areas V1 and V2 in the monkey. J Physiol (Paris) 1996; 90:217–20.
[9] Callaway EM. Local circuits in primary visual cortex of the macaque monkey. Annual Rev Neurosci 1998;21:47–74.
[10] Callaway EM, Katz LC. Emergence and refinement of clustered horizontal connections in cat striate cortex. J Neurosci 1990; 10:1134–53.
[11] Callaway EM, Wiser AK. Contributions of individual layer 2–5 spiny neurons to local circuits in macaque primary visual cortex. Vis Neurosci 1996;13:907–22.
[12] Carpenter GA. Distributed learning, recognition, and prediction by ART and ARTMAP neural networks. Neural Net 1997;8:1473–94.
[13] Carpenter GA, Grossberg S. Pattern recognition by self-organizing neural networks. Cambridge: MIT Press, 1991.
[14] Carpenter GA, Ross WD. ART-EMAP: a neural network architecture for object recognition by evidence accumulation. IEEE Trans. Neural Net 1995;6:805–18.
[15] Chey J, Grossberg S, Mingolla E. Neural dynamics of motion grouping: from aperture ambiguity to object speed and direction. J Optical Soc America A 1997;14:2570–94.
[16] Chey J, Grossberg S, Mingolla E. Neural dynamics of motion processing and speed discrimination. Vis Res 1998;38:2769–86.
[17] Das A, Gilbert CD. Long-range horizontal connections and their role in cortical reorganization revealed by optical recording of cat primary visual cortex. Nat 1995;375:780–4.
[18] De Weerd P, Peralta MR, Desimone R, Ungerleider LG. Loss of attentional stimulus selection after extrastriate cortical lesions in macaques. Nat Neurosci 1999;2:753–8.
[19] Douglas RJ, Koch C, Mahowald M, Martin KAC, Suarez HH. Recurrent excitation in neocortical circuits. Sci 1995;269:981–5.
[20] Duncan J. Selective attention and the organization of visual information. J Exp Psych: Gen 1984;113:501–17.
[21] Felleman DJ, van Essen DC. Distributed hierarchical processing in the primate cerebral cortex. Cereb Cortex 1991;1:1–47.
[22] Ferster D, Chung S, Wheat H. Orientation selectivity of thalamic input to simple cells of cat visual cortex. Nat 1996;380:249–52.
[23] Finkel LH, Edelman GM. Integration of distributed cortical systems by reentry: a computer simulation of interactive functionally segregated visual areas. J Neurosci 1989;9:3188–208.
[24] Fitzpatrick D. The functional organization of local circuits in visual cortex: insights from the study of tree shrew striate cortex. Cereb Cortex 1996;6:329–41.
[25] Fitzpatrick D, Lund JS, Blasdel GG. Intrinsic connections of macaque striate cortex: afferent and efferent connections of laminar 4C. J Neurosci 1985;5:3329–49.
[26] Francis G, Grossberg S, Mingolla E. Cortical dynamics of feature binding and reset: Control of visual persistence. Vis Res 1994;34:1089–104.
[27] Francis G, Grossberg S. Cortical dynamics of from and motion integration: persistence, apparent motion, and illusory contours. Vis Res 1996;36:149–73.
[28] Galuske RAW, Singer W. The origin and topography of long-range intrinsic projections in cat visual cortex: a developmental study. Cereb Cortex 1996;6:417–30.
[29] Gilbert CD, Wiesel TN. Morphology and intracortical projections of functionally characterised neurones in the cat visual cortex. Nat 1979;280:120–5.
[30] Gilbert CD, Wiesel TN. Receptive field dynamics in adult primary visual cortex. Nat 1992;356:150–2.
[31] Glass L. Moire effect from random dots. Nat 1969;223:578–89.
[32] Grinvald A, Lieke EE, Frostig RD, Hildesheim R. Cortical point-spread function and long-range lateral interactions revealed by real-time optical imaging of macaque monkey primary visual cortex. J Neurosci 1994;14:2545–68.
[33] Grosof DH, Shapley RM, Hawken MJ. Macaque V1 neurons can signal 'illusory' contours. Nat 1993;365:550–2.
[34] Grossberg S. How does a brain build a cognitive code. Psych Rev 1980;87:1–51.
[35] Grossberg S. 3-Division and figure–ground separation by visual cortex. Percep & Psychophy 1994;55:48–120.
[36] Grossberg S. Cortical dynamics of three-dimensional figure–ground perception of two-dimensional pictures. Psych Rev 1997;104:618–58.
[37] Grossberg S. How is a moving target continuously tracked behind occluding cover? In: Watanabe T, editor. High-level motion processing: computational, neurobiological, and psychophysical perspectives, Cambridge: MIT Press, 1998. p. 1–30.
[38] Grossberg S. How does the cerebral cortex work? Learning, attention, and grouping by the laminar circuits of visual cortex. Spat Vis 1999;12:163–85.
[39] Grossberg S. The link between brain learning, attention, and consciousness. Consci Cog 1999;8:1–44.
[40] Grossberg S, Boardman I, Cohen MA. Neural dynamics of variable-rate speech categorization. J Exp Psych: Human Percept and Perform 1997;23:481–503.
[41] Grossberg S, Grunewald A. Cortical synchronization and perceptual framing. J Cog Neurosci 1997;9:117–32.
[42] Grossberg S, Kelly F. Neural dynamics of binocular brightness perception. Vis Res 1999;39:3796–816.
[43] Grossberg S, McLoughlin NP. Cortical dynamics of three-dimensional surface perception: binocular and half-occluded scenic images. Neural Net 1997;10:1583–605.
[44] Grossberg S, Mingolla E, Ross WD. Visual brain and visual perception: how does the cortex do perceptual grouping? Trends Neurosci 1997;20:106–11.
[45] Grossberg S, Mingolla E, Viswanathan L. Neural dynamics of motion integration and segmentation within and across apertures. Vis Res 2001;41:2521–53.
[46] Grossberg S, Myers CW. The resonant dynamics of speech perception: Interword integration and duration-dependent backward effects. Psych Rev 2000;4:735–67.
[47] Grossberg S, Pessoa L. Texture segregation, surface representation, and figure–ground separation. Vis Res 1998;38:2657–84.
[48] Grossberg S, Raizada RDS. Contrast-sensitive perceptual grouping and object-based attention in the laminar circuits of primary visual cortex. Vis Res 2000;40:1413–32.
[49] Grossberg S, Somers D. Synchronized oscillations during cooperative feature linking in a cortical model of visual perception. Neural Net 1991;4:453–66.

[50] Grossberg S, Williamson JR. A self-organizing neural system for learning to recognize textured scenes. Vis Res 1999;39:1385–406.

[51] Grossberg S, Williamson JR. A neural model of how horizontal and interlaminar connections of visual cortex develop into adult circuits that carry out perceptual grouping and learning. Cereb Cortex 2001;11:37–58.

[52] Harth E, Unnikrishnan KP, Pandya AS. The inversion of sensory processing by feedback pathways: a model of visual cognitive functions. Sci 1987;237:184–7.

[53] Heitger F, von der Heydt R, Peterhans E, Rosenthaler L, Kubler O. Simulation of neural contour mechanisms: representing anomalous contours. Image and Vis Comput 1998;16:407–21.

[54] Hupé JM, James AC, Girard P, Bullier J. Feedback connections from V2 modulate intrinsic connectivity within. Soc Neurosci Abstracts 1997;23(1):1031 (No. 405.15).

[55] Kandel ER, O'Dell TJ. Are adult learning mechanisms also used for development? Sci 1992;258:243–5.

[56] Kapadia MK, Ito M, Gilbert CD, Westheimer G. Improvement in visual sensitivity by changes in local context: parallel studies in human observers and in V1 of alert monkeys. Neuron 1995;15: 843–56.

[57] Kelly FJ, Grossberg S. Neural dynamics of 3-D surface perception: Figure–ground separation and lightness perception. Percept & Psychophy 2000;62:1596–619.

[58] Kisvarday ZF, Cowey A, Smith AD, Somogyi P. Interlaminar and lateral excitatory amino acid connections in the striate cortex of monkey. J Neurosci 1989;9:667–82.

[59] Knierim JJ, van Essen DC. Neuronal responses to static texture patterns in area V1 of the alert macaque monkey. J Neurophysiol 1992;67:961–80.

[60] Lamme VAF. The neurophysiology of figure–ground segregation in primary visual cortex. J Neurosci 1998;15:1605–15.

[61] Lesher GW, Mingolla E. The role of edges and line-ends in illusory contour formation. Vis Res 1993;33:2253–70.

[62] Li Z. A neural model of contour integration in the primary visual cortex. Neural Comput 1998;10:903–40.

[63] Löwel S, Singer W. Neuronal responses to static texture patterns in area V1 of the alert macaque monkey. J Neurophysiol 1992;67:961–80.

[64] Luck S, Chelazzi L, Hillyard SA, Desimone R. Neural mechanisms of spatial selective attention in areas V1, V2, and V4 of macaque visual cortex. J Neurophysiol 1997;77:24–42.

[65] Lund JS, Boothe RG. Interlaminar connections and pyramidal neuron organisation in the visual cortex, area 17, of the macaque monkey. J Comp Neuro 1975;159:305–34.

[66] Martin JH. Neuroanatomy: text and atlas. Norwalk: Appleton and Lange, 1989.

[67] McGuire BA, Hornung JP, Gilbert CD, Wiesel TN. Patterns of synaptic input to layer 4 of cat striate cortex. J Neurosci 1984;4:3021–33.

[68] McLoughlin NP, Grossberg S. Cortical computation of stereo disparity. Vis Res 1998;38:91–9.

[69] Moore CM, Egeth H. Perception without attention: Evidence of grouping under conditions of inattention. J Exp Psych: Human Percept and Perform 1997;23:339–52.

[70] Moore CM, Yanstis S, Vaughan B. Object-based visual selection: evidence from perceptual completion. Psychol Sci 1998;9:104–10.

[71] Mountcastle VB. Modality and topographic properties of single neurons of cat somatic sensory cortex. J Neurophysiol 1957; 20:408–34.

[72] Mumford D. On the computational architecture of the neocortex. II. The role of cortico-cortical loops. Bio Cybernet 1992:241–51.

[73] Neumann H, Sepp W. Recurrent V1–V2 interaction in early visual boundary processing. Bio Cybernet 1999;81:425–44.

[74] Olshausen BA, Anderson CH, Van Essen DC. A neurobiological model of visual attention and invariant pattern recognition based on dynamic routing of information. J Neurosci 1993;13:4700–19.

[75] Peterhans E, von der Heydt R. Mechanisms of contour perception in monkey visual cortex. II. Contours bridging gaps. J Neurosci 1989;9:1749–63.

[76] Polat U, Mizobe K, Petter MW, Masamatsu T, Norcia AM. Collinear stimuli regulate visual responses depending on cells-contrast threshold. Nat 1998;391:580–4.

[77] Polat U, Sagi D. Lateral interactions between spatial channels: suppression and facilitation revealed by lateral masking experiments. Vis Res 1993;33:993–9.

[78] Posner MI. Orienting of attention. Quarterly J Exp Psych 1980; 32:3–25.

[79] Raizada RDS, Grossberg S. Context-sensitive binding by the laminar cicuits of V1 and V2: a unified model of perceptual grouping, attention, and orientation contrast. Vis Cog 2001, in press.

[80] Rao RPN, Ballard DH. Predictive coding in the visual cortex: A functionaal interpretation of some extra-classical receptive field effects. Nat Neurosci 1999;2:79–87.

[81] Redies C, Crook JM, Creutzfeldt OD. Neural responses to borders with and without luminance gradients in cat visual cortex and dLGN. Exp Brain Res 1986;61:469–81.

[82] Reynolds J, Chelazzi L, Desimone R. Competitive mechanisms subserve attention in macaque areas V2 and V4. J Neurosci 1999;19:1736–53.

[83] Rockland KS, Virga A. Terminal arbors of individual 'feedback' axons projecting from area V2 to V1 in the macaque monkey: a study using immunohistochemistry of anterogradely transported phaseolus vulgaris-leucoagglutinin. J Comp Neurol 1989;285:54–72.

[84] Roelfsema PR, Lamme VAF, Spekreijse H. Object-based attention in the primary visual cortex of the macaque monkey. Nat 1998; 395:376–81.

[85] Ruthazer ES, Stryker MP. The role of activity in the development of long-range horizontal connections in area 17 of the ferret. J Neurosci 1996;15:7253–69.

[86] Schmidt KE, Schlote W, Bratzke H, Rauen T, Singer W, Galuske RAW. Patterns of long range intrinsic connectivity in auditory and language areas of the human temporal cortex. Soc Neurosci Abstracts 1997;23(1):1058 (No. 415.13).

[87] Shipley TF, Kellman PJ. Strength of visual interpolation depends on the ratio of physically specified to total edge length. Percept & Psychophy 1992;52:97–106.

[88] Sillito AM, Jones HE, Gerstein GL, West DC. Feature-linked synchronization of thalamic relay cell firing induced by feedback from the visual cortex. Nat 1994;369:479–82.

[89] Somers DC, Todorov EV, Siapas AG, Toth LJ, Kim D, Sur M. A local circuit approach to understanding integration of long-range inputs in primary visual cortex. Cereb Cortex 1998;8:204–17.

[90] Stemmler M, Usher M, Niebur E. Lateral interactions in primary visual cortex: A model bridging physiology and psychophysics. Sci 1995;269:1877–80.

[91] Stratford KJ, Tarczy-Hornoch K, Martin KAC, Bannister NJ, Jack JJB. Excitatory synaptic inputs to spiny stellate cells in cat visual cortex. Nat 1996;382:258–61.

[92] Thorpe S, Fize D, Marlot C. Speed of processing in the human visual system. Nat 1996;381:520–2.

[93] Tsotsos J, Culhane S, Wai W, Lai Y, Davis N, Nuflo F. Modeling visual attention via selective tuning. Artificial Intell 1995;78:507–47.

[94] Ullman S. Sequence seeking and counter streams: a computational model for bidirectional information flow in the visual cortex. Cereb Cortex 1995;5:1–11.

[95] Usher M, Niebur E. Modeling the temporal dynamics of IT neurons in visual search: A mechanism for top-down selective attention. J Cog Neurosci 1996;8:311–27.

[96] Van Essen DC, Maunsell JHR. Hierarchical organization and functional streams in the visual cortex. Trends Neurosci 1983;6:370–5.

[97] Von der Heydt R, Peterhans E, Baumgartner G. Illusory contours and cortical neuron responses. Sci 1984;224:1260–2.

[98] Williams LR, Jacobs DW. Stochastic completion fields: A neural model of illusory contour shape and salience. Neural Comput 1997;9:837–58.

[99] Yen SC, Finkel LH. Extraction of perceptually salient contours by striate cortical networks. Vis Res 1998;38:719–41.

[100] Zeki S, Shipp S. The functional logic of cortical connections. Nat 1988;335:311–7.