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Linking Visual Development and Learning to Information Processing: Preattentive and Attentive Brain Dynamics

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Stephen Grossberg

December, 2004

Technical Report CAS/CNS-2004-017

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**Linking Visual Development and Learning to Information Processing:
Preattentive and Attentive Brain Dynamics**

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Invited article for

Plasticity in the Visual System: From Genes to Circuits

Peter De Weerd, Raphael Pinaud and Liisa Tremere, Eds.

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Introduction. Vision research is such a large and vigorous field that it has often advanced through parallel but non-interacting streams of work. Visual development has often been studied separately from adult visual perception. Even studies of adult perceptual learning have often not made contact with other studies of how vision works, and many psychophysical studies have been done without regard to their neurobiological mechanisms. Recently, theoretical advances in understanding the functional organization of visual cortex have begun to synthesize such parallel efforts into a unifying theoretical framework that has disclosed many new issues and, with them, ideas for novel types of experiments. This emerging framework has begun to clarify how the visual cortex autonomously develops, stabilizes its own development, and then gives rise to visual perception in the adult. A rapidly developing cortical model links processes of development in the infant to processes of perception and learning in the adult. This model sheds new light on how cortical circuits can be shaped by environmental statistics, and proposes how the cortex embodies more powerful and subtle computational principles than the Bayesian learning approaches that have recently gained such popularity; e.g., Kersten, Mamassian and Yuille (2004). In particular, the model clarifies the role of attention in learning, and also suggests when attention may not be needed for learning to occur. Cortical computation, I would claim, enables the brain to self-organize in response to ever-changing environmental statistics in a way that the priors and stationary probabilities of Bayesian thinking cannot fully capture. The present article summarizes some of these recent developments.

This emerging model of visual cortical dynamics, called the LAMINART model (Grossberg, 1999a; Grossberg and Howe, 2003; Grossberg, Mingolla, and Ross, 1997; Grossberg and Raizada, 2000; Raizada and Grossberg, 2001, 2003), suggests how the layered circuits of visual cortex interact to control cortical development and learning, notably how bottom-up, horizontal, and top-down circuits interact to control the formation of perceptual boundaries, or groupings. These studies include analyses of how the cortical layers develop their receptive field properties in a coordinated manner, how grouping and attentional circuits develop within these layers, and how cortical circuits embody statistical environmental constraints that support 3D vision (Grossberg and Seitz, 2003; Grossberg and Swaminathan, 2004; Grossberg and Williamson, 2001). The LAMINART models have hereby clarified how both pre-attentive and attentive feedback interactions may influence cortical development and learning (Grossberg, 1999a, 2003a). Related studies have clarified how learning tunes interactions between boundary circuits and the circuits that control the formation of perceptual surfaces. Indeed, properties of the well-known McCollough effect, or long-term orientation-specific color adaptation, have been traced to such learned boundary/surface interactions (Grossberg, Hwang, and Mingolla, 2002).

Computing with Boundaries and Surfaces. One reason for the disconnect between studies of visual development and learning and of adult visual perception has been insufficient understanding of the functional units that support adult visual perception. During the past two decades, experimental and theoretical evidence have provided increasing support for the prediction that the visual cortex builds percepts of object form using three-dimensional representations of perceptual *boundaries* and *surfaces*, notably representations that can separate figures from their backgrounds and complete the representations of partially occluded objects. It has been proposed that these boundary and surface representations are computed within the interblob and blob streams, respectively, between cortical areas V1 to V4 (see Grossberg (1994) for a review). These representations, in turn, are predicted to be the functional units that project to higher levels of the brain, notably inferotemporal and prefrontal cortex, where they are

categorized, or unitized, into object representations. All of these cortical areas and their representations are, moreover, linked with each other through feedback pathways.

Early modeling studies that identified boundaries and surfaces as basic perceptual units and suggested how they are computed by visual cortex were provided by the author and his colleagues; e.g., Cohen and Grossberg (1984), Grossberg (1984, 1987a, 1987b), Grossberg and Mingolla (1985a, 1985b), Grossberg and Todorovic (1988). Since that time, many experiments have lent support to this hypothesis (see Grossberg (1994, 1997) for reviews), and many authors have further modeled these boundary and surface processes; e.g., Cao and Grossberg, 2004; Douglas *et al.* (1995), Finkel and Edelman (1989), Grossberg (1994, 1997), Grossberg, Hwang, and Mingolla (2002), Grossberg and Howe (2003), Grossberg and Kelly (1999), Grossberg and McLoughlin (1997), Grossberg and Pessoa (1998), Grossberg and Yazdanbakhsh, 2004; Heitger *et al.* (1998), Kelly and Grossberg (2000), Li (1998), McLoughlin and Grossberg (1998), Mumford (1992), Pessoa, Mingolla, and Neumann (1995), Somers, Nelson and Sur (1995), Stemmler, Usher and Niebur (1995), and Ullman (1995). A parallel processing stream, through cortical area MT, helps to compute object motion and cues useful for visual navigation. A neural model of motion processing, called the 3D FORMOTION model, has been progressively developed by Chey, Grossberg, and Mingolla (1997, 1998), Grossberg, Mingolla, and Viswanathan (2001), and Berzhanskaya, Grossberg, and Mingolla (2004) but will not be further discussed in this chapter, except to mention one of its key untested predictions: The circuits in cortical areas MT/MST that help to accomplish pre-attentive motion capture are the same ones that carry out attentive motion-direction priming. This prediction is a variant of the *preattentive-attentive interface* prediction that is further discussed herein for the processing of visual form.

Development and Learning in Laminar Circuits for Filtering, Grouping, and Attention.

This chapter will first discuss aspects of how the visual cortex generates the perceptual boundaries that go into representations of visual object form. This process is also known as *perceptual grouping*, or the *binding problem*. These perceptual grouping processes already play an important role in how infants perceive the world. For example, neonates appear to perceive a partly occluded object as disjoint parts. The ability to process these fragments as coherent objects via perceptual grouping develops rapidly within the first two to four months of life (Kellman and Spelke, 1983; Johnson and Aslin, 1996; Johnson, 2001).

The LAMINART model clarifies how perceptual grouping circuits develop and learn, thereby giving rise to cortical circuits that are capable of explaining data about adult visual perception. A central issue in cortical development and learning concerns the *stability* of these processes; namely, how do cortical circuits protect previous development and learning from large-scale overwriting and obliteration by the changing statistics of inputs from the world? The same problem arises during adult learning. I call this problem the “stability-plasticity dilemma” since the brain needs to *balance* cortical plasticity and stability (e.g., Grossberg, 1980, 1982): The brain needs to adapt rapidly enough to improve survival chances, yet not just as rapidly erase useful memories in response to changing environmental inputs. This problem has since often been called the problem of “catastrophic forgetting”. Catastrophic forgetting does not refer to the controlled refinement and adjustment of circuits in response to fluctuations in environmental statistics. Such refinement is often important for successful behavior. Rather, it refers to large-scale erasure of still useful cortical circuit properties. Most neural models, such as the popular back propagation model (see Grossberg (1988) for a review), indeed all feedforward

neural models, experience catastrophic forgetting, unless they arbitrarily shut down their plasticity as time unfolds.

The LAMINART model proposes neural mechanisms that enable developing cortical circuits to dynamically stabilize themselves using properties of their self-organized circuit interactions. Remarkably, the same processes which help to stabilize development seem to control properties in the adult of perceptual grouping, attention, and learning. Many useful implications follow from this observation. One is that the laws of adult perception are strongly constrained by stability constraints on infant development. Another is that even early stages of visual cortical processing actively carry out such “emergent” processes as perceptual grouping and attentional selection.

The LAMINART model further clarifies why visual cortex, indeed all neocortex, is organized into layered circuits. This laminar organization is predicted to realize at least three interacting processes: (1) the developmental and learning processes whereby the cortex shapes its circuits to match environmental constraints in a *stable* way through time; (2) the binding process whereby cortex groups distributed data into coherent object representations that remain sensitive to analog properties of the environment (the property of “analog coherence”); and (3) the attentional process whereby cortex selectively processes important events. The model proposes that the mechanisms which achieve property (1) imply properties of (2) and (3). The LAMINART model also opens a path towards understanding how variations and specializations of these processes operate in other types of neocortex. This modeling perspective begins to unify three fields: infant cortical development, adult cortical neurophysiology and anatomy, and adult visual perception.

The model is called a LAMINART model because it clarifies how mechanisms of Adaptive Resonance Theory, or ART, can be realized within identified laminar cortical circuits. Earlier ART models were devoted to understanding how bottom-up and top-down cortical interactions work together to stably control cortical development, and learning during perception, and cognition. Although these studies successfully explained and predicted various behavioral and brain data, they did not show how these processes are realized within laminar cortical circuits. Grossberg (1999b) reviews some of these ART concepts and various data that they can explain. The LAMINART model extends these results by proposing how bottom-up, top-down, and *horizontal* interactions work together in *laminar* cortical circuits, and how they unify processes of development, learning, 3D grouping, and attention. LAMINART hereby joins concepts about ART learning and attention with concepts about perceptual grouping. This innovation was introduced in Grossberg (1999a).

Balancing Cortical Excitation and Inhibition: Stability, Intermittency, and Synchrony.

Subsequent work on the LAMINART model has clarified how excitatory and inhibitory connections in the cortex can develop stably by maintaining a *balance* between excitation and inhibition in multiple cortical circuits (Grossberg and Williamson, 2001). It is known, for example, that long-range excitatory horizontal connections between pyramidal cells in layer 2/3 of visual cortical areas play an important role in perceptual grouping (Figure 1). The model proposes how the laws that govern cortical development enable the strength of these long-range excitatory horizontal connections to be (approximately) balanced against the strength of short-range disynaptic inhibitory interneurons which input to the same target pyramidal cells. These balanced connections are proposed to realize properties of perceptual grouping in the adult. Figure 1 summarizes how these balanced connections enable perceptual groupings to form

between pairs, or greater numbers, of inducers in an image (the case of a Kanizsa square is here illustrated), but not outwardly from a single inducer, which would fill the percept with spurious boundaries.

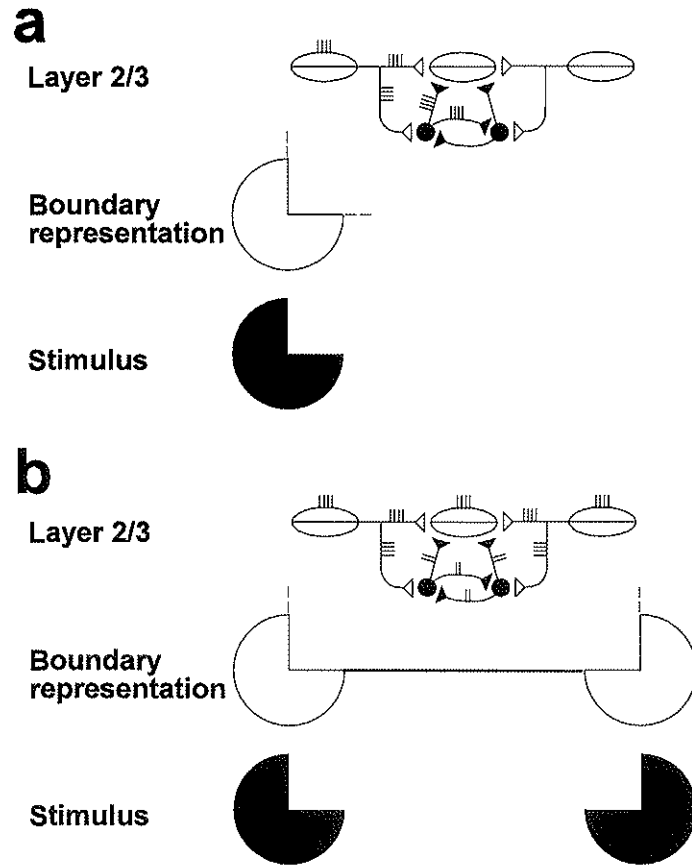


Figure 1. Schematic of the boundary grouping circuit in layer 2/3. Pyramidal cells with collinear, coaxial receptive fields (shown as ovals) excite each other via long-range horizontal axons (Bosking *et al.*, 1997; Schmidt *et al.*, 1997), which also give rise to short-range, disynaptic inhibition via pools of interneurons, shown filled-in black (McGuire *et al.*, 1991). This balance of excitation and inhibition helps to implement what we call the *bipole property*. **(a)** Illustration of how horizontal input coming in from just one side is insufficient to cause above-threshold excitation in a pyramidal cell (henceforth referred to as the target) whose receptive field does not itself receive any bottom-up input. The inducing stimulus (e.g. a Kanizsa ‘pacman’, shown here) excites the oriented receptive fields of layer 2/3 cells, which send out long-range horizontal excitation onto the target pyramidal. However, this excitation brings with it a commensurate amount of disynaptic inhibition. This creates a case of ‘one against one’, and the target pyramidal is not excited above-threshold. The boundary representation of the solitary pacman inducer produces only weak, sub-threshold collinear extensions (thin dashed lines). **(b)** When two collinearly aligned induced stimuli are present, one on each side of the target pyramidal’s receptive field, a boundary grouping can form. Long-range excitatory inputs fall onto the cell from both sides, and summate. However, these inputs fall onto a shared pool of inhibitory interneurons, which, as well as inhibiting the target pyramidal, also inhibit each other (Tamas, Somogyi and Buhl, 1998), thus normalizing the total amount of inhibition emanating from the interneuron pool, without any individual interneuron saturating. This summing excitation and normalizing inhibition together create a case of ‘two-against-one’, and the target pyramidal is excited above-threshold. This process occurs along the whole boundary grouping, which thereby becomes represented by a line of suprathreshold layer 2/3 cells (thick dotted line). Boundary strength scales in a graded analog manner with the strength of the inducing signals. [Reproduced with permission from Raizada and Grossberg (2001)].

The model also proposes that development enables the strength of excitatory connections from layer 6-to-4 is balanced against those of inhibitory interneuronal connections to the same layer 4 cells; see Figure 2. Due to this balance, the net excitatory effect of layer 6 on layer 4 is proposed to be modulatory. These (approximately) balanced excitatory and inhibitory connections exist within the on-center of an on-center off-surround network from layer 6-to-4. The off-surround cells can strongly inhibit their target cells, even though the on-center cells can only provide excitatory modulation of their target cells.

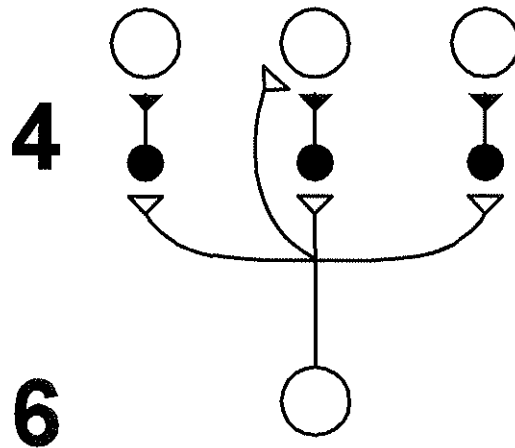


Figure 2. Schematic of the modulatory layer 6-to-layer 4 on-center off-surround path. Pyramidal cells in layer 6 give on-center excitation to layer 4 spiny stellates in the column above them, but also make medium-range connections onto layer 4 inhibitory interneurons, shown filled-in black (Ahmed *et al.*, 1997; McGuire *et al.*, 1984). These interneurons synapse onto the spiny stellates, creating a 6-to-4 off-surround, and also onto each other (connection not illustrated), thereby helping to normalize the total amount of inhibition (Ahmed *et al.*, 1997). Note that the 6-to-4 off-surround inhibition spatially overlaps with the excitatory on-center, with the consequence that the 6-to-4 excitation is inhibited down into being modulatory, *i.e.* priming or subthreshold (Callaway, 1998b; Stratford *et al.*, 1996). [Reproduced with permission from Raizada and Grossberg (2001)].

The model proposes how this layer 6-to-4 circuit functions as a “selection circuit” because it can help to select the groupings that enter conscious attention. Grouping cells in layer 2/3 can activate the layer 6-to-4 selection circuit via excitatory connections from layer 2/3 to layer 6; see Figure 3a. When ambiguous and complex scenes are being processed, many possible groupings can start to form using the horizontal connections within layer 2/3. The selection circuit enables the strongest groupings to inhibit weaker groupings via the 6-to-4 off-surrounds of the strongest groupings.

Top-down attention can bias this selection process, and thereby influence which groupings will enter conscious perception. In particular, it is proposed that top-down attentional signals from higher cortical areas, such as area V2, can also activate the layer 6-to-4 on-center off-surround network; see Figure 3b. This circuit is called a *folded feedback* circuit because the top-down feedback is “folded” into the bottom-up signal flow from layer 6-to-4. Attention can hereby modulate, or sensitize, cells in the attentional on-center, without fully activating them, because the excitatory and inhibitory signals in the on-center are balanced. Attention can also inhibit cells in the off-surround.

Because both grouping and attention share the same selection circuit, this anatomical arrangement enables attention to influence which groupings are selected. This circuit is called the

preattentive-attentive interface within the LAMINART model. Using this interface, attention can shift the excitatory/inhibitory balance that determines which groupings will enter consciousness. A dramatic example of this influence occurs when attention that is cast on one part of an object can flow selectively along the perceptual groupings that define the entire object. Roelfsema *et al.* (1998) have discovered such a flow of attention along a perceptual grouping during their neurophysiological recordings in macaque area V1. Because of this property, both infants and adults can focus their attention selectively upon whole objects, rather than just random subsets of visual features.

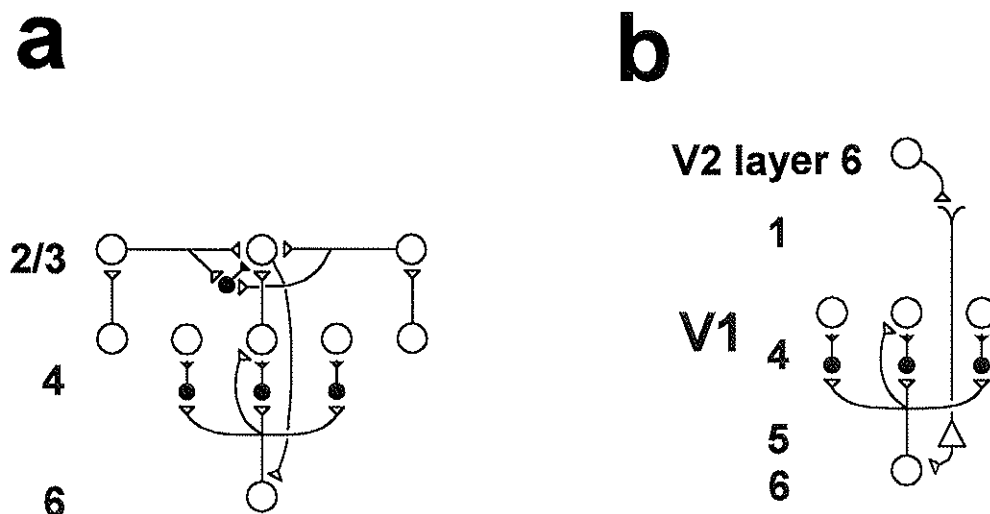


Figure 3. (a) Connecting the 6-to-4 on-center off-surround to the layer 2/3 grouping circuit: Like-oriented layer 4 simple cells with opposite contrast polarities compete (not shown) before generating half-wave rectified outputs that converge onto layer 2/3 complex cells in the column above them. Like attentional signals from higher cortex, groupings which form within layer 2/3 also send activation into the *folded feedback* path, to enhance their own positions in layer 4 beneath them via the 6→4 on-center, and to suppress input to other groupings via the 6to-4 off-surround. There exist direct layer 2/3-to-6 connections in macaque V1, as well as indirect routes via layer 5. (b) *Folded feedback* carries attentional signal from higher cortex into layer 4 of V1, via the modulatory 6→4 path. Corticocortical feedback axons tend preferentially to originate in layer 6 of the higher area and to terminate in the lower cortex's layer 1 (Salin and Bullier, 1995, p. 110), where they can excite the apical dendrites of layer 5 pyramidal cells whose axons send collaterals into layer 6. Several other routes through which feedback can pass into V1 layer exist. Having arrived in layer 6, the feedback is then 'folded' back up into the feedforward stream by passing through the 6-to-4 on-center off-surround path (Bullier *et al.*, 1996). [Reproduced with permission from Raizada and Grossberg (2001)].

The feedback circuits that govern the grouping and attentional selection processes are predicted to play a key role in helping to stabilize both development and adult learning within multiple cortical areas, including cortical areas V1 and V2. During development, the selection circuit (which itself is developing) helps to prevent the wrong combinations of cells from being co-activated, and thus from being associated, or wired, together. How this is predicted to happen will be discussed further in the next section.

Balanced excitatory and inhibitory connections help to explain the observed variability in the number and temporal distribution of spikes emitted by cortical neurons. Modeling studies have shown how balanced excitation and inhibition can produce the highly variable interspike intervals that are found in cortical data (Shadlen and Newsome, 1998; van Vreeswijk and

Sompolinsky, 1998). The LAMINART model suggests that such variability may reflect mechanisms that are needed to ensure stable development and learning by cortical circuits. Given that “stability implies variability,” the cortex is faced with the difficult problem that variable spikes are quite inefficient in driving responses from cortical neurons. When one analyses how these balanced excitatory and inhibitory connections generate perceptual groupings, it becomes clear that the grouping circuits automatically have the property of preferentially responding to synchronized inputs. Figure 1 illustrates why synchronously activated cells have a difficult time generating a perceptual grouping, whereas synchronously activated cells will not. According to Figure 1a, an asynchronous volley of horizontal signals from a single population of layer 2/3 cells will kill itself off due to balanced excitation and inhibition. According to Figure 1b, a synchronous volley from pairs of appropriately positioned cells will initiate grouping. Modeling studies have shown how both perceptual grouping and attentional circuits can actively resynchronize signals that have become partially desynchronized (Grossberg and Somers, 1991; Grossberg and Grunewald, 1997; Yazdanbakhsh and Grossberg, 2004). The model hereby discloses a previously unsuspected link between properties of stable development, adult learning, grouping, attention, and synchronous cortical processing.

The Link Between Attention and Learning: The Role of Adaptive Resonance. The solution that ART proposes to the stability-plasticity dilemma is to allow neural representations to be modified only by those incoming stimuli with which they form a sufficiently close match. If the match is close enough, then learning occurs. Precisely because the match is sufficiently close, this learning causes fine-tuning of the existing representation, rather than a radical overwriting. Matching gets started by initially endowing the top-down matching circuits with broadly distributed adaptive weights. Learning prunes these weights and makes them more selective. If the active neural representation does not match with the incoming stimulus, then its neural activity will be inhibited and hence unable to cause plastic changes. The network is designed so that inhibition of the initially active representation enables other representations to win the competition and become active instead. In other words, the network embodies a *search* mechanism that is typically realized by interacting matching and habituating processes (e.g., Carpenter and Grossberg, 1990; Grossberg and Seitz, 2003). Search either gives rise to a new match, thereby allowing learning, or a non-match, causing the search process to repeat until either a match is found or the incoming stimulus selects a totally new representation as a basis for learning.

A key mechanism that implements the matching process is top-down attentional feedback directed to behaviorally relevant sensory stimuli. The ART model predicted that top-down attentional signals exist that are expressed through a modulatory on-center off-surround network (Figure 3b), whose role is to select and enhance behaviorally relevant bottom-up sensory inputs (match), and suppress those that are irrelevant (non-match). Mutual excitation between the top-down feedback and the bottom-up signals that they match was predicted to amplify, synchronize, and maintain for a sufficient amount of time the matched neural activity pattern, thereby triggering learned synaptic changes. Thus, attentionally relevant stimuli are learned, while irrelevant stimuli are suppressed and hence prevented from destabilizing existing representations.

The attentional feedback pathway through layer 6-to-4 modulatory on-center off-surround network in the LAMINART model is predicted to implement ART matching in cortical laminar circuitry. The ART prediction raises two key questions: First, does top-down cortical

feedback have an on-center off-surround structure? Second, is there evidence that top-down feedback controls plasticity in the area to which it is directed?

The prediction that top-down attention has an on-center off-surround characteristic has received a considerable amount of psychological and neurobiological empirical confirmation in the visual system (Bullier *et al.*, 1996; Caputo and Guerra, 1998; Downing, 1988; Mounts, 2000; Reynolds, Chelazzi, and Desimone, 1999; Smith, Singh, and Greenlee, 2000; Somers *et al.*, 1999; Sillito *et al.*, 1994; Steinman, Steinman, and Lehmkuhle, 1995; Vanduffell, Tootell, and Orban, 2000). Based on such data, this conclusion has recently been restated, albeit without a precise anatomical realization, in terms of the concept of “biased competition” (Desimone, 1998; Kastner and Ungerleider, 2001), in which attention biases the competitive influences within the network. Feedback from auditory cortex to the medial geniculate nucleus (MGN) and the inferior colliculus (IC) also has an on-center off-surround form (Zhang *et al.*, 1997). Temereanca and Simons (2001) have produced reported a similar feedback scheme in the rodent barrel system.

The claim that bottom-up sensory activity is *enhanced* when matched by top-down signals is in accord with an extensive neurophysiological literature showing the facilitatory effect of attentional feedback (e.g., Luck *et al.*, 1997; Roelfsema, Lamme and Spekreijse, 1998) but not with models in which matches with top-down feedback cause suppression (e.g., Mumford, 1992; Rao and Ballard, 1999).

Recent data also support the ART claim that top-down feedback controls plasticity. Psychophysically, the role of attention in controlling adult plasticity and perceptual learning was demonstrated by Ahissar and Hochstein (1993). Neurophysiological evidence of Gao and Suga (1998) showed that acoustic stimuli caused plastic changes in the inferior colliculus of bats only when the IC received top-down feedback from auditory cortex. The authors also found that this plasticity is enhanced when the auditory stimuli were made behaviorally relevant, in accord with the ART proposal that top-down feedback allows attended—that is, relevant—stimuli to be learned, while suppressing unattended irrelevant ones. Evidence that cortical feedback also controls thalamic plasticity in the somatosensory system has been found by Nicolelis and colleagues (Krupa, Ghazanfar and Nicolelis, 1999) and by Parker and Dostrowsky (1999). Kaas (1999) reviews these findings.

Another predicted role of these feedback connections is to synchronize the firing patterns of higher and lower cortical areas. Given that “cells that fire together wire together”, synchronous firing of this sort would further increase the ability of the mutually excitatory resonant activity caused by ART matching to allow synaptic plasticity and learning to take place. It has elsewhere been shown that variants of the ART and LAMINART models are capable of rapidly synchronizing their activation patterns during both perceptual grouping and attentional focusing (Grossberg and Somers, 1991; Grossberg and Grunewald, 1997; Yazdanbakhsh and Grossberg, 2004). Recent discussions of top-down cortical feedback, synchrony, and how they support ART predictions are given by Engel, Fries, and Singer (2001), Fries *et al.*, (2001) and Pollen (1999).

Learning without Attention: The Role of Pre-attentive Resonance and Synchronization

The hypothesis that attentional feedback exerts a controlling influence over plasticity in sensory cortex does not imply that unattended stimuli can never be learned. Indeed, the LAMINART model has clarified how the stability of early development can be controlled, even before top-down attention may be able to modulate it (Grossberg, 1999a). During development, plastic changes in cortex are driven by stimuli that occur with high statistical regularity in the

environment (e.g., Grossberg and Swaminathan, 2004; Grossberg and Williamson, 2001). Given that there is experimental support for the ART prediction that top-down attention plays a matching role which helps to control cortical plasticity, how can we explain other data which, at the outset, seem to contradict this prediction by showing that perceptual learning can occur without attention under certain circumstances; e.g., Watanabe *et al.* (2001)? This issue can be understood by considering the following question: How can pre-attentive groupings form over positions that receive no bottom-up inputs, without destabilizing cortical development and learning?

This is an issue because, as described above, the ART matching rule has three aspects: First, incoming sensory signals that receive matching top-down excitatory feedback should be enhanced; second, non-matching inputs that do not receive excitatory feedback should be suppressed; and third, top-down feedback on its own should be only modulatory, that is, unable to produce above-threshold activity in the lower area in the absence of incoming bottom-up signals. The conceptual challenge is this: If ART matching is needed to stabilize cortical development and learning, and if ART matching requires that suprathreshold activation can occur only where there are bottom-up inputs, then does not the existence of illusory contours contradict the ART matching rule, since such groupings form over positions that receive no bottom-up inputs? Moreover, the horizontal connections that underlie such groupings are known to develop and learn in response to visual inputs, yet do not seem to destabilize cortical development or learning. How is this possible?

Here is where the laminar organization of the visual cortex, as conceptualized by the LAMINART model, offers a parsimonious and elegant solution by using the preattentive-attentive interface circuit that occurs between layers 6 and 4. When a horizontal grouping starts to form in layer 2/3, it also activates the *intracortical*, interlaminar feedback pathway from layer 2/3 to the modulatory on-center off-surround network from layer 6 to 4. This feedback pathway helps to select which cells will remain active to participate in a winning grouping. But this is the same network that ART requires attention to use when it stabilizes cortical development and learning. In other words, the layer 6-to-4 selection circuit, which in the adult helps to choose winning groupings, is also predicted, during brain development and learning, to ensure that the ART matching rule holds at every position along a grouping, including positions that receive no bottom-up input. Because the matching rule holds, only the correct combinations of cells can “fire together and wire together”, and hence stability is maintained. *Intracortical* feedback via layers 2/3-to-6-to-4-to-2/3 can realize this selection process even before *intercortical* attentional feedback can develop. This property is sometimes summarized with the phrase: “The pre-attentive grouping is its own attentional prime” (Grossberg, 1999a).

Experiments such as those of Watanabe *et al.* (2001) can be explained by noting that the pre-attentive resonances that support unattended learning are not inhibited by the attentive resonances that are activated by the experimental task. Indeed, in these experiments, a form identification task at the center of gaze attracts attention, whereas unattended perceptual learning of motion direction occurs at peripheral locations. These experiments illustrate that attentive resonance can influence learning at certain locations in the What stream (the form stimulus) even as pre-attentive resonance may influence learning at disjoint locations in the Where stream (the motion stimulus). Said in another way, the LAMINART model predicts that this experiment was cleverly set up so that the inhibitory effects of attention did not suppress some pre-attentive resonances at disjoint positions. Further tests of this hypothesis would systematically vary how much attentive inhibition would be expected to suppress learning in such non-attended locations.

Beyond Bayes: Self-Organizing Feedforward/Feedback and Digital/Analog Decisions. The LAMINART model brings into focus several new problems and proposed solutions thereof about the dynamics of cortical processing, including predicted links between balanced excitation and inhibition, synchrony, resonance, attention, and learning. The LAMINART model embodies a novel way to compute in several other senses as well, which illustrate my assertion that cortical dynamics are not adequately conceptualized by traditional concepts such as Bayesian computing. I claim that cortical computation represents a new type of hybrid between feedforward and feedback computing, and also between digital and analog computing for processing perceptual groupings as well as other types of distributed data. The LAMINART model predicts that these properties allow the fast but stable self-organization that is characteristic of cortical development and life-long learning.

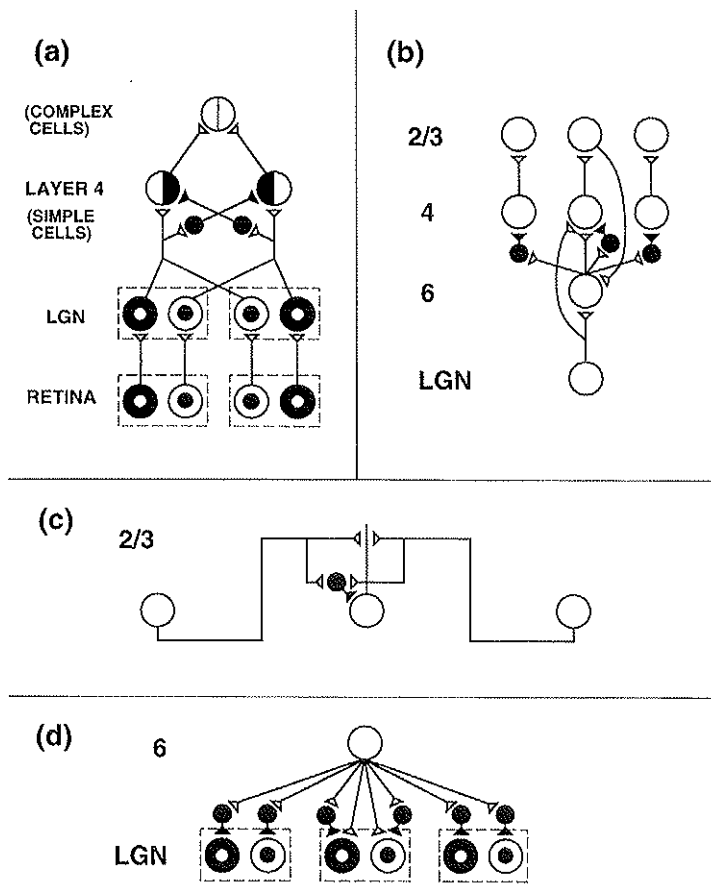


Figure 4. The adult network of retinal, V1, and lateral geniculate nucleus (LGN) neurons to which the developmental model converges: **(a)** Feedforward circuit from retina to LGN to cortical layer 4. **Retina:** Retinal ON cells have on-center off-surround organization (white disk surrounded by black annulus). Retinal OFF cells have an off-center on-surround organization (black disk surrounded by white annulus). **LGN:** The LGN ON and OFF cells receive feedforward ON and OFF cell inputs from the retina. **Layer 4:** LGN ON and OFF cell excitatory inputs to layer 4 establish oriented simple cell receptive fields. Like-oriented oriented layer 4 simple cells with opposite contrast polarities compete before generating half-wave rectified outputs. Pooled simple cell outputs enable complex cells to respond to both polarities. They hereby full-wave rectify the image. See text for details. **(b)** Cortical feedback loop between layers 4, 2/3, and 6: LGN activates layer 6 as well as layer 4. Layer 6 cells excite layer 4 cells with a narrow on-center and inhibit them using layer 4 inhibitory interneurons that span a broader off-surround. Layer 4 cells excite layer 2/3 cells, which send excitatory feedback signals back to layer 6 cells via

layer 5 (not shown). Layer 2/3 can hereby activate the feedforward layer 6-to-4 on-center off-surround network. **(c)** The horizontal interactions in layer 2/3 that initiate perceptual grouping: Layer 2/3 complex pyramidal cells monosynaptically excite one another via horizontal connections, primarily on their apical dendrites. They also inhibit one another via disinaptic inhibition that is mediated by model smooth stellate cells. Together these interactions can realize the “bipole property” which enables groupings to form inwardly across the space between two or more inducers, but not outwardly from a single inducer. **(d)** Top-down corticogeniculate feedback from layer 6: LGN ON and OFF cells receive topographic excitatory feedback from layer 6, 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. See the text for further details. [Reproduced with permission from Grossberg and Williamson (2001)].

The new hybrid between feedforward and feedback processing works as follows: When an unambiguous scene is processed, the LAMINART model can quickly group the scene in a fast feedforward sweep of activation that passes directly through layer 4 to 2/3 and then on to layers 4 to 2/3 in subsequent cortical areas (see Figures 3 and 4). This property clarifies how recognition can be so fast in response to unambiguous scenes; e.g., Thorpe *et al.* (1996). On the other hand, if there are multiple possible groupings in a scene, as in a complex textured scene, then competition among these possibilities due to inhibitory interactions in layers 4 and 2/3 can cause all cell activities to become smaller. This happens because the competitive circuits in the model are *self-normalizing*; that is, they tend to conserve the total activity of the circuit: When some activities get bigger, others must get smaller. This self-normalizing property is related to the ability of the shunting on-center off-surround networks that realize these competitive circuits to realize the property of *contrast normalization*; that is, to process input contrasts over a large dynamic range without saturation (Douglas *et al.*, 1995; Grossberg, 1973, 1980; Heeger, 1992). In other words, these self-normalizing circuits carry out a type of real-time probability theory in which the amplitude of cell activity covaries with the certainty of the network's selection, or decision, about a grouping.

Cell activation amplitude is, in turn, translated into processing speed. Low activation greatly slows down the feedforward processing in the circuit because it takes longer for cell activities to exceed output thresholds and to activate subsequent cells above threshold. In the model, network uncertainty is resolved through feedback: Weakly active layer 2/3 grouping cells feed back signals to layers 6-then-4-then-2/3 to close an intracortical cortical feedback loop that rapidly contrast enhances and amplifies the winning grouping. This is the feedback circuit that embodies the prediction that "The pre-attentive grouping is its own attentional prime", and thus the circuit that is predicted to stabilize cortical development and learning when attention is not available. As the winner is selected, and weaker groupings are suppressed, its cells become more active, hence can again rapidly send the cortical decision to subsequent processing stages.

In summary, the LAMINART circuit behaves like a real-time probabilistic decision circuit that operates in a fast feedforward mode when there is little uncertainty, and automatically switches to a slower feedback mode when there is uncertainty. Feedback selects a winning decision that enables the circuit to speed up again. In all, activation amplitude and processing speed both increase with certainty. The large activation amplitude of a winning grouping is facilitated by the synchronization that occurs as the winning grouping is selected. Bayes may be able to compute probabilities whose values embody variable degrees of uncertainty, but does not have the power to self-time decision-making until contentions are automatically resolved.

The LAMINART circuit also embodies a novel kind of hybrid computing that simultaneously realizes the stability of digital computing and the sensitivity of analog computing. This is true because the feedback loop between layers 2/3-6-4/-2/3 that selects or confirms a winning grouping has the property of *analog coherence* (Grossberg, 1999a; Grossberg, Mingolla, and Ross, 1997; Grossberg and Raizada, 2000; Yazdanbakhsh and Grossberg, 2004); namely, this feedback loop can synchronously store a winning grouping without losing analog sensitivity to amplitude differences in the input pattern. The coherence that is derived from synchronous storage in the feedback loop provides the stability of digital computing, while preserving the sensitivity of analog computation. Bayes may be able to compute the analog values of its probabilities, but does not have the coherence needed to bind them together into emergent perceptually meaningful structures, indeed structures that can spontaneously complete missing information, as in the case of illusory contours.

All of these properties are predicted to be a manifestation of the ability of cortical laminar circuits to stabilize development and learning using the *intracortical* feedback loop between layers 2/3-6-4-2/3 by selecting cells that fire together to wire together. The same *intracortical* decision circuit is predicted to help stabilize development in the infant and learning throughout life, as well as to select winning groupings in the adult (Grossberg, 1999a). Thus, properties of perceptual grouping in the adult are predicted to be constrained by the requirements of stable development in the infant. This intracortical circuit can work even before *intercortical* attentional feedback can develop to also stabilize cortical development and learning. Bayesian learning typically requires that priors and stationary probabilities exist. In contrast, LAMINART circuits are designed to develop and learn in a stable way in response to changing world statistics.

Development of Perceptual Grouping and Learning Circuits. Three types of quantitative modeling studies support the conclusions drawn in this article. These models are more extensively reviewed in Grossberg (2003b). One type of study concerns how horizontal and interlaminar connections develop within cortical layers 2/3, 4, and 6 in cortical area V1, and by extension to V2 and higher cortical regions (Grossberg and Swaminathan, 2004; Grossberg and Williamson, 2001). These interactions are often cited as the basis of "non-classical" receptive fields that are sensitive to the context in which individual features are found (von der Heydt, Peterhans, and Baumgartner, 1984; Peterhans and von der Heydt, 1989; Born and Tootell, 1991; Knierim and van Essen, 1992). In these modeling studies, it was assumed that receptive fields of individual simple and complex cells in layers 4 and 2/3, respectively, have already substantially developed. Grossberg and Williamson (2001) simulated development of the layer 2/3 horizontal connections that carry out collinear perceptual grouping, and the layer 6-to-4 inhibitory connections that control the preattentive-attentive interface, using the model summarized in Figure 4. Grossberg and Swaminathan (2004) simulated how the same laws of cortical development that lead to bipole cell connections for colinear grouping within a single depth can also lead to the development of angle cells (Hedge and Van Essen, 2000; Shevelev, 1998) and disparity gradient cells (Hinkle and Connor, 2001; Thomas, Cumming, and Parker, 2002) that span multiple depths. The different types of cells develop in response to different feature combinations in the visual environment. This study also showed how interactions among the angle cells and disparity gradient cells can contextually disambiguate locally ambiguous visual cells to form unambiguous boundary and surface representations of 3D slanted and curved objects, including percepts of bistable Necker cubes.

The second model (Olson and Grossberg, 1998) investigated the question of how cortical area V1 develops simple cells that respond to different eyes or different orientations at different positions on the retina within the familiar cortical maps of orientation and ocular dominance (Hubel and Wiesel, 1962, 1963, 1968). This organization is called a *map* because cell tuning to orientation and ocular dominance varies in a systematic way as the cortex is traversed in a horizontal direction. Such maps exhibit properties that are called singularities, fractures, and linear zones (Blasdel, 1992a, 1992b; Obeymeyer and Blasdel, 1993). The model showed how these features of cortical maps develop. A number of earlier models also studied how simple cells develop their orientationally tuned receptive fields within maps of orientation and ocular dominance (e.g., von der Malsburg, 1973; Grossberg, 1976a; Willshaw and von der Malsburg, 1976; Swindale, 1980, 1982, 1992; Linsker, 1986a, 1986b; Rojer and Schwartz, 1989, 1990; Durbin and Mitchison, 1990; Obermayer, Ritter and Schulten, 1990, Obermayer, Blasdel and Schulten, 1992; Miller, 1992, 1994; Grossberg and Olson, 1994; Sirosh and Miikkulainen, 1994).

The Olson and Grossberg (1998) model showed, in addition, how nearby pairs of simple cells develop that are sensitive to the same orientation but opposite contrast polarities (Liu *et al.*, 1992). Such a model is called a *Triple-O Map* model because it shows how Orientation, Ocular Dominance, and Opposite Contrast Polarities all develop together. Earlier models were either Single-O or Double-O Map models, and many did not represent the dynamics of the cells whose connections were undergoing development. The Triple-O model clarifies how nearby simple cells that are sensitive to opposite contrast polarities could, in principle, cooperate to activate a shared complex cell.

The third model proposed how nearby pairs of simple cells that are sensitive to opposite contrast polarities develop connections to shared complex cells (Grunewald and Grossberg, 1998). In addition to being tuned to position, size, orientation, and pooled contrast polarities, the complex cells in the model, and *in vivo*, are also tuned to binocular disparity, which is a well-known cue to object depth (Julesz, 1971). These complex cell properties help to explain how depth-sensitive perceptual groupings can form over objects that are seen in front of textured backgrounds, and also how figure-ground properties emerge (Grossberg, 1994). A key question for this model concerned how oppositely polarized simple cells, whose activations are *anti-correlated* in time (if a contrast at a given position is dark-to-light, it cannot also be light-to-dark, and conversely), can nonetheless develop connections to a shared complex cell, and thereby become *correlated*.

Grossberg and Seitz (2003) began to unify these three types of models into a more comprehensive model of how cortical development of cells occurs in a coordinated manner across cell layers, guided by signals from the cortical subplate.

Several mechanisms in addition to those summarized in the preceding sections play a role in these models of cortical development. One mechanism causes *antagonist rebounds* to occur between simple cells that are sensitive to opposite contrast polarities but the same positions and orientations. For example, when a simple cell that has been on for awhile in response to a dark-to-light contrast shuts off, an opponent simple cell, that is sensitive to a light-to-dark contrast, briefly turns on. Such rebounds are proposed to be due to the chemical transmitters that carry signals between model cells. These transmitters habituate, or inactivate, when they are released by signals in their pathways, or axons (Abbott, Varela, Sen, and Nelson, 1997; Francis, Grossberg, and Mingolla, 1994; Grossberg, 1972). Such habituating transmitters play a role in the models of how simple cell maps develop (they help the map to form by preventing the developmental process from getting “stuck” in representations that develop soonest), how complex cells get activated by oppositely polarized simple cells (a rebounding simple cell can get correlated with an active complex cell that was initially activated by a simple cell of opposite contrast polarity), and how bistable percepts can occur in the adult (when two representations activate competitive processes in a balanced way, the one that wins habituates and enables the other to win later), notably percepts of bistable Necker cubes.

Grunewald and Grossberg (1998) also modeled how learned feedback from cortical area V1 to the LGN may carry out a matching process that helps to stabilize the development of disparity tuning in cortical complex cells and, by extension, the cortical map itself; see Figure 4d. This V1-to-LGN feedback is homologous to the attentional feedback that is proposed to occur from cortical area V2 to V1 (Figure 3b), and by extension other cortical areas as well. These model interactions clarify how complex cells can binocularly match left and right eye image features with the same contrast polarity, yet can also pool signals with opposite contrast

polarities, consistent with psychophysical and neurobiological data about adult 3D vision; e.g., Cao and Grossberg (2004) and Grossberg and Howe (2003).

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