

CHAPTER 6

Towards a unified theory of neocortex: laminar cortical circuits for vision and cognition

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Abstract: A key goal of computational neuroscience is to link brain mechanisms to behavioral functions. The present article describes recent progress towards explaining how laminar neocortical circuits give rise to biological intelligence. These circuits embody two new and revolutionary computational paradigms: Complementary Computing and Laminar Computing. Circuit properties include a novel synthesis of feedforward and feedback processing, of digital and analog processing, and of preattentive and attentive processing. This synthesis clarifies the appeal of Bayesian approaches but has a far greater predictive range that naturally extends to self-organizing processes. Examples from vision and cognition are summarized. A LAMINART architecture unifies properties of visual development, learning, perceptual grouping, attention, and 3D vision. A key modeling theme is that the mechanisms which enable development and learning to occur in a stable way imply properties of adult behavior. It is noted how higher-order attentional constraints can influence multiple cortical regions, and how spatial and object attention work together to learn view-invariant object categories. In particular, a form-fitting spatial attentional shroud can allow an emerging view-invariant object category to remain active while multiple view categories are associated with it during sequences of saccadic eye movements. Finally, the chapter summarizes recent work on the LIST PARSE model of cognitive information processing by the laminar circuits of prefrontal cortex. LIST PARSE models the short-term storage of event sequences in working memory, their unitization through learning into sequence, or list, chunks, and their read-out in planned sequential performance that is under volitional control. LIST PARSE provides a laminar embodiment of Item and Order working memories, also called Competitive Queuing models, that have been supported by both psychophysical and neurobiological data. These examples show how variations of a common laminar cortical design can embody properties of visual and cognitive intelligence that seem, at least on the surface, to be mechanistically unrelated.

Keywords: neocortex; laminar circuits; learning; grouping; attention; 3D vision; working memory; categorization; V1; V2; V4; prefrontal cortex

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Introduction

Although there has been enormous experimental and theoretical progress on understanding brain or mind in the fields of neuroscience and psychology, establishing a mechanistic link between them has been very difficult, if only because these two levels of description often seem to be so different. Yet establishing a link between brain and mind is crucial in any mature theory of how a brain or mind works. Without such a link, the mechanisms of the brain have no functional significance, and the functions of behavior have no mechanistic explanation. Throughout the history of psychology and neuroscience, some researchers have tried to establish such a link by the use of metaphors or the application of classical concepts to the brain. These have included hydraulic systems, digital computers, holograms, control theory circuits, and Bayesian networks, to name a few. None of these approaches has managed to explicate the unique design principles and mechanisms that characterize biological intelligence. The present chapter summarizes aspects of a rapidly developing theory of neocortex that links explanations of behavioral functions to underlying biophysical, neurophysiological, and anatomical mechanisms. Progress has been particularly rapid towards understanding how the laminar circuits of visual cortex see (Grossberg et al., 1997; Grossberg, 1999a, 2003a; Grossberg and Raizada, 2000; Raizada and Grossberg, 2001, 2003; Grossberg and Howe, 2003; Grossberg and Seitz, 2003; Grossberg and Swaminathan, 2004; Yazdanbakhsh and Grossberg, 2004; Cao and Grossberg, 2005; Grossberg and Yazdanbakhsh, 2005; Grossberg and Hong, 2006).

This progress illustrates the introduction of qualitatively new computational paradigms, as might have been expected, given how long these problems have remained unsolved. These results overcome a conceptual impasse that is illustrated by the popular proposal that our brains possess independent modules, as in a digital computer. The brain's organization into distinct anatomical areas and processing streams supports the idea that brain processing is specialized, but that, in itself, does not imply that these streams contain independent modules. This hypothesis gained

dominance despite the fact that much behavioral data argue against independent modules. For example, during visual perception, strong interactions are known to occur between perceptual qualities (Kanizsa, 1974; Egusa, 1983; Faubert and von Grunau, 1995; Smallman and McKee, 1995; Pessoa et al., 1996). In particular, form and motion can interact, as can brightness and depth, among other combinations of qualities.

Complementary Computing and Laminar Computing

At least two new computational paradigms have gradually been identified from the cumulative experiences of modeling many kinds of brain and behavior data over the past three decades: Complementary Computing and Laminar Computing (Grossberg, 1999a, 2000). *Complementary Computing* concerns the discovery that pairs of parallel cortical processing streams compute complementary properties in the brain. Each stream has complementary computational strengths and weaknesses, much as in physical principles like the Heisenberg Uncertainty Principle. Each cortical stream can also possess multiple processing stages. These stages realize a *hierarchical resolution of uncertainty*. "Uncertainty" here means that computing one set of properties at a given stage can suppress information about a complementary set of properties at that stage. The computational unit of brain processing that has behavioral significance is thus not a single processing stage, or any smaller entity such as the potential of a single cell, or spike or burst of spikes. Instead, hierarchical interactions within a stream and parallel interactions between streams resolve their complementary deficiencies to compute complete information about a particular type of biological intelligence. These interactions have been used to clarify many of the data that do not support the hypothesis of independent modules. To model how the brain controls behavior, one thus needs to know how these complementary streams are organized with respect to one another.

Understanding how the brain sees is one area where experimental and modeling work have advanced the furthest, and illustrate several types of

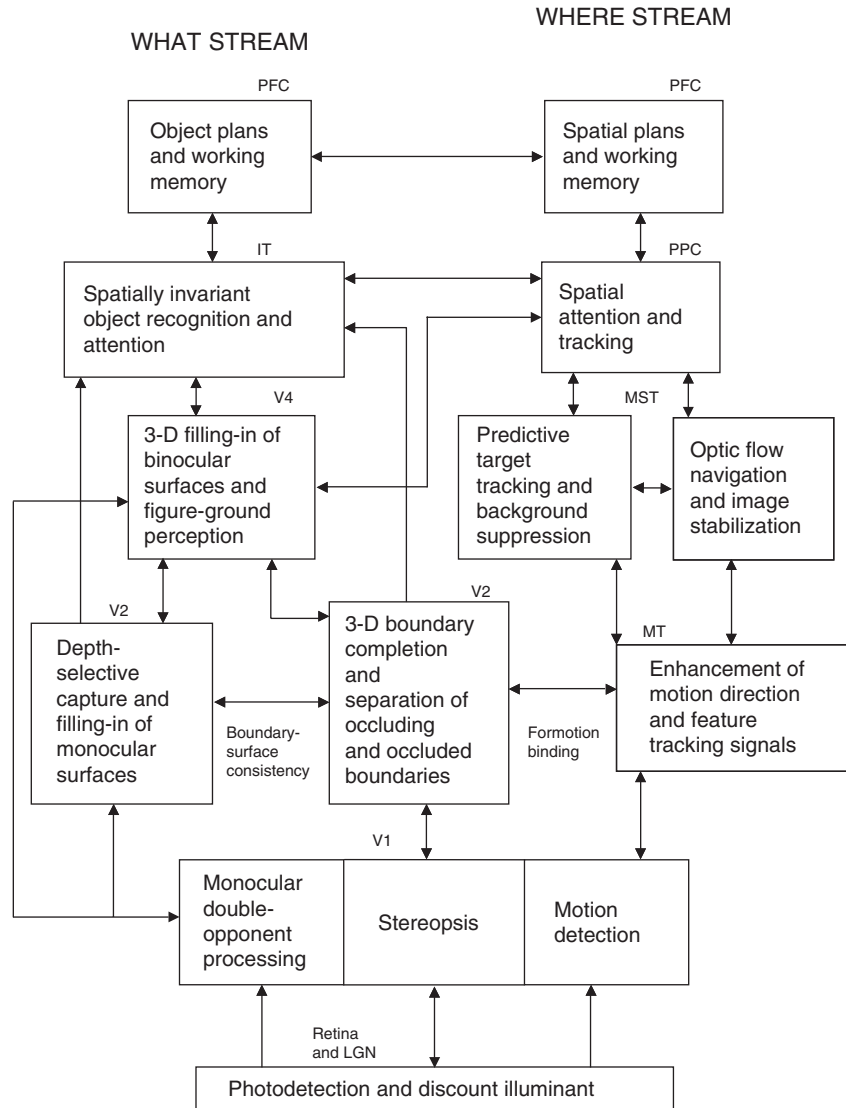


Fig. 1. Some visual processes and their anatomical substrates that are being modeled as part of a unified vision system. LGN: Lateral Geniculate Nucleus; V1: striate visual cortex; V2, V4, MT, MST: prestriate visual cortex; IT: inferotemporal cortex; PPC: posterior parietal cortex; PFC: prefrontal cortex.

complementary interactions. Figure 1 provides a schematic macrocircuit of the types of processes that are being assembled into a unified theory of how the brain sees, including processes of vision, recognition, navigation, tracking, and visual cognition. In particular, matching and learning processes within the What and Where cortical streams have been proposed to be complementary: The What stream,

through cortical areas V1-V2-V4-IT-PFC, learns to recognize *what* objects and events occur. The Where stream, through cortical areas V1-MT-MST-PPC-PFC, spatially localizes *where* they are, and acts upon them. Complementary processes also occur within each stream: What stream boundary grouping via the (V1 interblob)-(V2 pale stripe)-V4 stages, and surface formation via the (V1 blob)-(V2 thin

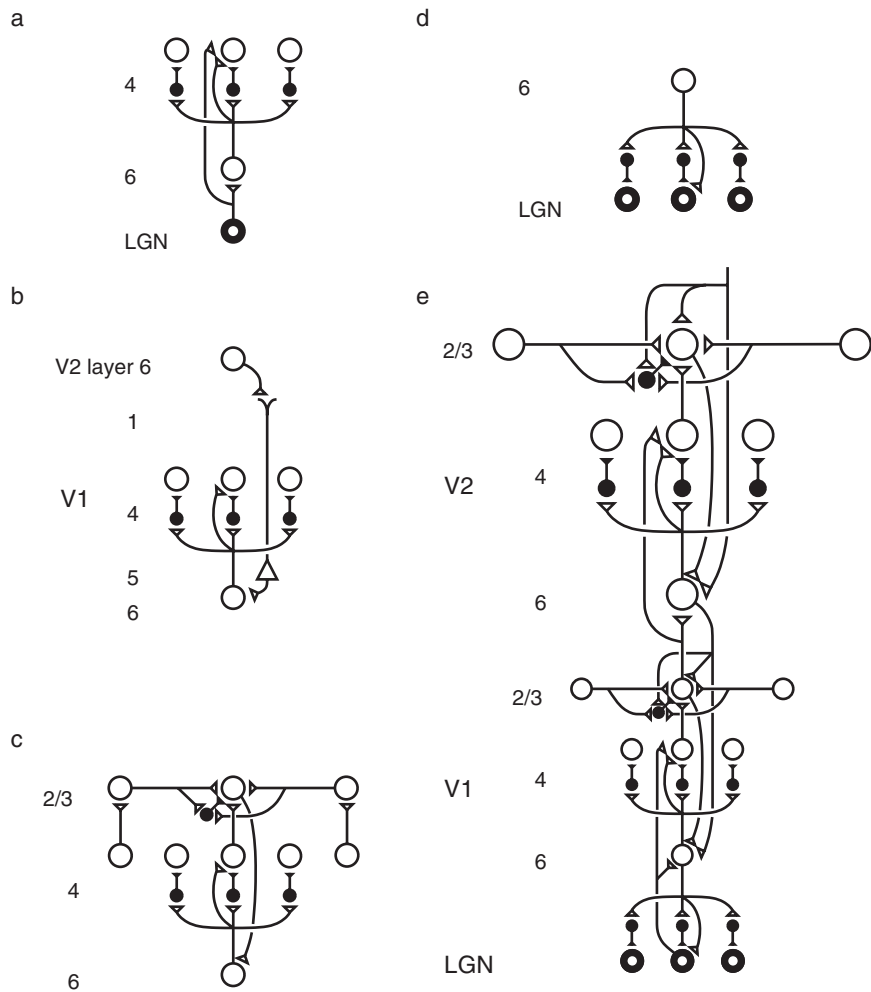
stripe)-V4 stages, have complementary properties. Where stream target tracking via MT-(MST ventral) and navigation via MT-(MST dorsal) have complementary properties. Such complementary processes are predicted to arise from symmetry-breaking operations during cortical development.

Laminar Computing concerns the fact that cerebral cortex is organized into layered circuits (usually six main layers) which undergo characteristic bottom-up, top-down, and horizontal interactions, which have been classified into more than 50 divisions, or areas, of neocortex (Brodmann, 1909; Martin, 1989). The functional utility of such a laminar organization in the control of behavior has remained a mystery until recently. Understanding

how different parts of the neocortex specialize the same underlying laminar circuit design in order to achieve all the highest forms of biological intelligence remains a long-term goal, although challenging data about both vision and cognitive information processing (Grossberg and Pearson, 2006; Pearson and Grossberg, 2005) have now been modeled as variations of this design.

Laminar computing by visual cortex: unifying adaptive filtering, grouping, and attention

A number of models have been proposed (Douglas et al., 1995; Stemmler et al., 1995; Li, 1998;



Somers et al., 1998; Yen and Finkel, 1998) to simulate aspects of visual cortical dynamics, but these models have not articulated why cortex has a laminar architecture. Our own group's breakthrough on this problem (Grossberg et al., 1997; Grossberg, 1999a) began with the suggestion that the laminar organization of visual cortex accomplishes at least three things: (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; and (3) the attentional process whereby cortex selectively processes important events.

These results further develop the proposal that even the earliest stages of visual cortex are not merely a bottom-up filtering device, as in the classical model of Hubel and Wiesel (1977). Instead, bottom-up filtering, horizontal grouping, and top-down attention are all joined together in laminar cortical circuits. Perceptual grouping, the process

that binds spatially distributed and incomplete information into 3D object representations, starts at an early cortical stage; see Fig. 2c. These grouping 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 et al., 1984; Peterhans and von der Heydt, 1989; Knierim and van Essen, 1992; Grosz et al., 1993; Kapadia et al., 1995; Sillito et al., 1995; Sheth et al., 1996; Bosking et al., 1997; Polat et al., 1998). Likewise, even early visual processing is modulated by system goals via top-down expectations and attention (Motter, 1993; Sillito et al., 1994; Roelfsema et al., 1998; Watanabe et al., 1998; Somers et al., 1999). The model proposes how mechanisms governing (1) in the infant lead to properties (2) and (3) in the adult, and properties (2) and (3) interact together intimately as a result.

The laminar model proposes that there is no strict separation of preattentive data-driven bottom-up filtering and grouping, from attentive task-directed top-down processes. The model shows how these processes may come together at a shared

Fig. 2. How known cortical connections join the layer 6→4 and layer 2/3 circuits to form an entire V1/V2 laminar model. Inhibitory interneurons are shown filled-in black. (a) The LGN provides bottom-up activation to layer 4 via two routes. First, it makes a strong connection directly into layer 4. Second, LGN axons send collaterals into layer 6, and thereby also activate layer 4 via the layer 6 → layer 4 on-center off-surround path. The combined effect of the bottom-up LGN pathways is to stimulate layer 4 via an on-center off-surround, which provides divisive contrast normalization (Grossberg, 1973, 1980; Heeger, 1992) of layer 4 cell responses. (b) Feedback carries attentional signals from higher cortex, via the modulatory layer 6 → layer 4 path, into layer 4 of V1. Because of the bend in this feedback pathway, I have called it “folded feedback.” Corticocortical feedback axons tend preferentially to originate in layer 6 of the higher area and to terminate in layer 1 of the lower cortex (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. The triangle in the figure represents such a layer 5 pyramidal cell. Several other routes through which feedback can pass into V1 layer 6 exist (see Raizada and Grossberg (2001) for a review). Having arrived in layer 6, the feedback is then “folded” back up into the feedforward stream by passing through the 6 → 4 on-center off-surround path (Bullier et al., 1996). (c) Connecting the 6→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. Just like attentional signals from higher cortex, as shown in (b), groupings that 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 6→4 off-surround. There exist direct layer 2/3→6 connections in macaque V1, as well as indirect routes via layer 5. (d) Top-down corticogeniculate feedback from V1 layer 6 to LGN also has an on-center off-surround anatomy, similar to the 6→4 path. The on-center feedback selectively enhances LGN cells that are consistent with the activation that they cause (Sillito et al., 1994), and the off-surround contributes to length-sensitive (endstopped) responses that facilitate grouping perpendicular to line ends. (e) The entire V1/V2 circuit: V2 repeats the laminar pattern of V1 circuitry, but at a larger spatial scale. In particular, the horizontal layer 2/3 connections have a longer range in V2, allowing above-threshold perceptual groupings between more widely spaced inducing stimuli to form (Amir et al., 1993). V1 layer 2/3 projects up to V2 layers 6 and 4, just as LGN projects to layers 6 and 4 of V1. Higher cortical areas send feedback into V2 which ultimately reaches layer 6, just as V2 feedback acts on layer 6 of V1 (Sandell and Schiller, 1982). Feedback paths from higher cortical areas straight into V1 (not shown) can complement and enhance feedback from V2 into V1. Top-down attention can also modulate layer 2/3 pyramidal cells directly by activating both the pyramidal cells and inhibitory interneurons in that layer. The inhibition tends to balance the excitation, leading to a modulatory effect. These top-down attentional pathways tend to synapse in layer 1, as shown in Fig. 2b. Their synapses on apical dendrites in layer 1 are not shown, for simplicity. (Adapted with permission from Raizada and Grossberg (2001).)

circuit, or interface, that is called the *preattentive-attentive interface*, which exists between layers 6 and 4 (Fig. 2a–c, e). Significantly, by indicating how mechanisms whereby the cortex can develop and learn in a stable way impose computational constraints that *define* key properties of adult visual information processing, the model begins to unify the fields of cortical development and adult perceptual learning and information processing. The model is called a LAMINART model (Fig. 2; Grossberg, 1999a; Raizada and Grossberg, 2003) because it clarifies how mechanisms of Adaptive Resonance Theory (ART), which have previously been predicted to stabilize cortical development and learning of bottom-up adaptive filters and top-down attentive expectations (Grossberg, 1980, 1999c; Carpenter and Grossberg, 1993) can be joined together in laminar circuits to processes of perceptual grouping through long-range horizontal interactions (Grossberg and Mingolla, 1985b).

A new way to compute: feedforward and feedback, speed and uncertainty, digital and analog

The LAMINART model proposes how laminar neocortex embodies a novel way to compute which exhibits at least three major new computational properties (Grossberg, 2003a). These new properties allow the fast, but stable, autonomous self-organization that is characteristic of cortical development and life-long learning in response to changing and uncertain environments. They go beyond the types of Bayesian cortical models that are so popular today, but also clarify the intuitive appeal of these models (Pilly and Grossberg, 2005; Grossberg and Pilly, 2007).

The first property concerns a new type of hybrid between *feedforward and feedback computing*. In particular, 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. This property clarifies how recognition can be fast in response to unambiguous scenes; e.g., Thorpe et al. (1996). If, however, there are multiple possible groupings, say in response to 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. This self-normalizing property emerges from on-center off-surround networks of cells that obey membrane, or *shunting*, equations. Such networks are capable of processing input contrasts over a large dynamic range without saturation (Grossberg, 1973, 1980; Heeger, 1992; Douglas et al., 1995).

In other words, these self-normalizing circuits carry out a type of real-time probability theory in which the amplitude and coherence of cell activity covaries with the certainty of the network's selection, or decision, about a grouping. Amplitude also covaries with 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 a cortical feedback loop that rapidly contrast enhances and amplifies a winning grouping. As the winner is selected, and weaker groupings are suppressed, its cells become more active, hence can again more rapidly exceed output thresholds and 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 significant uncertainty. Feedback selects a winning decision that enables the circuit to speed up again. 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.

These concepts are illustrated within an emerging unified model of how cortical form and motion processes interact. This 3D FORMOTION model has quantitatively simulated and predicted the temporal dynamics of how the visual cortex responds to motion stimuli, including motion stimuli

whose coherence is probabilistically defined (Chey et al., 1997; Grossberg et al., 2001; Berzhanskaya et al., 2007; Grossberg and Pilly, 2007). Grossberg and Pilly (2007) have, in particular, proposed a how Retina/LGN-V1-MT-MST-LIP-Basal Ganglia interactions can quantitatively explain and simulate data about probabilistic decision-making in LIP (Shadlen and Newsome, 2001; Roitman and Shadlen, 2002). These experiments have been presented as supportive of Bayesian processing.

The second property concerns 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 intracortical feedback loop between layers 2/3-6-4-2/3 that selects or confirms a winning grouping has the property of *analog coherence* (Grossberg et al., 1997; Grossberg, 1999a; Grossberg and Raizada, 2000); namely, this feedback loop can synchronously store a winning grouping without losing analog sensitivity to amplitude differences in the input pattern. The coherence of synchronous selection and storage provides the stability of digital computing. The sensitivity of analog computation can be traced to how excitatory and inhibitory interactions are balanced within layers 4 and 2/3, and to the shunting dynamics of the inhibitory interactions within these layers.

The third property concerns its ability to self-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. As further discussed below, this 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).

The critical role of the layer 6-to-4 decision circuits in the realization of all three properties clarifies that they are all different expressions of a shared circuit design.

Linking stable development to synchrony

The LAMINART model clarifies how excitatory and inhibitory connections in the cortex can develop in a stable way by achieving and maintaining

a *balance* between excitation and inhibition (Grossberg and Williamson, 2001). Long-range excitatory horizontal connections between pyramidal cells in layer 2/3 of visual cortical areas play an important role in perceptual grouping (Hirsch and Gilbert, 1991; McGuire et al., 1991). The LAMINART model proposes how development enables the strength of long-range excitatory horizontal signals to become balanced against inhibitory signals that are mediated by short-range disynaptic inhibitory interneurons which target the same pyramidal cells (Fig. 2c). These balanced connections are proposed to realize properties of perceptual grouping in the adult. In a similar way, development enables the strength of excitatory connections from layer 6-to-4 to be balanced against those of inhibitory interneuronal connections (Wittmer et al., 1997); see Fig. 2a, c. Thus, 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 a *modulatory* on-center, off-surround network from layer 6-to-4. This network plays at least three functional roles that are intimately linked: maintaining a contrast-normalized response to bottom-up inputs at layer 4 (Fig. 2a); forming perceptual groupings in layer 2/3 that maintain their sensitivity to analog properties of the world (Fig. 2c); and biasing groupings via top-down attention from higher cortical areas (Fig. 2b; also see Fig. 2d, e).

Balanced excitatory and inhibitory connections have been proposed by several models to explain the observed variability in the number and temporal distribution of spikes emitted by cortical neurons (Shadlen and Newsome, 1998; van Vreeswijk and Sompolinsky, 1998). The LAMINART model proposes that such variability may reflect mechanisms that are needed to ensure stable development and learning. If indeed “stability implies variability,” how does the cortex convert these variable spikes, which are inefficient in driving responses from cortical neurons, into reliable responses to visual inputs? Within LAMINART circuits, such balanced excitatory and inhibitory connections respond to inputs by rapidly synchronizing their responses to input stimuli (Yazdanbakhsh and Grossberg, 2004; Grossberg and Versace, 2007; see also Grossberg and Somers, 1991;

Grossberg and Grunewald, 1997). In fact, the article that introduced ART predicted a role for synchronous cortical processing, including synchronous oscillations, which were there called “order-preserving limit cycles,” as part of the process of establishing resonant states (Grossberg, 1976). Since the early experimental reports of Eckhorn et al. (1988) and Gray and Singer (1989), many neurophysiological experiments have reported synchronous cortical processing; e.g., Engel et al. (2001), Fries et al. (2001), and Sarnthein et al. (1998). The ART model further predicted a functional link between properties of stable development, adult perceptual learning, attention, and synchronous cortical processing, to which the LAMINART model adds perceptual grouping in laminar cortical circuits.

The Synchronous Matching ART (SMART) model of Grossberg and Versace (2005, 2006, 2007) further develops LAMINART to clarify how multiple levels of brain organization work together, ranging from individual spikes, through local field potentials and inter-areal synchronization, to cognitive learning dynamics. SMART proposes how higher-order specific and nonspecific thalamic nuclei are coordinated with multiple stages of cortical processing to control stable spike-timing-dependent plasticity (STDP). The model proposes how gamma oscillations can facilitate STDP learning, and how slower beta oscillations may be generated during reset events. It furthermore predicts that reset is mediated by the deeper layers of cortex. The model hereby predicts that “more gamma” can be expected through time in the superficial layers of cortex than the deeper layers.

Attention arises from top-down cooperative-competitive matching

Attention typically modulates an ongoing process. In order for the concept of attention to be scientifically useful, these processes need to be articulated and the way in which attention modulates them needs to be mechanistically explained. LAMINART, and ART before it, predicted that an intimate link exists between processes of attention, competition, and bottom-up/top-down

matching. LAMINART predicts, in particular, that top-down signals from higher cortical areas, such as area V2, can attentionally prime, or modulate, layer 4 cells in area V1 by activating the on-center off-surround network from layer 6-to-4 (Fig. 2b, e). Because the excitatory and inhibitory signals in the on-center are balanced, attention can sensitize, or modulate, cells in the attentional on-center, without fully activating them, while also inhibiting cells in the off-surround.

The importance of the conclusion that top-down attention is often expressed through a top-down, modulatory on-center, off-surround network cannot be overstated. Because of this organization, top-down attention can typically provide only excitatory modulation to cells in the on-center, while it can strongly inhibit cells in the off-surround. As Hupé et al. (1997, p. 1031) have noted: “feedback connections from area V2 modulate but do not create center-surround interactions in V1 neurons.” When the top-down on-center matches bottom-up signals, it can amplify and synchronize them, while strongly suppressing mismatched signals in the off-surround. This prediction was first made as part of ART in the 1970s (Grossberg, 1976, 1978, 1980, 1999a, 1999c). It has since received both of psychological and neurobiological empirical confirmation in the visual system (Downing, 1988; Sillito et al., 1994; Steinman et al., 1995; Bullier et al., 1996; Caputo and Guerra, 1998; Somers et al., 1999; Reynolds et al., 1999; Mounts, 2000; Smith et al., 2000; Vanduffel et al., 2000). Based on such data, this property 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. Figure 3 summarizes data of Reynolds et al. (1999) and a simulation of these data from Grossberg and Raizada (2000) that illustrate the on-center off-surround character of attention in macaque V2.

The preattentive–attentive interface and object-based attention

Top-down attention and preattentive perceptual grouping interact within the cortical layers to

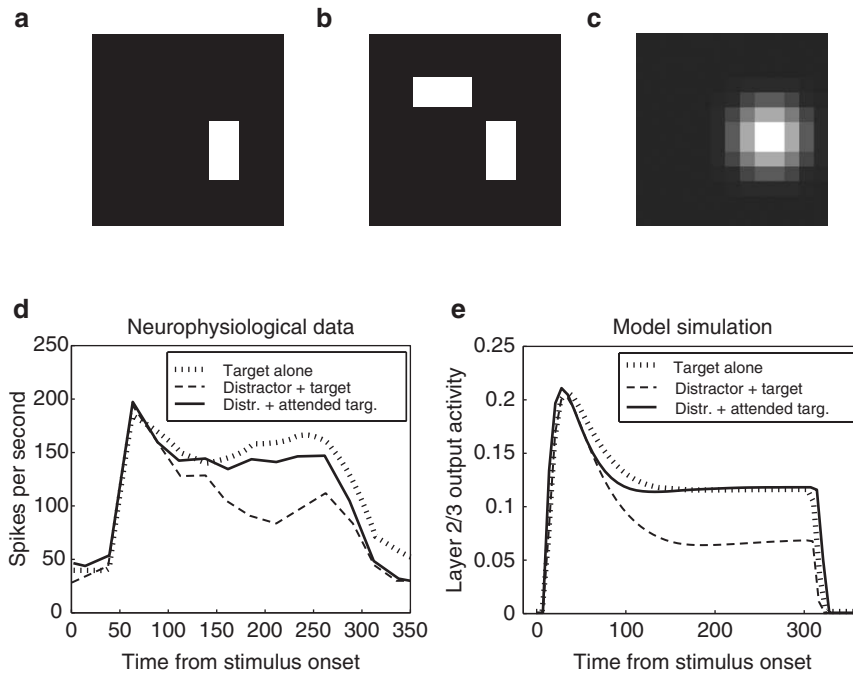


Fig. 3. The effect of attention on competition between visual stimuli. A target stimulus, presented on its own (a), elicits strong neural activity at the recorded cell. When a second, distractor stimulus is presented nearby (b), it competes against the target, and activity is reduced. Directing spatial attention to the location of the target stimulus (c), protects the target from this competition, and restores neural activity to the levels elicited by the target on its own. The stimuli shown here, based on those used in the neurophysiological experiments of Reynolds et al. (1999), were presented to the model neural network. Spatial attention (c), was implemented as a Gaussian of activity fed back into layer 6. (d) Neurophysiological data from macaque V2 that illustrate the recorded activity patterns described above: strong responses to an isolated target (dotted line), weaker responses when a competing distractor is placed nearby (dashed line) and restored levels of activity when the target is attended (solid line). (Adapted with permission from Reynolds et al., 1999, Fig. 5; see also Reynolds et al., 1995). (e) Model simulation of the Reynolds et al. data. The time-courses illustrated show the activity of a vertically oriented cell stimulated by the target bar. If only the horizontal distractor bar were presented on its own, this cell would respond very weakly. If both target and distractor were presented, but with the horizontal distractor attended, the cell would respond, but more weakly than the illustrated case where the distractor and target are presented together, with neither attended. (Adapted with permission from Grossberg and Raizada (2000).)

enable attention to focus on an entire object boundary, thereby enabling whole object boundaries to be selectively attended and recognized. This happens because the same layer 6-to-4 competition, or selection, circuit may be activated both by preattentive grouping cells in layer 2/3, and by top-down attentional pathways (Fig. 2b, c). Layer 4 cells can then, in turn, reactivate layer 2/3 cells (Fig. 2c). This layer 6-to-4 circuit “folds” the feedback from top-down attention or a layer 2/3 grouping back into the feedforward flow of bottom-up inputs to layer 4. It is thus said to embody a “folded feedback” process (Grossberg, 1999a). Thus, when ambiguous complex scenes

are being processed, *intracortical* folded feedback enables stronger groupings in layer 2/3 to inhibit weaker groupings, whereas *intercortical* folded feedback enables higher-order attentive constraints to bias which groupings will be selected.

Figure 2e summarizes the hypothesis that top-down attentional signals to layer 1 may also directly modulate groupings via apical dendrites of both excitatory and inhibitory layer 2/3 cells in layer 1 (Rockland and Virga, 1989; Lund and Wu, 1997). By activating both excitatory and inhibitory cells in layer 2/3, the inhibitory cells may balance the excitatory cell activation, thereby enabling attention to directly modulate grouping cells in layer 2/3.

Because the cortex uses the same circuits to select groupings and to prime attention, attention can flow along perceptual groupings, as reported by Roelfsema et al. (1998). In particular, when attention causes an excitatory modulatory bias at some cells in layer 4, groupings that form in layer 2/3 can be enhanced by this modulation via their positive feedback loops from 2/3-to-6-to-4-to-2/3. The direct modulation of layer 2/3 by attention can also enhance these groupings. Figure 4 summarizes a LAMINART simulation of data from Roelfsema et al. (1998) of the spread of visual attention along an object boundary grouping. LAMINART has

also been used to simulate the flow of attention along an illusory contour (Raizada and Grossberg, 2001), consistent with experimental data of Moore et al. (1998). The ability of attention to selectively light up entire object representations has an obviously important survival value in adults. It is thus of particular interest that the intracortical and intercortical feedback circuits that control this property have been shown in modeling studies to play a key role in stabilizing infant development and adult perceptual learning within multiple cortical areas, including cortical areas V1 and V2.

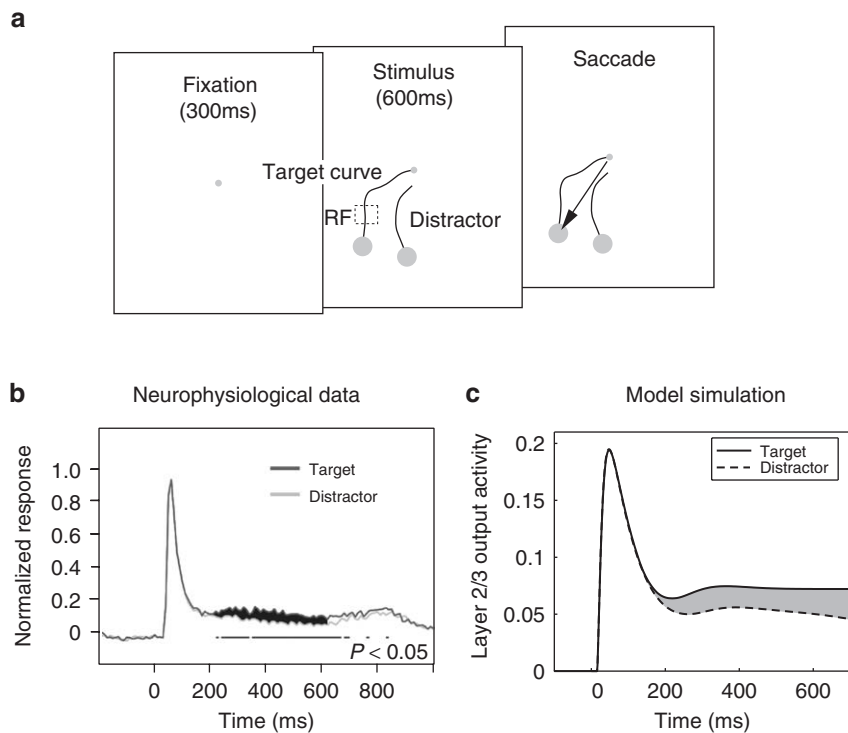


Fig. 4. Spread of visual attention along an object boundary grouping, from an experiment by Roelfsema et al. (1998). (a) The experimental paradigm. Macaque monkeys were trained to perform a mental curve-tracing task, during which physiological recordings were made in V1: A fixation spot was presented 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 trace 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 (RF) lay on the target curve, as opposed to the distractor. Note that the 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. (1998).) (c) Model simulation of the Roelfsema et al. data. (Adapted with permission from Grossberg and Raizada (2000).)

Stable development and learning through adaptive resonance

ART (Grossberg, 1980, 1995, 1999c; Pollen, 1999; Engel et al., 2001) is a cognitive and neural theory which addresses a general problem that faces all adaptive brain processes; namely, the *stability–plasticity dilemma*: how can brain circuits be plastic enough to be rapidly fine-tuned by new experiences, and yet simultaneously stable enough that they do not get catastrophically overwritten by the new stimuli with which they are continually bombarded?

The solution that ART proposes to this problem is to allow neural representations to be rapidly modified only by those incoming stimuli with which they form a sufficiently close match. If the match is close enough, then learning occurs. Because an approximate match is required, such learning fine-tunes the memories of existing representations, so that outliers cannot radically overwrite an already learned representation. ART proposes how a learning individual can flexibly vary the criterion, called *vigilance*, of how good a match is needed between bottom-up and top-down information in order for the presently active representation to be refined through learning. When coarse matches are allowed (low vigilance), the learned representations can represent general and abstract information. When only fine matches are allowed (high vigilance), the representations are more specific and concrete. If the active neural representation does not match with the incoming stimulus, then its neural activity is extinguished and hence unable to cause plastic changes. Suppression of an active representation enables mismatch-mediated memory search, or hypothesis-testing, to ensue whereby some other representation can become active through bottom-up signaling. This representation, in turn, reads out top-down signals that either gives rise to a match, thereby allowing learning, or a nonmatch, causing the search process to repeat until either a match is found or the incoming stimulus causes a totally new representation to be formed. For this to work, top-down expectations have large enough adaptive memory traces to enable an initial match to occur with a newly selected representation. It has been

suggested that breakdowns in vigilance control can contribute to various disorders, including medial temporal amnesia (abnormally low vigilance; Carpenter and Grossberg, 1993) and autism (abnormally high vigilance; Grossberg and Seidman, 2006).

In both ART and its elaboration into LAMINART, attention is mediated by a top-down, modulatory on-center, off-surround network (e.g., Grossberg, 1980, 1982, 1999b), whose role is to select and enhance behaviorally relevant bottom-up sensory inputs (match), and suppress those that are irrelevant (nonmatch). Mutual excitation between the top-down feedback and the bottom-up signals that they match can amplify, synchronize, and maintain existing neural activity in a resonant state long enough for rapid synaptic changes to occur. Thus, attentionally relevant stimuli are learned, while irrelevant stimuli are suppressed and prevented from destabilizing existing representations. Hence the name *adaptive resonance*. Grossberg (1999c, 2003a) provides more detailed reviews.

The folded feedback layer 6-to-4 modulatory on-center, off-surround attentional pathway in the LAMINART model (Fig. 2b) satisfies the predicted properties of ART matching. 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 (Sillito et al., 1994; Luck et al., 1997; Roelfsema et al., 1998), but not with models in which matches with top-down feedback cause suppression (Mumford, 1992; Rao and Ballard, 1999). The ART proposal raises two key questions: First, does top-down cortical feedback have the predicted top-down, modulatory on-center, off-surround structure in other neocortical structures, where again the stabilizing role of top-down feedback in learning would be required? Second, is there evidence that top-down feedback controls plasticity in the area to which it is directed?

Zhang et al. (1997) have shown that feedback from auditory cortex to the medial geniculate nucleus (MGN) and the inferior colliculus (IC) also has an on-center off-surround form, and Temereanca and Simons (2001) have produced

evidence for a similar feedback architecture in the rodent barrel somatosensory system.

The link between attention and learning

Accumulating evidence also shows that top-down feedback helps to control cortical plasticity. Psychophysically, the role of attention in controlling adult plasticity and perceptual learning was demonstrated by Ahissar and Hochstein (1993). Gao and Suga (1998) reported physiological evidence that acoustic stimuli caused plastic changes in the IC of bats only when the IC received top-down feedback from auditory cortex. Plasticity is enhanced when the auditory stimuli were made behaviorally relevant, consistent with the ART proposal that top-down feedback allows attended, and thus relevant, stimuli to be learned, while suppressing unattended irrelevant ones. Cortical feedback also controls thalamic plasticity in the somatosensory system (Krupa et al., 1999; Parker and Dostrovsky, 1999). See Kaas (1999) for a review.

Models of intracortical feedback due to grouping, and of corticocortical and thalamocortical feedback due to attention, have shown that either type of feedback can rapidly synchronize the firing patterns of higher and lower cortical areas (Grossberg and Somers, 1991; Grossberg and Grunewald, 1997; Yazdanbakhsh and Grossberg, 2004; Grossberg and Versace, 2007). ART predicts that such synchronization phenomena underlie the type of resonances that can trigger cortical learning by enhancing the probability that “cells that fire together wire together.” Engel et al. (2001) review data and related models that are consistent with the proposal that synchrony, attention, and learning are related.

View-invariant object category learning: coordinating object attention and surface-based spatial attention shrouds

The above summary has focused on object attention. It did not discuss spatial attention, how spatial and object attention work together, or how attention is hierarchically organized. The above summary also talks about category learning, but

not the fact that view-invariant object categories may be learned from combinations of multiple object views. The present section sketches some results concerning these more global issues about brain organization.

One way in which attention may globally influence many brain regions is illustrated in Fig. 2e, which shows how attention can leap from higher cortical levels to multiple lower cortical areas via their layers 6. This anatomy proposes a solution to an otherwise challenging problem: How can attention prime so many cortical areas with higher-order constraints without inadvertently firing them all? Figure 2e shows that attention can leap between the layers 6 of different cortical areas without firing them all, because the layer 6-to-4 circuits that act intracortically are modulatory.

The above example illustrates how attention can act “vertically” between cortical regions. Many studies have analyzed how attention is spread “horizontally” across a given level of cortical processing, including how spatial attention may be simultaneously divided among several targets (Pylyshyn and Storm, 1988; Yantis, 1992), and how object and spatial attention may both influence visual perception (Posner, 1980; Duncan, 1984). The distinction between object and spatial attention reflects the organization of visual cortex into parallel What and Where processing streams (Fig. 1). Many cognitive neuroscience experiments have supported the hypotheses of Ungerleider and Mishkin (1982; see also Mishkin et al. (1983)) and of Goodale and Milner (1992) that inferotemporal cortex and its cortical projections learn to categorize and recognize what objects are in the world, whereas the parietal cortex and its cortical projections learn to determine where they are and how to deal with them by locating them in space, tracking them through time, and directing actions towards them. This design into parallel streams separates sensory and cognitive processing from spatial and motor processing.

The What stream strives to generate object representations that are independent of their spatial coordinates, whereas the Where stream generates representations of object location and action. The streams must thus interact to act upon recognized objects. Indeed, both object and spatial attention

are needed to search a scene for visual targets and distracters using saccadic eye movements. Grossberg et al. (1994) illustrated how object and spatial attention may interact by quantitatively fitting a large human psychophysical database about visual search with a model, called the Spatial Object Search (SOS) model, that proposes how 3D boundary groupings and surface representations interact with object attention and spatial attention to find targets amid distracters. This analysis proposed that surface properties may engage spatial attention, as when search is restricted to all occurrences of a color on a prescribed depth plane (Egeth et al., 1984; Nakayama and Silverman, 1986; Wolfe and Friedman-Hill, 1992).

More recent modeling work has advanced the theoretical analysis of how spatial and object attention are coordinated by surface and boundary representations, by showing how they support the learning of view-invariant object categories (Fazl et al., 2005, 2006, 2007). This work advances the solution of the following problem: What is an object? How does the brain learn what an object is under both unsupervised and supervised learning conditions? How does the brain learn to bind multiple views of an object into a view-invariant representation of a complex object while scanning its various parts with active eye movements? How does the brain avoid the problem of erroneously classifying views of different objects as belonging to a single object, even before it has a concept of what the object is? How does the brain direct the eyes to explore an object's surface even before it has a concept of the object? The ARTSCAN model predicts how spatial and object attention work together to direct eye movements to explore object surfaces and to enable learning of view-invariant object categories from the multiple view categories that are thereby learned.

In particular, ARTSCAN predicts that spatial attention employs an *attentional shroud*, or form-fitting distribution of spatial attention, that is derived through feedback interactions with an object's surface representation. ARTSCAN modifies the original Tyler and Kontsevich (1995) concept of an attentional shroud in which the shroud was introduced as an alternative to the perception of simultaneous transparency, with evidence that

only one plane is seen at a time within the perceptual moment. This concept focuses on object perception. ARTSCAN proposes that an attentional shroud also plays a fundamental role in regulating object learning.

Such a shroud is proposed to persist within the Where stream during active scanning of an object with attentional shifts and eye movements. This claim raises the basic question: How can the shroud persist during active scanning of an object, if the brain has not yet learned that there is an object there? ARTSCAN proposes how a *preattentively* formed surface representation leads to activation of a shroud, even before the brain can recognize the surface as representing a particular object. Such a shroud can be formed starting with either bottom-up or top-down signals. In the bottom-up route, a surface representation (e.g., in visual cortical area V4) directly activates a shroud, which conforms its shape to that of the surface, in a spatial attention cortical area (e.g., posterior parietal cortex). The shroud, in turn, can topographically prime the surface representation via top-down feedback. A surface-shroud resonance can hereby develop. In the top-down route, a volitionally controlled, local focus of spatial attention (an attentional spotlight) can send a top-down attentional signal to a surface representation. This spotlight of enhanced activation can then fill-in across the entire surface, being contained only by the surface boundary (Grossberg and Mingolla, 1985b). Surface filling-in generates a higher level of filled-in surface activation than did the bottom-up input to the surface alone. The filling-in of such a top-down attentional spotlight can hereby have an effect on the total filled-in surface activity that is similar to that caused by a higher bottom-up stimulus contrast (Reynolds and Desimone, 2003). The more highly active surface representation can reactivate the spatial attention region to define a surface form-fitting spatial locus of spatial attention; that is, a shroud. Again, the shroud is defined by a surface-shroud resonance.

Any surface in a scene can potentially sustain an attentional shroud, and surface representations dynamically compete for spatial attention. The winner of the competition at a given moment gains more activity and becomes the shroud.

As saccadic eye movements explore an object's surface, the surface-induced shroud modulates object learning in the What stream by maintaining activity of an emerging view-invariant category representation while multiple view-specific representations are linked to it through learning. Output from the shroud also helps to select the boundary and surface features to which eye movements will be directed, via a surface contour process that is predicted to play a key role in 3D figure-ground separation (Grossberg, 1994, 1997) and to be mediated via cortical area V3A (Nakamura and Colby, 2000a, b).

The model postulates that an active shroud weakens through time due to self-inhibitory inputs at selected target locations ("inhibition of return"; Grossberg, 1978; Koch and Ullman, 1985), combined with chemical transmitters that habituate, or are depressed, in an activity-dependent way (Grossberg, 1968; Francis et al., 1994; Abbott et al., 1997) and gate the signals that sustain the shroud. When an active shroud is weakened enough, it collapses and cannot any longer inhibit a tonically active reset signal. When a reset signal is disinhibited, it inhibits the active view-invariant object category in the What Stream, thereby preventing it from erroneously being linked to the view categories of subsequently foveated objects. Then a new shroud, corresponding to some other surface, is selected in the Where stream, as a new object category is activated in the What stream by the first view of the new object.

While a shroud remains active, the usual ART mechanisms direct object attention to ensure that new view categories and the emerging view-invariant object category are learned in a stable way through time. ARTSCAN hereby provides a new proposal for how surface-based spatial attention and object attention are coordinated to learn view-invariant object categories.

The ARTSCAN model learns with 98.1% accuracy on a letter database whose letters vary in size, position, and orientation. It does this while achieving a compression factor of 430 in the number of its category representations, compared to what would be required to learn the database without the view-invariant categories. The model also simulates reaction times (RTs) in human data

about object-based attention: RTs are faster when responding to the noncued end of an attended object compared to a location outside the object, and slower engagement of attention to a new object occurs if attention has to first be disengaged from another object first (Brown and Denney, *in press*; Egly et al., 1994).

Learning without attention: the preattentive grouping is its own attentional prime

The fact that attentional feedback can influence cortical plasticity does not imply that unattended stimuli can never be learned. Indeed, abundant plasticity occurs during early development, before top-down attention has even come into being. Grossberg (1999a) noted that, were this not possible, an infinite regress could be created, since a lower cortical level like V1 might then not be able to stably develop unless it received attentional feedback from V2, but V2 itself could not develop unless it had received reliable bottom-up signals from V1. How does the cortex avoid this infinite regress so that, during development, plastic changes in cortex may be driven by stimuli that occur with high statistical regularity in the environment without causing massive instability, as modeled in the LAMINART simulations of Grossberg and Williamson (2001)? How does this process continue to fine-tune sensory representations in adulthood, even in cases where task-selective attention and awareness do not occur (Watanabe et al., 2001; Seitz and Watanabe, 2003)?

The LAMINART model clarifies how attention is used to help stabilize learning, while also allowing learning to slowly occur without task-selective attention and awareness. It also links these properties to properties of preattentive vision that are not obviously related to them. For example, how can preattentive groupings, such as illusory contours, form over positions that receive no bottom-up inputs? Although we take such percepts for granted, illusory contours seem to contradict the ART matching rule, which says that bottom-up inputs are needed to fire cells, while top-down feedback is modulatory. How, then, can cells that represent the illusory contour fire at positions that do not receive

bottom-up inputs without destabilizing cortical development and learning? If the brain had not solved this problem, anyone could roam through the streets of a city and destabilize the brains of pedestrians by showing them images of Kanizsa squares! The absurdity of this possibility indicates how fundamental the issue at hand really is.

The LAMINART model proposes how the brain uses its laminar circuits to solve this problem using a *preattentive–attentive interface* in which both intercortical attentional feedback and *intracortical* grouping feedback share the same selection circuit from layer 6-to-4: When a grouping starts to form in layer 2/3, it activates the intracortical feedback pathway from layer 2/3-to-6, which activates the modulatory on-center, off-surround network from layer 6-to-4. This intracortical feedback pathway helps to select which cells will remain active in a winning grouping. Attention uses this same network to stabilize cortical development and learning through intercortical interactions. In other words, the intracortical layer 6-to-4 selection circuit, which in the adult helps to choose winning groupings, is also predicted to help stabilize visually induced brain development by assuring that the ART matching rule holds at every position along a grouping. Because the matching rule holds, only the correct combinations of cells can “fire together and wire together,” and hence stability is achieved. Intracortical feedback via layers 2/3-to-6-to-4-to-2/3 realizes this selection process even before intercortical attentional feedback can develop. I like to say that: “The preattentive grouping is its own attentional prime” (Grossberg, 1999a).

The LAMINART model hereby shows how, by joining together bottom-up (interlaminar) adaptive filtering, horizontal (intralaminar) grouping, top-down intracortical (but interlaminar) preattentive feedback, and top-down intercortical (and interlaminar) attentive feedback, some developmental and learning processes can be stabilized without top-down attention. This is realized by using intracortical feedback processes that activate the same stabilizing networks that top-down intercortical attentional processes use. Because of this intimate link between intracortical and intercortical feedback processes, attention can modulate the selection and activation level of

preattentive grouping processes, as in the case of the Roelfsema et al. (1998) data.

Balanced excitatory and inhibitory circuits as a cortical design principle

The circuits that realize grouping and attentional processes compute balanced excitatory and inhibitory interactions. The excitatory/inhibitory balance within layer 2/3 circuits helps achieve perceptual grouping. The balance between excitatory and inhibitory interactions within the on-center of the network from layer 6-to-4 helps to do several things, among them render top-down attention modulatory. Figure 2 shows only these two types of balanced excitatory and inhibitory circuits. Other cortical interactions also balance excitation and inhibition, including the interactions that realize *monocular* simple cell receptive fields in layer 4 (data: Palmer and Davis, 1981; Pollen and Ronner, 1981; Liu et al., 1992; model: Olson and Grossberg, 1998). Balanced excitatory/inhibitory interactions within layer 3B also give rise to *binocular* simple cells that initiate stereopsis by matching monocular inputs from different eyes (Grossberg and Howe, 2003; Cao and Grossberg, 2005).

The balanced interactions within layer 2/3, and those from layer 6-to-4, as in Fig. 2, can explain data in which the excitatory/inhibitory balance is altered by sensory inputs. Figure 5 summarizes data of Polat et al. (1998) on contrast-dependent perceptual grouping in primary visual cortex, and a model simulation of Grossberg and Raizada (2000). The excitatory effects that enable colinear flankers to facilitate activation in response to a low-contrast target are mediated by layer 2/3 interactions, and the inhibitory effects that cause colinear flankers to depress activation in response to a high-contrast target are mediated by the layer 6-to-4 off-surround. These two types of effects propagate throughout the network via layer 4-to-2/3 and layer 2/3-to-6 interactions, among others. An important factor in the model simulation is that the inhibitory interactions are of shunting type (Grossberg, 1973, 1980; Heeger, 1992;

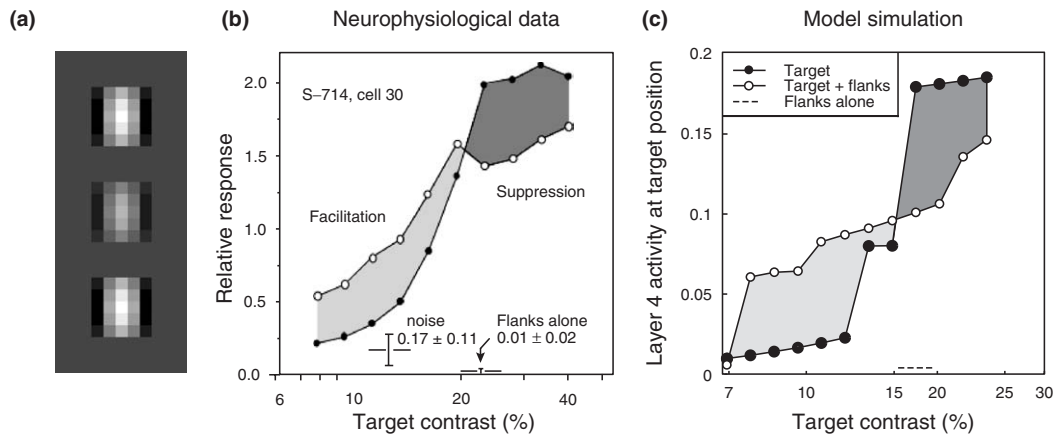


Fig. 5. Contrast-dependent perceptual grouping in primary visual cortex. (a) Illustrative visual stimuli. A variable-contrast oriented Gabor patch (middle stimulus pattern) stimulates the classical receptive field (CRF), with collinear flanking Gabors of fixed high-contrast outside of the CRF (the two end stimulus patterns). The stimulus shown here, based on those used (Polat et al., 1998), was presented to the model neural network. (b) Neural responses recorded from cat V1. The colinear flankers have a net facilitatory effect on weak targets which are close to the contrast-threshold of the cell, 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. (Adapted with permission from Polat et al. (1998).) (c) Model simulation of the Polat et al. data. (Adapted with permission from Grossberg and Raizada (2000).)

Douglas et al., 1995) and thereby compute cell activations that are contrast-normalized.

How can perceptual grouping data be explained as a manifestation of excitatory/inhibitory balance? In cortical area V2 of monkeys, approximately colinear interactions from approximately co-oriented cells are capable of firing a cell that does not receive bottom-up inputs (von der Heydt et al., 1984; Peterhans and von der Heydt, 1989), as occurs when an illusory contour is perceived. The von der Heydt et al. (1984) experiment confirmed a prediction of Grossberg and colleagues (Cohen and Grossberg, 1984; Grossberg, 1984; Grossberg and Mingolla, 1985a, b) that perceptual grouping obeys a *bipole property* (Fig. 6); namely, such a cell can fire if it gets approximately colinear horizontal inputs from approximately co-oriented cells on both sides of its receptive field, even if it does not receive bottom-up input; or it can fire in response to bottom-up input alone, or to bottom-up input plus any combination of horizontal signals. The predicted bipole receptive field structure has been supported by later psychophysical experiments; e.g., Field et al. (1993) and Kellman and Shipley (1991), and anatomical experiments; e.g., Bosking et al. (1997). The LAMINART model

(Grossberg et al., 1997; Grossberg, 1999a) extended this analysis by predicting how the bipole property may be realized by balanced excitatory/inhibitory interactions within layer 2/3, as summarized in Fig. 6. Without these balanced inhibitory interactions, the growth of horizontal connections during development could proliferate uncontrollably if inhibition is too weak, or could be suppressed entirely if inhibition is too strong (Grossberg and Williamson, 2001).

A synthesis of 3D vision, attention, and grouping

Our discussion so far has not considered how the brain sees the world in depth. Since the original LAMINART breakthrough in the mid-1990s, the model has been consistently extended into the 3D LAMINART model of 3D vision and figure-ground perception. This step was achieved by unifying two previous models: the LAMINART model, which had until that time focused on cortical development, learning, grouping, and attention, but did not consider binocular interactions and 3D vision; and the non-laminar FACADE model of 3D vision and figure-ground

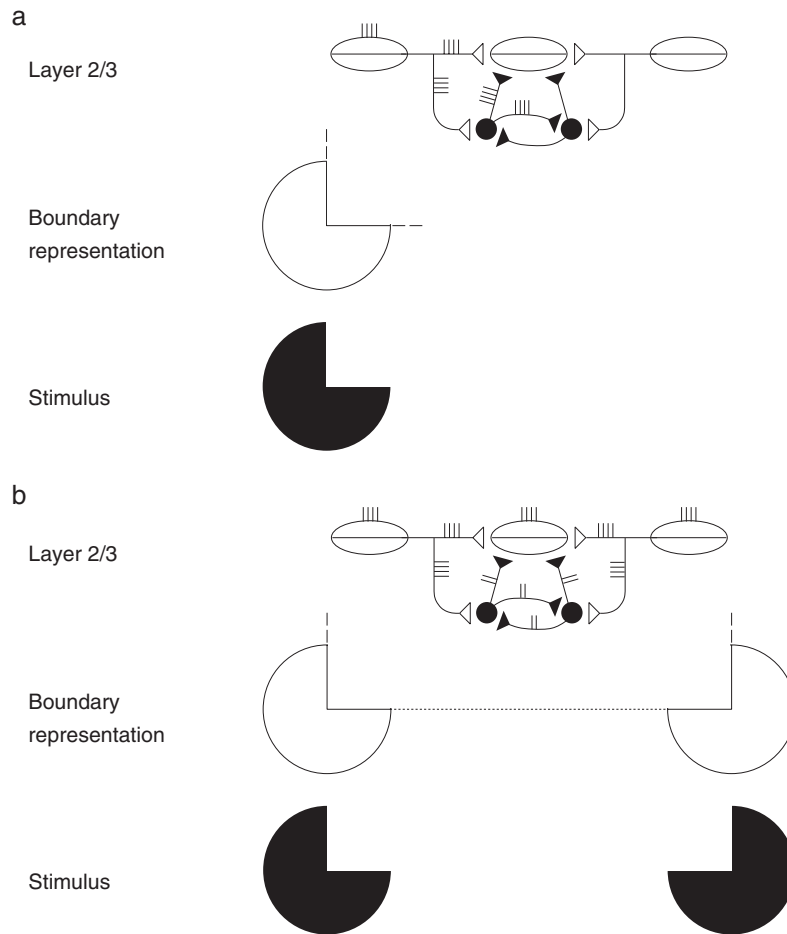


Fig. 6. Schematic of the boundary grouping circuit in layer 2/3. Pyramidal cells with colinear, co-oriented receptive fields (shown as ovals) excite each other via long-range horizontal axons (Bosking et al., 1997; Schmidt et al., 1997), which also give rise to short-range, disynaptic inhibition via pools of interneurons, shown filled-in black (McGuire et al., 1991). This balance of excitation and inhibition helps to implement the *bipole property*. (a) Illustration of how horizontal input coming in from just one side is insufficient to cause above-threshold excitation in a pyramidal cell (henceforth referred to as the target) whose receptive field does not itself receive any bottom-up input. The inducing stimulus (e.g., a Kanizsa 'pacman') excites the oriented receptive fields of layer 2/3 cells, which send out long-range horizontal excitation onto the target pyramidal. This excitation brings with it a commensurate amount of disynaptic inhibition. This balance of "one-against-one" prevents the target pyramidal cell from being excited above-threshold. The boundary representation of the solitary pacman inducer produces only weak, subthreshold colinear extensions (thin dashed lines). (b) When two colinearly aligned inducer stimuli are present, one on each side of the target pyramidal cell receptive field, a boundary grouping can form. Long-range excitatory inputs fall onto the cell from both sides, and summate. However, these inputs fall onto a shared pool of inhibitory interneurons, which, as well as inhibiting the target pyramidal, also inhibit each other (Tamas et al., 1998), thus normalizing the total amount of inhibition emanating from the interneuron pool, without any individual interneuron saturating. The combination of 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 supra-threshold-activated layer 2/3 cells (thick dotted line). Boundary strength scales in a graded analog manner with the strength of the inducing signals. (Adapted with permission from Grossberg and Raizada (2000).)

perception (Grossberg, 1994, 1997; Grossberg and McLoughlin, 1997; McLoughlin and Grossberg, 1998; Kelly and Grossberg, 2000). The resulting unification was able to build upon LAMINART without having to discard any of its mechanisms, and to achieve a much broader explanatory and predictive range. Through this synthesis, the 3D LAMINART model has clarified how the laminar circuits of cortical areas V1, V2, and V4 are organized for purposes of stereopsis, 3D surface perception, and 3D figure-ground perception (Grossberg and Howe, 2003; Grossberg and Swaminathan, 2004; Cao and Grossberg, 2005; Fang and Grossberg, 2005; Grossberg and Yazdanbakhsh, 2005). As a result, the 3D LAMINART model predicts how cellular and network mechanisms of 3D vision and figure-ground perception are linked to mechanisms of development, learning, grouping, and attention. The following discussion merely hints at how this generalization builds seamlessly upon the already available LAMINART foundation. The original articles should be consulted for data support and model explanations and simulations of 3D vision data.

In the 3D LAMINART model, layer 4 no longer directly activates layer 2/3, as in Fig. 2c. Instead, layer 4 monocular simple cells first activate layer 3B binocular simple cells, which in turn activate layer 2/3A binocular complex cells, as shown in Fig. 7. The layer 2/3A cells can then interact via horizontal interactions, like those summarized in Figs. 2c, e, to enhance cell activations due to approximately co-oriented and colinear inputs. Second, binocular complex cells in layer 2/3A can represent different disparities, and thus different relative depths from an observer. Interactions between layer 2/3A cells that represent the same relative depth from the observer can be used to complete boundaries between object contours that lie at that depth.

Because binocular fusion begins already in layer 3B, the binocular boundaries that are formed in layers 3B and 2/3A may be positionally displaced, or shifted, relative to their monocular input signals from layers 6 and 4. Figure 2c illustrates that these layer 2/3 boundaries feed signals back to layer 6 in order to select the winning groupings that are formed in layer 2/3, but issues about binocular

shifts did not need to be considered in data explanations of the original LAMINART model. Signals from the monocular layer 4 cells activate positionally shifted binocular cells in layer 3B, which in turn activate layer 2/3A binocular complex cells. This raises the question: How can the positionally displaced binocular boundaries in layer 2/3A of Fig. 6 contact the correct monocularly activated cells in layers 6 and 4, so that they can complete the feedback loop between layers 2/3-6-4-3B-2/3A that can select winning 3D groupings?

The 3D LAMINART model proposes that horizontal connections, which are known to occur in layers 5 and 6 (Callaway and Wiser, 1996), accomplish this. Feedback signals from layer 2/3A propagate vertically to layer 5, whose cells activate horizontal axons in this layer that contact the appropriate layer 6 cells. These layer 5-to-6 horizontal contacts are assumed to be selectively formed during development. Grossberg and Williamson (2001) and Grossberg and Seitz (2003) have simulated how layer 2/3 connections and layer 6-to-4 connections may be formed during development. The selective layer 5-to-6 contacts are proposed to form according to similar laws. In summary, *inward* horizontal layer 4-to-3B and 2/3A-to-2/3A connections are proposed to form binocular cells and their groupings, while *outward* layer 5-to-6 connections are proposed to close the feedback loops that help to select the correct 3D groupings.

Given how 3D groupings in layer 2/3A contact the correct layer 6 cells, the preattentive—attentive interface problem forces a proposal for how attention fits into the 3D circuit: namely, top-down attentional outputs from layer 6 of a higher cortical level like V2 activates the same layer 5 cells that contact monocular input sources in layer 6 via horizontal connections. Then the layer 6-to-4 modulatory on-center, off-surround network controls attentional priming and matching, just like in Fig. 2b. This proposal raises the question of how the top-down pathways from layer 6 of a higher cortical level know how to converge on the same layer 5 cells to which the layer 2/3 cells project at the lower cortical level? Since firing of the layer 2/3 cells activates the layer 5 cells as well as the layer 6 cells of the higher cortical level, this may occur due to associative learning.

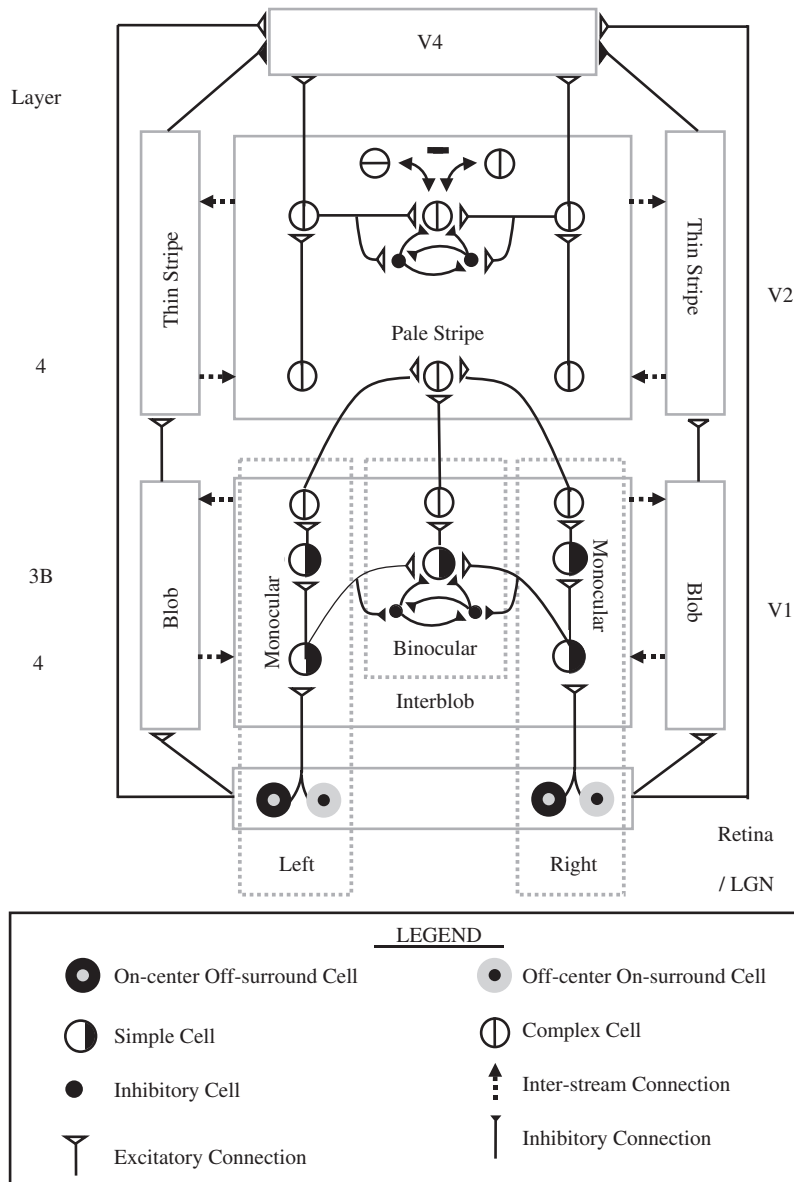


Fig. 7. Model circuit diagram. The full 3D LAMINART model consists of a boundary stream that includes V1 interblobs, V2 pale stripes, and part of V4, and computes 3D perceptual groupings; and a surface stream that includes V1 blobs, V2 thin stripes, and part of V4, and computes 3D surfaces that are infused with color and lightness in depth. These two streams both receive illuminant-discounted signals from Retina/LGN cells, and interact with each other to overcome their complementary deficiencies to create consistent 3D boundary and surface percepts in cortical area V4. Also, 3D boundary and surface representations formed in the pale stripes and thin stripes of cortical area V2, respectively, are amodally completed, and provide neural support for the object recognition process in inferotemporal cortex.

As noted above, Grossberg and Versace (2005, 2006, 2007) have proposed an elaboration of the LAMINART model, called the Synchronous Matching Adaptive Resonance Theory (SMART)

model, in which such learning processes are studied down to the level of individual spikes and dendrites. This model extends laminar cortical modeling in a different direction by investigating

how synchronization of neuronal spiking occurs within and across multiple brain regions, including how neocortical areas interact with higher-order specific and nonspecific thalamic nuclei, and how synchronization abets synaptic plasticity using STDP. The SMART extension of LAMINART also proposes a functional explanation for the differential expression of oscillation frequencies, notably gamma and beta, during match (gamma) or mismatch (beta) between bottom-up thalamic input and top-down cortical expectations, and of aggregate cell recordings such as current-source densities and local field potentials. The main fact for our present review is that a rational extension of LAMINART can bridge between all the processing levels that join individual spikes to cognitive information processing, and that SMART has begun to quantitatively simulate, and functionally rationalize, data on all these organizational levels.

Habituation, development, reset, and bistability

In addition to fast mechanisms of activation and slower mechanisms of learning, another intermediate time scale is needed to control cortical dynamics; notably, activity-dependent habituation mechanisms, as was noted above in the discussion of attentional shrouds. In particular, habituation of chemical transmitter gates has proved to be essential in studies of cortical development (Grunewald and Grossberg, 1998; Olson and Grossberg, 1998; Grossberg and Seitz, 2003); see Grossberg (2003b) for a review. The habituation mechanisms prevent the developmental process from “getting stuck” into activating, over and over, the cells that initially win the competition. Such perseveration would prevent multiple feature combinations from getting represented in a distributed fashion throughout the network. Habituation interactions help to solve this problem because habituation is activity-dependent: only those cells or connections habituate that are in active use. Thus, when habituation acts, it selectively weakens the competitive advantage of the initial winners, so that other cells can become activated to represent different input features.

Habituation mechanisms play an important role in adult vision by helping to *reset* previously active visual representations when the scenes or images that induced them change or disappear. Without such an active reset process, visual representations could easily persist for a long time due to the hysteresis that could otherwise occur in circuits with as many feedback loops as those in Figs. 2 and 7. In many examples of this reset process, offset of a previously active input leads to an *antagonistic rebound* of activation of previously inactive cells, and these newly activated cells help to inhibit the previously active cells, including grouping cells in layer 2/3. This reset process is not perfect, however, and there are large perceptual databases concerning residual effects of previously active representations. In fact, such a reset process has elsewhere been used to explain psychophysical data about visual aftereffects (Francis and Grossberg, 1996; Grunewald and Lankheet, 1996), visual persistence (Francis et al., 1994), and binocular rivalry (Grossberg, 1987; Arrington, 1993, 1995, 1996; Liang and Chow, 2002), among other data that are all proposed to be manifestations of the reset process. Ringach et al. (1999) have reported direct neurophysiological evidence for rebound phenomena using reverse correlation techniques to analyze orientational tuning in neurons of cortical area V1. Abbott et al. (1997) have provided direct experimental evidence in visual cortex of the habituation mechanisms that were predicted to cause the reset (Grossberg, 1968, 1969, 1980). Grossberg (1980, 1999b) also predicted that such reset processes play a role in driving the reset and memory search processes that help the adult brain to rapidly discover and learn new representations of the world, as part of ART.

The same habituation mechanisms that usually phasically reset active brain representations can also lead to persistent multistable percepts when two or more 3D interpretations of a 2D image are approximately equally salient, as in Necker cube percepts, and also during binocular rivalry. Grossberg and Swaminathan (2004) have used the same habituation and competitive mechanisms to simulate development of disparity-gradient cell receptive fields and how a 2D Necker cube image generates bi-stable 3D boundary and surface representations.

In summary, there is a predicted link, mediated by habituating transmitter mechanisms, between processes of cortical development in the infant and processes of perceptual and cognitive reset, learning, and bistability in the adult. This link is worthy of a lot more experimental study than it has received to date.

Towards a unified theory of laminar neocortex: from vision to cognition

The results above focus on vision, which is a spatial process, or more accurately, a SPATIO-temporal process. Can LAMINART principles be used to explain data about the temporal dynamics of cognitive information processing, which involves more spatio-TEMPORAL processes? In particular, how do the layered circuits of prefrontal and motor cortex carry out working memory storage, sequence learning, and voluntary, variable-rate performance of event sequences? A neural model called LIST PARSE (Pearson and Grossberg, 2005; Grossberg and Pearson, 2006) proposes an answer to this question that unifies the explanation of cognitive, neurophysiological, and anatomical data from humans and monkeys. It quantitatively simulates human cognitive data about immediate serial recall and free recall, and monkey neurophysiological data from the prefrontal cortex obtained during sequential sensory-motor imitation and planned performance. The human cognitive data include bowing of the serial position performance curves, error-type distributions, temporal limitations upon recall accuracy, and list length effects. LIST PARSE also qualitatively explains cognitive effects related to attention, temporal grouping, variable presentation rates, phonemic similarity, presentation of non-words, word frequency/item familiarity and list strength, distracters and modality effects.

The model builds upon earlier working memory models that predict why both spatial and nonspatial working memories share the same type of circuit design (Grossberg, 1978). These Item and Order working memories, also called Competitive Queuing models (Houghton, 1990), propose rules for the storage of event sequences in working

memory as evolving spatial patterns of activation. LIST PARSE proposes how to embody an Item and Order cognitive working memory model into the laminar circuits of ventrolateral prefrontal cortex. Such Competitive Queuing models have gradually become the dominant model for how to temporarily store sequences of events in working memory.

Grossberg (1978) derived this class of models from an analysis of how to store sequences of speech or motor items in working memory in a manner that can be stably coded in long-term memory (e.g., word, language, and skill learning) without destabilizing previously learned list categories that are subcategories of the new ones being learned. For example, how do you learn a list category for the novel word MYSELF when you already know the words MY, SELF, and ELF? The main design principle is called the LTM Invariance Principle. An exciting consequence of the LTM Invariance Principle is that the following types of activity patterns naturally emerge across the items that are stored in working memory: (1) primacy gradients of activity across the stored items wherein the earliest items are stored with the greatest activity — a primacy gradient can control the correct order of recall; (2) recency gradients, which control a backwards order of recall; and (3) bowed gradients, which permit recall of items at the list ends before the items near the list middle, and with higher probability than the list middle. Even if a primacy gradient is stored for a short list, a bowed gradient will then always emerge for a sufficiently long list. As just noted, bowing means that the system is not able to reproduce the correct order from working memory, because items near the list end will be recalled before items in the middle. Thus, the inability to read-out the correct order of long lists from working memory can be traced to a constraint on the design of working memories that ensures stable learning of list categories, or chunks.

Any model of working memory needs to confront the question of how it evolved during natural selection. Happily, the LTM Invariance Principle can be realized by the same sort of shunting on-center off-surround network that is so frequently found in other parts of the brain, notably the

visual cortex (Bradski et al., 1992; Grossberg, 1978, 1994). These on-center off-surround networks must be recurrent, or feedback, networks whose positive and negative feedback signals establish and store the spatial patterns of activity that represent the stored working memory. Specialization of how these recurrent networks sequentially rehearse their stored patterns and reset each rehearsed item is what sets them apart from other recurrent shunting on-center off-surround networks across the brain.

LIST PARSE is a LAMINART-style model that illustrates how variations on granular laminar cortical circuits can quantitatively simulate data about spatio-TEMPORAL cognitive processes as well as SPATIO-temporal visual processes. The family of LAMINART models now allows us to understand as variations of a shared cortical design brain processes that seem to be totally unrelated on the level of behavioral function. As just one example, LAMINART predicts that the volitional mechanism which allows humans to experience visual imagery and fantasy, is the same mechanism, suitably specialized, that regulates the storage of event sequences in working memory. The volitional gain control mechanism that is predicted to carry out this function may be realized by inhibition of inhibitory interneurons in layer 4 of both cortical areas. It remains to be seen how such LAMINART mechanisms are specialized within the laminar circuits of other cortical areas to realize a variety of intelligent behaviors.

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