CHAPTER

107

Linking Attention to Learning, Expectation, Competition, and Consciousness

Stephen Grossberg

ABSTRACT

The concept of attention has been used in many senses, often without clarifying how or why attention works as it does. Attention, like consciousness, is often described in a disembodied way. The present article summarizes neural models and supportive data about how attention is linked to processes of learning, expectation, competition, and consciousness. A key theme is that attention modulates cortical self-organization and stability. The perceptual and cognitive neocortex is organized into six main cell layers, with characteristic sublamina. Attention is part of a unified design of bottom-up, horizontal, and top-down interactions among identified cells in laminar cortical circuits. Neural models clarify how attention may be allocated during processes of visual perception, learning, and search; auditory streaming and speech perception; movement target selection during sensory-motor control; mental imagery and fantasy; and hallucinations during mental disorders, among other processes.

I. INTRODUCTION

Attention is a behavioral concept, but one whose properties arise from brain mechanisms. To fully understand how attention works, we need to mechanistically link brain mechanisms to the attentive behavioral functions that they control. Building brain-behavior links for processes of attention is particularly challenging because attention is typically a modulatory process that can sensitize, or prime, an observer to expect an object to occur at a given location or with particular stimulus properties (Posner, 1980; Duncan, 1984). Were attention, by itself, able to routinely activate fully formed perceptual representations, then we could not tell the difference between external reality and internal fantasy or hallucination. Thus, to fully understand attention, we need to explain the brain processes that attention is modulating. A rapidly growing number of models can now quantitatively simulate the neurophysiologically recorded dynamics of identified nerve cells in known anatomies *and* the behaviors that they control, and these models naturally include attentional processes.

This article emphasizes models and data about how attention is realized within the laminar circuits of neocortex. Neural system models have also clarified how attention may be allocated during many different tasks.

II. LINKING ATTENTION TO LEARNING, EXPECTATION, COMPETITION, SYNCHRONIZATION, AND CONSCIOUSNESS

Neural models of perception and cognition have predicted that top-down attention is a key mechanism for solving the stability-plasticity dilemma (Grossberg, 1980, 1999b), which concerns the fact that brains can rapidly learn enormous amounts of information throughout life without just as rapidly forgetting what they already know. How do attentive processes within neocortex help to stabilize cortical learning and memory through time so that they are not catastrophically overwritten by the new stimuli with which they are continually bombarded?

Adaptive Resonance Theory (ART) proposes to explain how attention helps to solves the stability-plasticity dilemma by modeling how bottom-up signals activate top-down expectations whose signals are matched against bottom-up data. Both the bottom-up and top-down pathways contain adaptive weights, or long-term memory traces, that may be modified by experience (Fig. 107.1A). The learned top-down expectations focus attention on information that matches them (Fig. 107.1B). They select, synchronize, and amplify the activities of cells within the attentional focus while suppressing the activities of irrelevant cells that which could otherwise be incorporated into previously learned memories and thereby destabilize them. The cell activities that survive such top-down attentional focusing rapidly reactivate bottom-up pathways (Fig. 107.1A), thereby generating a feedback resonance between bottom-up and top-down signal exchanges. Such resonances rapidly bind distributed information at multiple levels of brain processing into context-sensitive representations of objects and events. These resonances are proposed to support slower processes of learning, hence the name adaptive resonance. ART also predicts that "All conscious states are resonant states." Thus, ART links attention to processes of learning, expectation, competition, synchronization, and consciousness.

Since these predictions were made in the 1970*s*, many experimental and modeling studies have provided support for them. Some relevant experiments are summarized here. Other chapters in this volume provide additional supportive evidence (e.g., Chapters 25, 44, 49, 50, 66, 81, and 88).

Mathematical analyses have proved how easily learning can lead to catastrophic forgetting in response to a changing world and how top-down attention can stabilize learning if it satisfies four properties (Carpenter and Grossberg, 1991), which together are called the ART Matching Rule:

Bottom-up automatic activation. A cell, or cell population, can become active enough to generate output signals if it receives a large enough bottom-up input, other things being equal. Such an input can drive the cell to suprathreshold levels of activation.

Top-down priming. A cell cannot fire if it receives only a large top-down expectation input. Such a top-down signal can modulate, prime, or sensitize the cell and thereby prepare it to react more quickly and vigorously to subsequent bottom-up inputs that approximately match the top-down expectation. A top-down signal can also shift the baseline firing rate of the cell. It cannot, however, generate large behaviorally significant output signals from the cell.

Match. A cell can fire if it receives large convergent bottom-up and top-down inputs. Such a matching process can generate enhanced and synchronized cell activation as resonance takes hold.

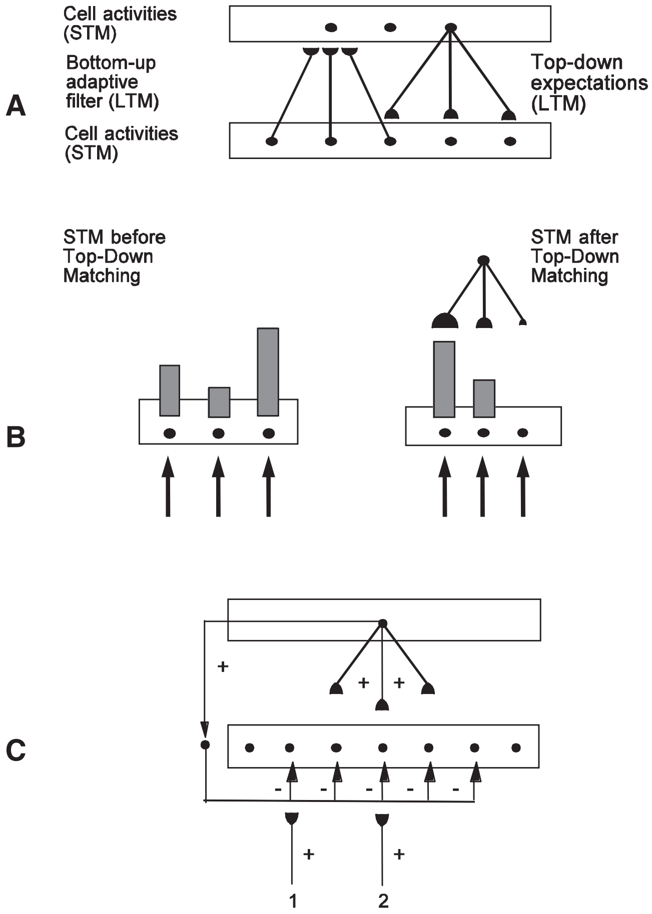

FIGURE 107.1 (A) Patterns of activation, or short-term memory (STM), on a lower processing level send bottom-up signals to a higher processing level. These signals are multiplied by adaptive weights, or learned long-term memory (LTM) traces, which influence the activation of the cells at the higher processing level. These latter cells, in turn, activate top-town expectation signals that are also multiplied by learned LTM traces. These top-down expectations are matched against the STM pattern that is active at the lower level. (B) This matching processes, confirms, amplifies, and synchronizes STM activations that are supported by large LTM traces in an active top-down expectation and suppresses STM activations that do not get top-down support, thereby focusing attention on the representations encoded by the selected cells. The size of the hemidisks at the end of the top-down pathways represents the strength of the learned LTM trace that is stored in that pathway. (C) The ART Matching Rule may be realized by a top-down modulatory on-center off-surround network. (Reprinted with permission from Grossberg, 1999a).

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

The simplest mathematically possible circuit (Carpenter and Grossberg, 1991), a top-down modulatory on-center off-surround network (Fig. 107.1), has successfully been used to simulate a variety of behavioral and brain data (Grossberg, 1999b). In such a circuit, when only bottom-up signals are active, all cells can fire that receive large enough inputs. When only top-down attention is active, cells in the off-surround that receive inhibition but no excitation can get strongly inhibited, whereas cells in the on-center that receive a combination of excitation and inhibition can get at most subliminally activated due to an approximate balance between excitation and inhibition. When bottom-up and top-down inputs match (pathway 2 in Fig. 107.1C), the two excitatory sources of excitation (bottom-up and top-down) that converge at the cell can overwhelm the one inhibitory source; it is a case of two against one that can lead to synchronous firing. When bottom-up and top-down inputs mismatch (pathway 1 in Fig. 107.1C), the top-down inhibition can neutralize the bottom-up excitation; it is a case of one against one.

III. ATTENTION IS MODULATORY

The ART Matching Rule predicts that top-down attention accomplishes modulatory priming and matching by using competitive mechanisms such as the top-down modulatory on-center off-surround network in Fig. 107.1C. Data compatible with this prediction were gradually reported over the years, with an acceleration of experiments during the past 5 years. For example, Zeki and Shipp (1988, 316) wrote that "backward connections seem not to excite cells in lower areas, but instead influence the way they respond to stimuli." Likewise, the data of Sillito et al. (1994, 479–482) on attentional feedback from V1 to LGN led them to conclude that "the cortico-thalamic input is only strong enough to exert an effect on those dLGN cells that are additionally polarized by their retinal input. . . . the feedback circuit searches for correlations that support the 'hypothesis' represented by a particular pattern of cortical activity." Their experiments demonstrated all of the properties of the ART Matching Rule—they found in addition that "cortically induced correlation of relay cell activity produces coherent firing in those groups of relay cells with receptive-field alignments appropriate to signal the particular orientation of the moving contour to the cortex. . . . this increases the gain of the input for feature-linked events detected by the cortex." In other words, top-down signaling, by itself, cannot fully activate LGN cells; it needs matched bottom-up retinal inputs to do so, and those LGN cells whose bottom-up signals support cortical activity may get synchronized and amplified by this feedback. In addition, anatomical studies have shown that the top-down V1 to LGN pathway realizes a top-down on-center off-surround network (Dubin and Cleland, 1977; Weber et al., 1989; see Fig. 107.2D).

IV. LAMINAR ORGANIZATION OF BOTTOM-UP, HORIZONTAL, AND TOP-DOWN CONNECTIONS

How are top-down attentional circuits realized within the brain, in particular within perceptual and cognitive neocortex? All the sensory and cognitive neocortex is organized into six main layers of cells. A recent family of LAMINART models (Fig. 107.2) proposes a detailed answer to this question for the interblob stream of visual cortex and, by extension, to other neocortical areas by characterizing how bottom-up, top-down, and horizontal interactions are organized within cortical layers to generate percepts of visual form. In particular, LAMINART shows how these interactions help visual cortex to realize: (1) stable development and learning of circuit connections and weights in response to a changing environment, (2) coherent grouping or binding of distributed information into boundary representations of objects and events without a loss of analog sensitivity—the property of analog coherence, and (3) attentional focusing on important object representations at the expense of less important representations (Grossberg, 1999a; Grossberg, Mingolla, et al., 1997; Grossberg and Raizada, 2000; Grossberg and Seitz, 2003; Grossberg and Williamson, 2001; Raizada and Grossberg, 2001). Three important implications of this result are as follows.

First, biological vision systems are not merely bottom-up filtering devices, as Hubel and Wiesel proposed in their classical analysis of early vision. Rather, even early stages of visual cortex join together bottom-up filtering, horizontal grouping, and top-down attention. Perceptual grouping, the process that binds spatially distributed and incomplete information into 3D object representations, starts at an early cortical stage; see Fig. 107.2C. These grouping interactions are often cited as the basis of nonclassical receptive fields that are sensitive to the context in which individual features are found (Bosking et al., 1997; Grosof et al.,

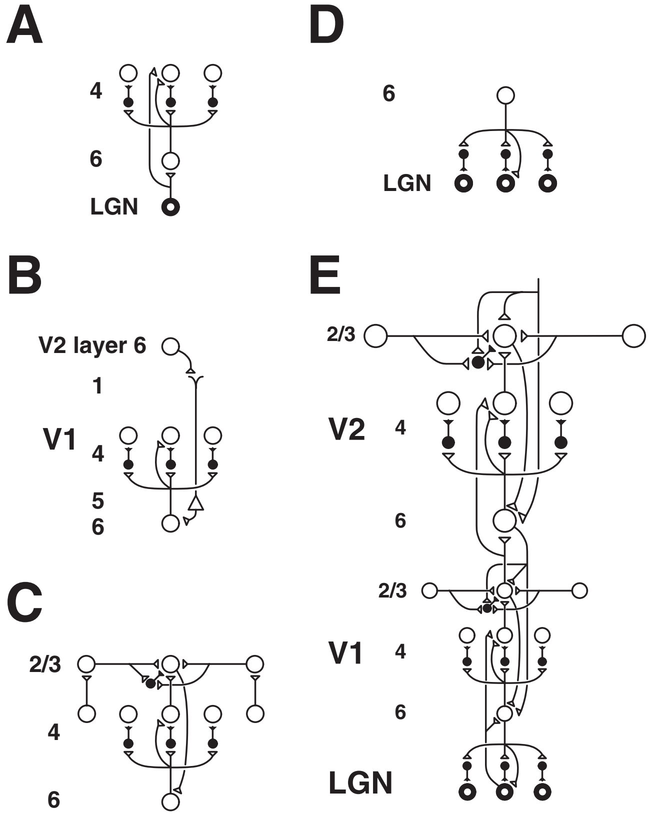

FIGURE 107.2 How known cortical connections join layer 6 → 4 and layer 2/3 circuits to form a laminar V1 and V2 model. Inhibitory interneurons are shown as solid black. (A) The LGN provides bottom-up activation to layer 4 via two routes. First, it makes a strong connection directly into layer 4. Second, LGN axons send collaterals into layer 6 and thereby also activate layer 4 via the 6 → 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, 1980; Heeger, 1992) of layer 4 cell responses. (B) Folded feedback carries attentional signals 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 layer 1 of the lower cortex, where they can excite the apical dendrites of layer 5 pyramidal cells whose axons send collaterals into layer 6. The triangle represents such a layer 5 pyramidal cell. Several other routes through which feedback can pass into V1 layer 6 exist. 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. (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. Direct layer 2/3 → 6 connections in macaque V1 exist, 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, and the off-surround contributes to length-sensitive (end-stopped) 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. 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 (B). Their synapses on apical dendrites in layer 1 are not shown, for simplicity. (Reprinted with permission from Raizada and Grossberg 2001, where supportive data references are cited).

1993; Kapadia et al., 1995; Knierim and van Essen, 1992; Peterhans and von der Heydt, 1989; Polat et al., 1998; Sheth et al., 1996; von der Heydt et al., 1984; Sillito et al., 1995).

Second, even early visual processing is modulated by system goals via top-down expectations and attention (Motter, 1993; Roelfsema et al., 1998; Sillito et al., 1994; Somers et al., 1999; Watanabe et al., 1998). In particular, Fig. 107.2B illustrates how layer 6 of a higher cortical area can modulate layer 4 of a lower cortical area via a top-down on-center off-surround circuit. It can do so, for example, by activating apical dendrites in layer 1 of layer 5 cells, which activate layer 6 cells. Layer 6 cells, in turn, can activate layer 4 through a modulatory on-center off-surround network. Such a circuit exemplifies folded feedback (Grossberg, 1999a); namely, top-down signals are folded back into the feedforward flow of visual information processing. The 6-to-4 network is thus predicted to be an interface, called the preattentive-attentive interface, where data-driven bottom-up pre-attentive processing and task-directed top-down attentive processing are fused together via a shared decision circuit.

This layer 6-to-4 modulatory decision circuit realizes at least three functional roles in the model: contrast normalization of bottom-up inputs from earlier processing levels (Fig. 107.2A), selection of winning groupings that start to form in layer 2/3 via horizontal connections while preserving their analog coherence in response to intracortical feedback (C), and attentional priming in response to intercortical feedback from a higher cortical level (B). In particular, attention shares the same decision circuit as pre-attentive filtering and grouping, which is how attention can do its work. Attention can also directly modulate layer 2/3 groupings by activating the dendrites in layer 1 of excitatory and inhibitory cells in layer 2/3 (Lund and Wu, 1997; Rockland, and Virga, 1989). A balance between excitation and inhibition has been predicted to be a basic design principle in perceptual grouping (Grossberg, 1999a; Grossberg and Raizada, 2000). By activating both excitatory and inhibitory cells in layer 2/3, inhibitory interneurons that synapse on excitatory cells may balance their activation, thereby enabling attention to directly modulate the responses of grouping cells in layer 2/3.

Third, mechanisms governing property (1) in the infant lead to properties (2) and (3) in the adult. Thus, mechanisms that enable the cortex to learn in a stable way *define* key properties of adult visual information processing. This last result shows that learning and information processing need to be codesigned for either to work well in a novel environment.

V. ATTENTION, COMPETITION, AND MATCHING

Both ART and LAMINART predict that attention from higher cortical areas, such as area V2, acts on cells in area V1 via a top-down modulatory on-center off-surround network. Experiments of Hupé et al. (1997, 1031) support this prediction by showing that "feedback connections from area V2 modulate but do not create center-surround interactions in V1 neurons." More generally, 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 et al., 1999; Smith et al., 2000; Somers et al., 1999; Sillito et al., 1994; Steinman et al., 1995; Vanduffell et al., 2000). In particular, the claim that bottom-up sensory activity is enhanced when matched by top-down on-center signals is in accord with an extensive neurophysiological literature showing the facilitatory effect of attentional feedback (Luck et al., 1997; Roelfsema et al., 1998; Sillito et al., 1994), but not with models in which matches with top-down feedback cause suppression (Mumford, 1992; Rao and Ballard, 1999). ART predicts that on-center off-surround attentional feedback should exist in all sensory and cognitive systems that are capable of stable online learning. In particular, 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), as does feedback in the rodent barrel system (Temereanca and Simons, 2001).

Top-down attention through competitive matching has also been used to explain data about 3D figure-ground separation (Kelly and Grossberg, 2000), visual object learning and recognition (Bradski and Grossberg, 1995; Carpenter and Ross, 1995; Grossberg, 1999b), visual search (Grossberg et al., 1994), visual motion perception (Chey et al., 1997; Grossberg, Mingolla, and Viswanathan, 2001), auditory streaming (Grossberg, 1999b), speech perception and word recognition (Grossberg et al., 1997; Grossberg and Myers, 2000; Grossberg and Stone, 1986), selection of eye movement targets (Grossberg, Roberts, et al., 1997), and imagery, fantasy, and hallucinations (Grossberg, 2000).

The ART prediction that attention is mediated through competitive mechanisms has recently been restated in terms of the concept of biased competition (Desimone, 1998; see Chapter 50), in which attention biases the competitive influences within the network.

Figure 107.3 summarizes data in 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.

VI. OBJECT-BASED ATTENTION VIA THE PRE-ATTENTIVE-ATTENTIVE INTERFACE

When images that contain unambiguous groupings are processed, the laminar circuit in Fig. 107.2E can react quickly with a fast feedforward sweep of activation through layers 4-to-2/3 in one cortical area then to 4-to-2/3 in a higher cortical area, and so on (Thorpe et al., 1996). When ambiguous and complex scenes are being processed, competitive interactions in layers 4 and 2/3 are predicted to attenuate amplitude and processing rate of cell activation in layer 2/3. Intracortical feedback from layer 2/3-to-6 to 4-to-2/3 enables stronger groupings in layer 2/3 to be contrast-enhanced while they quickly inhibit weaker groupings and then to fire vigorously to higher cortical levels.

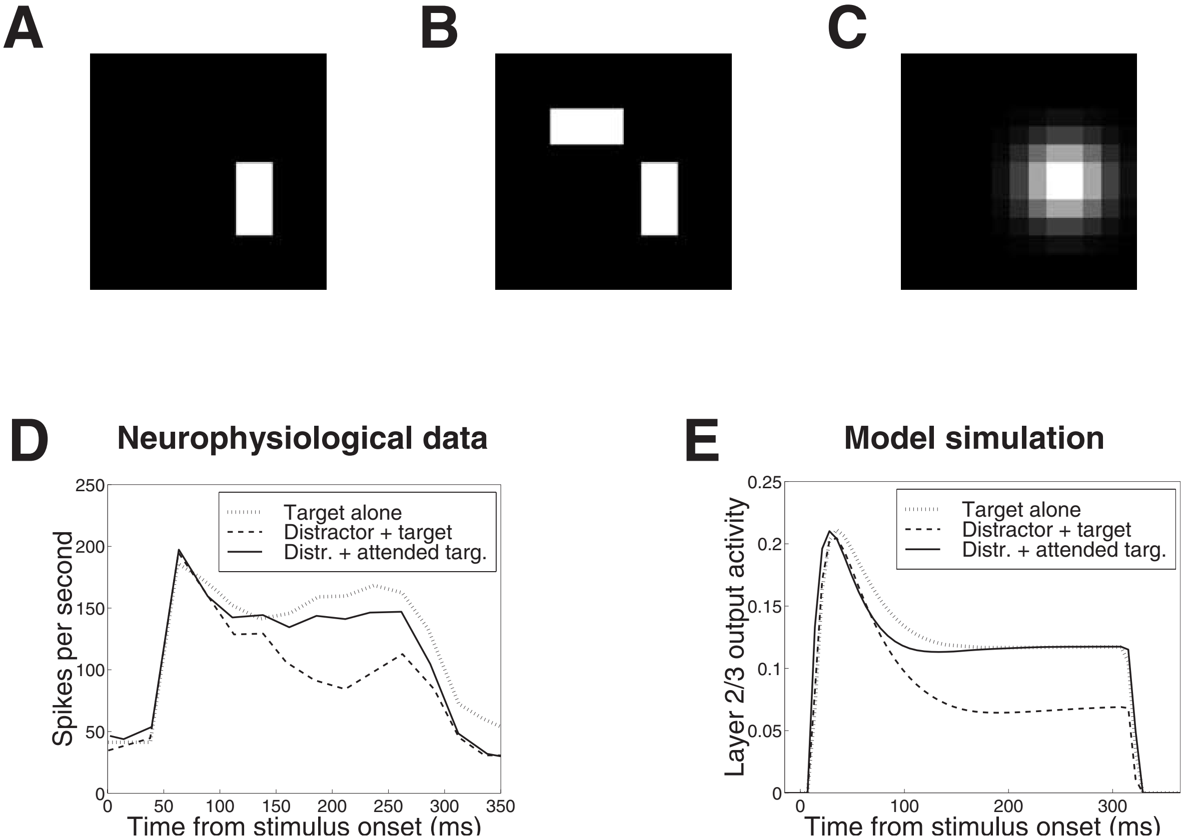

FIGURE 107.3 The effect of attention on competition between visual stimuli. A target stimulus, presented on its own (A), elicits strong neural activity at the recorded cell. When a second, distractor stimulus is presented nearby (B), it competes against the target and activity is reduced. Directing spatial 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 in 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 just described: 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. 107.5.) (E) Model simulation of the Reynolds et al. (1999) 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 in which the distractor and target are presented together, with neither attended. (Reprinted with permission from Grossberg and Raizada, 2000.)

Because the cortex uses the same circuits to select groupings (Fig. 107.2C), and to prime attention (B), attention can selectively focus on an entire object by flowing along the perceptual groupings that define the object boundary (Roelfsema et al., 1998; see Fig. 107.4A, B). 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 107.4C summarizes a LAMINART simulation of the Roelfsema et al. (1998) data. LAMINART also simulates the spread of attention along an illusory contour (Raizada and Grossberg, 2001), consistent with experimental data in Moore et al. (1998), thereby illustrating how the cortex can attend incomplete object data.

The ability of attention to selectively light up entire object representations has an obviously important survival value. It is thus of interest that the intracortical and intercortical feedback circuits that control this property have been shown in modeling studies to help stabilize infant development and adult perceptual learning within multiple cortical areas, including cortical areas V1 and V2 (Carpenter and Grossberg, 1991;

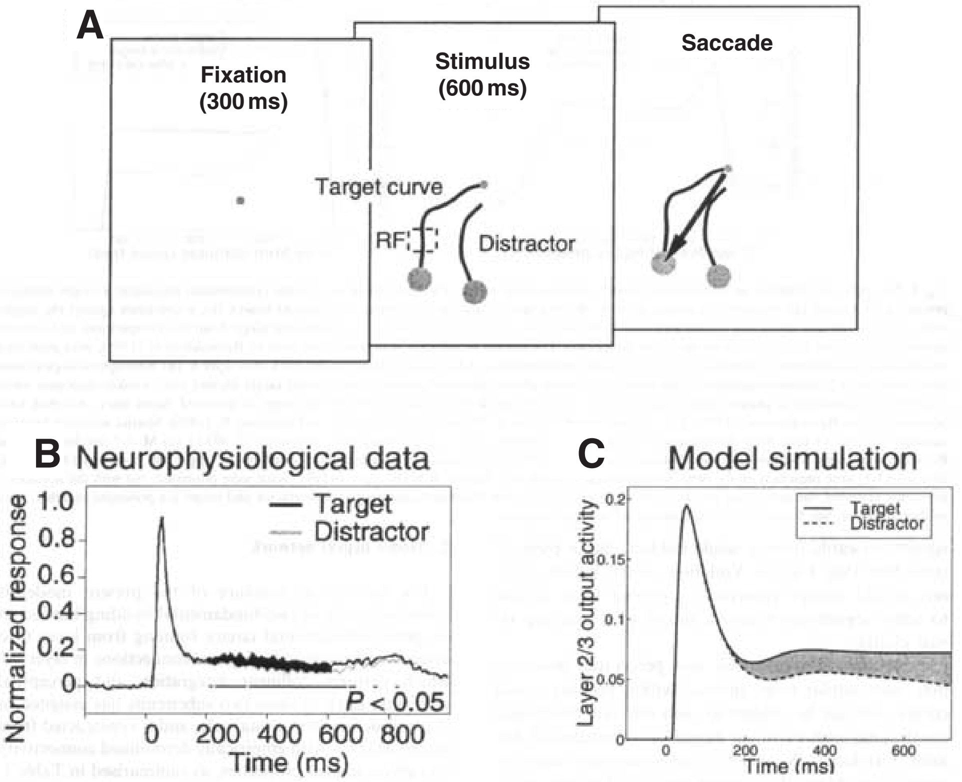

FIGURE 107.4 Spread of visual attention along an object boundary grouping, from an experiment by Roelfsema et al. (1998). (A) The experimental paradigm. Macaque monkeys performed a curve-tracing task, during which physiological recordings were made in V1. A fixation spot was presented for 300 ms, followed by a target curve and a distractor curve presented simultaneously. The target was connected at one end to the fixation point. While maintaining fixation, the monkeys had to trace the target curve and then, after 600 ms, make a saccade to its end point. (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 approximately 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, pers. comm.). This suggests that attentional signals propagate along the length of the target curve. (A and B adapted with permission from Roelfsema et al., 1998.) (C) Model simulation of the Roelfsema et al. data. (Reprinted with permission from Grossberg and Raizada, 2000.)

Grossberg, 1999a, 1999b; Grossberg and Williamson, 2001).

VII. THE LINK BETWEEN ATTENTION AND LEARNING

The ART proposal that attention helps to stabilize cortical development and learning, thereby preventing catastrophic forgetting, suggests that top-down attentional mechanisms should be present in *every* cortical area where these processes occur. The ART solution to the stability-plasticity problem 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 resonance and learning occurs. Precisely because the match is sufficiently close, such learning fine-tunes the memories of existing representations. In this way, outliers cannot cause a radical overwriting of an already learned representation.

ART also proposes how, at higher levels of perceptual and cognitive processing, including inferotemporal and prefrontal cortex, a learning individual can flexibly vary the criterion of how good a match is needed between bottom-up and top-down information in order for presently active recognition categories and their top-down expectations to be refined through learning (Carpenter and Grossberg, 1987; Grossberg, 1999b). This can be achieved by a process called vigilance control, which can alter the criterion of how good a match is needed for resonance to occur. When coarse matches are allowed, a top-down expectation, say from prefrontal to inferotemporal cortex, can learn a prototype that is capable of focusing attention on general and abstract information. When only fine matches are allowed, learned prototypes are more specific and concrete and can focus attention even on individual exemplars, such as particular views of particular faces (Desimone and Ungerleider, 1989; Gochin et al., 1991; Harries and Perrett, 1991).

If the active top-down prototype does not match well enough with the bottom-up input, then its neural activity is extinguished and hence unable to cause plastic changes. Suppression of an active representation enables a memory search to ensue, whereby a different representation can become active instead 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. ART proposes how such a memory search can be mediated by corticohippocampal interactions (Carpenter and Grossberg, 1991, 1993; Grossberg and Merrill, 1996).

This summary of ART-based recognition learning shows how the focus of object attention may become either abstract or concrete, depending on the task-constraints that are imposed. Compatible data from recordings in inferotemporal cortex were reported by Spitzer et al. (1988), who exposed monkeys to easy and difficult discriminations, and showed "in the difficult condition the animals adopted a stricter internal criterion for discriminating matching from nonmatching stimuli. . . . the animals' internal representations of the stimuli were better separated, independent of the criterion used to discriminate them. . . . increased effort appears to cause enhancement of the responses and sharpened selectivity for attended stimuli" (339–340).

Other experiments have also supported the predicted link between attention and learning. 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. These authors also reported that 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. Evidence that cortical feedback also controls thalamic plasticity in the somatosensory system has been found by Krupa et al. (1999) and by Parker and Dostrovsky (1999). These findings are reviewed by Kaas (1999).

Studies of *inter*cortical attention-activated feedback and *intra*cortical grouping-activated feedback have also shown that either type of feedback can rapidly synchronize the firing patterns of higher and lower cortical areas (Grossberg and Grunewald, 1997; Grossberg and Somers, 1991; Yazdanbakhsh and Grossberg, 2004). ART puts this result into perspective by suggesting that resonance may lead to synchronization, which may facilitate cortical learning by enhancing the probability that "cells that fire together wire together." Engel et al. (2001) review data about top-down cortical feedback and synchrony (see also Chapter 87). The cortex also includes circuits that enable development and learning to self-stabilize without top-down *inter*cortical attention by using the *intra*cortical pathway from layer 2/3-to-6 to 4-to-2/3 (see Fig. 107.2C) to act as a selection circuit that inhibits outliers before they can cause catastrophic forgetting; see Raizada and Grossberg (2003) for further discussion.

VIII. DIVIDED, OBJECT VERSUS SPATIAL, AND HIERARCHICAL ATTENTION

Although bottom-up inputs that arrive in the off-surround of an active top-down attentional prime may be suppressed, inputs outside the off-surround may not be suppressed. This is already clear in some conditions of the Reynolds et al. (1999) experiment that is summarized in Fig. 107.3. In fact, many studies have shown that attention may be simultaneously divided among several targets (e.g., Pylyshyn and Storm, 1988; Yantis, 1992). In addition, both object and spatial attention may influence visual perception (Duncan, 1984; Posner, 1980). The distinction between object and spatial attention reflects the organization of visual cortex into parallel "what" and "where" processing streams. Many cognitive neuroscience experiments support the hypotheses of Ungerleider and Mishkin (1982) and Goodale and Milner (1992) that inferotemporal cortex and its cortical projections learn to categorize and recognize what objects are in the world, whereas parietal cortex and its cortical projections learn to determine where they are in space and how to act with respect to them. Because the "what" stream strives to generate invariant object representations that are independent of spatial coordinates, whereas the "where" stream generates representations of object location, these streams must interact to control actions aimed at recognized objects. Indeed, both object and spatial attention are needed to search for visual targets amid distractors. Grossberg et al. (1994) quantitatively fit a large human psychophysical database about visual search with a Spatial Object Search (SOS) model that proposes the way that 3D boundary groupings and surface representations interact with object attention and spatial attention to find targets amid distractors. In this analysis, object and spatial attention must be sensitive to perceptual groupings as well as to surface properties such as all occurrences of a color on a prescribed depth plane (Grossberg, 1994).

The present article focuses on the microarchitecture of attention but is consistent with, and clarifies, how attention may be globally organized across many brain regions acting together. In particular, laminar cortical circuits (Fig. 107.2E) clarify how attention can leap between brain regions via their layers 6 and thereby modulate cells in multiple cortical areas without firing them.

Acknowledgment

Supported in part by the Air Force Office of Scientific Research (AFOSR F49620-01-1-0397) the National Science Foundation (SBE-0354378) and the Office of Naval Research (ONR N00014-01-1-0624).

References

Ahissar, M., and Hochstein, S. (1993). Attentional control of early perceptual learning. *Proc. Natl. Acad. Sci. U.S.*A. **90**, 5718–5722.

Bosking, W. H., Zhang, Y., Schofield, B., and Fitzpatrick, D. (1997). Orientation selectivity and the arrangement of horizontal connections in the tree shrew striate cortex. *J. Neurosci.* **17**, 2112–2127.

Bradski, G., and Grossberg, S. (1995). Fast-learning VIEWNET architectures for recognizing three-dimensional objects from multiple two-dimensional views. *Neural Net.* **8**, 1053–1080.

Bullier, J., Hupé, J. M., James, A., and Girard, P. (1996). Functional interactions between areas V1 and V2 in the monkey. *J. Physiol.* **90**, 217–220.

Caputo, G., and Guerra, S. (1998). Attentional selection by distractor suppression. *Vis. Res.* **38**, 669–689.

Carpenter, G. A., and Grossberg, S. (1987). A massively parallel architecture for a self-organizing neural pattern recognition machine. *Comput. Vis. Graphics Image Processing* **37**, 54–115.

Carpenter, G. A., and Grossberg, S. (eds.) (1991). "Pattern Recognition by Self-Organizing Neural Networks." MIT Press, Cambridge, MA.

Carpenter, G. A., and Grossberg, S. (1993). Normal and amnesic learning, recognition, and memory by a model of cortico-hippocampal interactions. *Trends Neurosci.* **16**, 131–137.

Carpenter, G. A., and Ross, W. D. (1995). ART-EMAP: A neural network architecture for object recognition by evidence accumulation. *IEEE Trans. Neural Net.* **6**, 805–818.

Chey, J., Grossberg, S., and Mingolla, E. (1997). Neural dynamics of motion grouping: From aperture ambiguity to object speed and direction. *J. Opt. Soc. Am. A1* **4**, 2570–2594.

Desimone, R. (1998). Visual attention mediated by biased competition in extrastriate visual cortex. *Phil. Trans. Roy. Soc. London* **353**, 1245–1255.

Desimone, R., and Ungerleider, L. G. (1989). Neural mechanisms of visual processing in monkeys. *In* "Handbook of Neuropsychology" (F. Boller and J. Grafman, eds.), Vol. 2, pp. 267–299. Elsevier, Amsterdam.

Downing, C. J. (1988). Expectancy and visual-spatial attention: Effects on perceptual quality. *J. Exp. Psych. Hum. Perception Performance* **14**, 188–202.

Dubin, M. W., and Cleland, B. G. (1977). Organization of visual inputs to interneurons of lateral geniculate nucleus of the cat. *J. Neurophysiol.* **40**, 410–427.

Duncan, J. (1984). Selective attention and the organization of visual information. *J. Exp. Psych. Gen.* **113**, 501–517.

Engel, A. K., Fries, P., and Singer, W. (2001). Dynamic predictions: Oscillations and synchrony in top-down processing. *Nat. Rev. Neurosci.* **2**, 704–716.

Gao, E., and Suga, N. (1998). Experience-dependent corticofugal adjustment of midbrain frequency map in bat auditory system. *Proc. Natl. Acad. Sci. U.S.A.* **95**, 12663–12670.

Gochin, P. M., Miller, E. K., Gross, C. G., and Gerstein, G. L. (1991). Functional interactions among neurons in inferior temporal cortex of the awake macaque. *Exp. Brain Res.* **84**, 505–516.

Goodale, M. A., and Milner, D. (1992). Separate visual pathways for perception and action. *Trends Neurosci.* **15**, 10–25.

Grosof, D. H., Shapley, R. M., and Hawken, M. J. (1993). Macaque V1 neurons can signal "illusory" contours. *Nature* **365**, 550–552.

Grossberg, S. (1980). How does a brain build a cognitive code? *Psych. Rev.* **87**, 1–51.

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

Grossberg, S. (1999a). How does the cerebral cortex work? Learning, attention, and grouping by the laminar circuits of visual cortex. *Spat. Vis.* **12**, 163–187.

Grossberg, S. (1999b). The link between brain learning, attention, and consciousness. *Consci. Cogn.* **8**, 1–44.

Grossberg, S. (2000). How hallucinations may arise from brain mechanisms of learning, attention, and volition. *J. Intl. Neuropsych. Soc.* **6**, 583–592.

Grossberg, S., Boardman, I., and Cohen, M. A. (1997). Neural dynamics of variable-rate speech categorization. *J. Exp. Psych. Hum. Perception Performance* **23**, 481–503.

Grossberg, S., and Grunewald, A. (1997). Cortical synchronization and perceptual framing. *J. Cogn. Neurosci.* **9**, 117–132.

Grossberg, S., and Merrill, J. W. L. (1996). The hippocampus and cerebellum in adaptively timed learning, recognition, and movement. *J. Cogn. Neurosci.* **8**, 257–277.

Grossberg, S., Mingolla, E., and Ross, W. D. (1994). A neural theory of attentive visual search: Interactions of boundary, surface, spatial, and object representations. *Psych. Rev.* **101**, 470–489.

Grossberg, S., Mingolla, E., and Ross, W. D. (1997). Visual brain and visual perception: How does the cortex do perceptual grouping? *Trends Neurosci.* **20**, 106–111.

Grossberg, S., Mingolla, E., and Viswanathan, L. (2001). Neural dynamics of motion integration and segmentation within and across apertures. *Vis. Res.* **41**, 2521–2553.

Grossberg, S., and Myers, C. W. (2000). The resonant dynamics of speech perception: Interword integration and duration-dependent backward effects. *Psych. Rev.* **4**, 735–767.

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

Grossberg, S., Roberts, K., Aguilar, M., and Bullock, D. (1997). A neural model of multimodal adaptive saccadic eye movement control by superior colliculus. *J. Neurosci.* **17**, 9706–9725.

Grossberg, S., and Seitz, A. (2003). Laminar development of receptive fields, maps, and columns in visual cortex: The coordinating role of the subplate. *Cereb. Cortex.* **13**, 852–863.

Grossberg, S., and Somers, D. (1991). Synchronized oscillations during cooperative feature linking in a cortical model of visual perception. *Neural Net.* **4**, 453–466.

Grossberg, S., and Stone, G. O. (1986). Neural dynamics of word recognition and recall: Attentional priming, learning, and resonance. *Psych. Rev.* **93**, 46–74.

Grossberg, S., and Williamson, J. R. (2001). A neural model of how horizontal and interlaminar connections of visual cortex develop into adult circuits that carry out perceptual groupings and learning. *Cereb. Cortex* **11**, 37–58.

Harries, M. H., and Perrett, D. I. (1991). Visual processing of faces in temporal cortex: Physiological evidence for a modular organization and possible anatomical correlates. *J. Cogn. Neurosci.* **3**, 9–24.

Heeger, D. J. (1992). Normalization of cell responses in cat striate cortex. *Vis. Neurosci.* **9**, 181–197.

Hupé, J. M., James, A. C., Girard, D. C., and Bullier, J. (1997). Feedback connections from V2 modulate intrinsic connectivity within V1. *Soc. Neurosci. Abstracts* 406.15, 1031.

Kaas, J. H. (1999). Is most of neural plasticity in the thalamus cortical? *Proc. Natl. Acad. Sci. U.S.A.* **96**, 7622–7623.

Kapadia, M. K., Ito, M., Gilbert, C. D., and Westheimer, G. (1995). Improvement in visual sensitivity by changes in local context: parallel studies in human observers and in V1 of alert monkeys. *Neuron* **15**, 843–856.

Kelly, F., and Grossberg, S. (2000). Neural dynamics of 3-D surface perception: Figure-ground separation and lightness perception. *Perception Psychophys.* **62**, 1596–1618.

Knierim, J. J., and Van Essen, D. C. (1992). Neuronal responses to static texture patterns in area V1 of the alert macaque monkey. *J. Neurophysiol.* **67**, 961–980.

Krupa, D. J., Ghazanfar, A. A., and Nicolelis, M. A. (1999). Immediate thalamic sensory plasticity depends on corticothalamic feedback. *Proc. Natl. Acad. Sci. U.S.A.* **96**, 8200–8205.

Luck, S. J., Chelazzi, L., Hillyard, S. A., and Desimone, R. (1997). Neural mechanisms of spatial selective attention in areas V1, V2, and V4 of macaque visual cortex. *J. Neurophysiol.* **77**, 24–42.

Lund, J. S., and Wu, C. Q. (1997). Local circuit neurons of macaque monkey striate cortex: IV. Neurons of laminae 1–3A. *J. Comp. Neurol.* **384**, 109–126.

Moore, C. M., Yantis, S., and Vaughan, B. (1998). Object-based visual selection: Evidence from perceptual completion. *Psych. Sci.* **9**, 104–110.

Motter, B. C. (1993). Focal attention produces spatially selective processing in visual cortical areas V1, V2 and V4 in the presence of competing stimuli. *J. Neurophysiol.* **70**, 909–919.

Mounts, J. R. W. (2000). Evidence for suppressive mechanisms in attentional selection: Feature singletons produce inhibitory surrounds. *Perception Psychophys.* **62**, 969–983.

Mumford, D. (1992). On the computational architecture of the neocortex, II. The role of corticocortical loops. *Biol. Cybernet.* **66**, 241–251.

Parker, J. L., and Dostrovsky, J. O. (1999). Cortical involvement in the induction, but not expression, of thalamic plasticity. *J. Neurosci.* **19**, 8623–8629.

Peterhans, E., and von der Heydt, R. (1989). Mechanisms of contour perception in monkey visual cortex, II. Contours bridging gaps. *J. Neurosci.* **9**, 1749–1763.

Polat, U., Mizobe, K., Pettet, M. W., Kasamatsu, T., and Norcia, A. M. (1998). Collinear stimuli regulate visual responses depending on cell's contrast threshold. *Nature* **391**, 580–584.

Posner, M. I. (1980). Orienting of attention. *Q. J. Exp. Psychol.* **32**, 2–25.

Pylyshyn, Z. W., and Storm, R. W. (1988). Tracking multiple independent targets: Evidence for a parallel tracking mechanism. *Spat. Vis.* **3**, 179–197.

Raizada, R., and Grossberg, S. (2001). Context-sensitive bindings by the laminar circuits of V1 and V2: A unified model of perceptual grouping, attention, and orientation contrast. *Vis. Cogn.* **8**, 341–466.

Raizada, R., and Grossberg, S. (2003). Towards a theory of the laminar architecture of cerebral cortex: Computational clues from the visual system. *Cereb. Cortex* **13**, 100–113.

Rao, R. P. N., and Ballard, D. H. (1999). Predictive coding in the visual cortex: A functional interpretation of some extra-classical receptive field effects. *Nat. Neurosci.* **2**, 79–87.

Reynolds, J., Chelazzi, L., and Desimone, R. (1999). Competitive mechanisms subserve attention in macaque areas V2 and V4. *J. Neurosci.* **19**, 1736–1753.

Rockland, K. S., and Virga, A. (1989). Terminal arbors of individual "feedback" axons projecting from area V2 to V1 in the macaque monkey: A study using immunohistochemistry of anterogradely transported phaseolus vulgaris-leucoagglutinin. *J. Comp. Neurol.* **285**, 54–72.

Roelfsema, P. R., Lamme, V. A. F., and Spekreijse, H. (1998). Object-based attention in the primary visual cortex of the macaque monkey. *Nature* **395**, 376–381.

Sandell, J. H., and Schiller, P. H. (1982). Effect of cooling area 18 on striate cortex cells in the squirrel monkey. *J. Neurophysiol.* **48**, 38–48.

Sheth, B. R., Sharma, J., Rao, S. C., and Sur, M. (1996). Orientation maps of subjective contours in visual cortex. *Science* **274**, 2110–2115.

Sillito, A. M., Grieve, K. L., Jones, H. E., Cudeiro, J., and Davis, J. (1995). Visual cortical mechanisms detecting focal orientation discontinuities. *Nature* **378**, 492–496.

Sillito, A. M., Jones, H. E., Gerstein, G. L., and West, D. C. (1994). Feature-linked synchronization of thalamic relay cell firing induced by feedback from the visual cortex. *Nature* **369**, 479–482.

Smith, A. T., Singh, K. D., and Greenlee, M. W. (2000). Attentional suppression of activity in the human visual cortex. *Neurorepetition* **11**, 271–277.

Somers, D. C., Dale, A. M., Seiffert, A. E., and Tootell, R. B. (1999). Functional MRI reveals spatially specific attentional modulation in human primary visual cortex. *Proc. Natl. Acad. Sci. U.S.A.* **96**, 1663–1668.

Spitzer, H., Desimone, R., and Moran, J. (1988). Increased attention enhances both behavioral and neuronal performance. *Science* **240**, 338–340.

Steinman, B. A., Steinman, S. B., and Lehmkuhle, S. (1995). Visual attention mechanisms show a canter-surround organization. *Vis. Res.* **35**, 1859–1869.

Temereanca, S., and Simons, D. J. (2001). Topographic specificity in the functional effects of corticofugal feedback in the whisker/barrel system. *Soc. Neurosci. Abstracts* 393.6.

Thorpe, S., Fize, D., and Marlot, C. (1996). Speed of processing in the human visual system. *Nature* **381**, 520–522.

Ungerleider, L. G., and Mishkin, M. (1982). Two cortical visual systems: Separation of appearance and location of objects. *In* "Analysis of Visual Behavior" (D. L. Ingle, M. A. Goodale, and R. J. W. Mansfield, eds.), pp. 549–586. MIT Press, Cambridge, MA.

Vanduffel, W., Tootell, R. B., and Orban, G. A. (2000). Attention-dependent suppression of meta-bolic activity in the early stages of the macaque visual system. *Cereb. Cortex* **10**, 109–126.

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

Watanabe, T., Sasaki, Y., Nielsen, M., Takino, R., and Miyakawa, S. (1998). Attention-regulated activity in human primary visual cortex. *J. Neurophysiol.* **79**, 2218–2221.

Weber, A. J., Kalil, R. E., and Behan, M. (1989). Synaptic connections between coricogeniculate axons and interneurons in the dorsal lateral geniculate nucleus of the cat. *J. Comp. Neurol.* **289**, 156–164.

Yantis, S. (1992). Multielement visual tracking: Attention and perceptual organization. *Cogn. Psychol.* **24**, 295–340.

Yazdanbakhsh, A., and Grossberg, S. (2004). Fast synchronization of perceptual grouping in laminar visual cortical circuits. *Neural Networks* **17**, 707–718.

Zeki, S., and Shipp, S. (1988). The functional logic of cortical connections. *Nature* **335**, 311–317.

Zhang, Y., Suga, N., and Yan, J. (1997). Corticofugal modulation of frequency processing in bat auditory system. *Nature* **387**, 900–903.