



Integrating Top-Down and Bottom-Up Sensory Processing by Somato-Dendritic Interactions

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Abstract. The classical view of cortical information processing is that of a bottom-up process in a feedforward hierarchy. However, psychophysical, anatomical, and physiological evidence suggests that top-down effects play a crucial role in the processing of input stimuli. Not much is known about the neural mechanisms underlying these effects. Here we investigate a physiologically inspired model of two reciprocally connected cortical areas. Each area receives bottom-up as well as top-down information. This information is integrated by a mechanism that exploits recent findings on somato-dendritic interactions. (1) This results in a burst signal that is robust in the context of noise in bottom-up signals. (2) Investigating the influence of additional top-down information, priming-like effects on the processing of bottom-up input can be demonstrated. (3) In accordance with recent physiological findings, interareal coupling in low-frequency ranges is characteristically enhanced by top-down mechanisms. The proposed scheme combines a qualitative influence of top-down directed signals on the temporal dynamics of neuronal activity with a limited effect on the mean firing rate of the targeted neurons. As it gives an account of the system properties on the cellular level, it is possible to derive several experimentally testable predictions.

Keywords: top-down processing, feedback, backpropagating action potential, visual cortex, oscillation, active dendrites

1. Introduction

The cortical processing of sensory information is traditionally thought of as being performed in a feedforward manner. The information about actual stimuli propagates through a bottom-up pathway from lower to higher cortical areas (e.g., Oram and Perret, 1994). Although this paradigm has been remarkably successful as an approach to understanding sensory processing in the cortex, it neglects key features in cortical processing (König and Luksch, 1998). Indeed, anatomical and psychophysical studies indicate that top-down effects play a crucial role in the processing of sensory information.

Anatomical investigations have shown that the interareal connectivity is highly reciprocal and that the proportions of synapses formed by feedforward

versus feedback projections on the respective target neurons are of the same order of magnitude (Rockland and Virga, 1989; Felleman and van Essen, 1991; Salin et al., 1993; Salin and Bullier, 1995; Johnson and Burkhalter, 1997; Budd, 1998). Numerous psychophysical studies have demonstrated top-down effects on the processing of sensory information. Firmly demonstrated are, for example, effects of priming (Stins and van Leeuwen, 1993), stimulus context (Adelson, 1993; Bar and Ullman, 1996), expectancy (Downing, 1988) and object-centered attention (Lavie and Driver, 1996; Driver and Spence, 1998). These findings suggest that the processing and subjective perception of external stimuli are not merely a passive bottom-up process depending on the actual stimulus but are also determined by

internal brain states like expectation, attention, or past experiences.

While detailed physiological and anatomical investigations revealed important insights into the function of bottom-up processes, understanding of the neural mechanisms underlying top-down effects is still poor. Several studies addressed the physiology of top-down mechanisms in the visual system considering the effects of attention (Moran and Desimone, 1985; Posner and Petersen, 1990; Desimone and Duncan, 1995; Luck et al., 1997), stimulus context (Lamme, 1995; Lamme et al., 1998; Roelfsema et al., 1998), mental imagery (Le Bihan et al., 1993; Kosslyn et al., 1995; Goebel et al., 1998; Watanabe et al., 1998), and lesioning or cooling of higher cortical areas (Sandell and Schiller, 1982; Mignard and Malpeli, 1991; Hupe et al., 1998). In general, these studies revealed rather subtle effects of higher cortical areas on receptive field properties and firing rates of neurons in the primary visual cortex. Thus, it has been suggested that feedback projections have modulatory effects while activity is mainly driven by the bottom-up pathway. In spite of these data, however, the underlying mechanisms and the origin of the remarkable difference between effects of bottom-up and top-down signals are unresolved.

Taking a particular approach to investigate top-down interactions in the temporal domain, recent experiments in awake behaving cats show that coupling between cortical areas at different hierarchical levels depends on the behavioral context of the animal (von Stein et al., 1998). The prominent effect is an enhancement of coupling in low-frequency ranges (θ/α -band 4 to 12 Hz) depending on the behavioral context, and it has been suggested that this enhancement of coupling is due to top-down processing. These results suggest that the effects of top-down signals on the temporal structure of neuronal activity need to be further explored.

Here we investigate the interaction of top-down and bottom-up pathways in a model capturing temporal dynamics on a millisecond time scale.¹ Important aspects of the model are inspired by recent physiological experiments demonstrating the backpropagation of action potentials into the apical dendrite, regenerative dendritic calcium currents and the impact of these effects on somato-dendritic interactions (Stuart and Sakmann, 1994; Stuart et al., 1997a, 1997b; Schiller et al., 1997; Buzsaki and Kandel, 1998; Larkum et al., 1999). These phenomena lead to interesting computational properties. We investigate how they support the integration of bottom-up and top-down signals in a cooperative

process, allow the influence of prior knowledge on the processing, and effect the temporal pattern of neuronal activity.

2. The Simulated Network

A hierarchical network of reciprocally connected areas consisting of different parallel pathways is shown in Fig. 1A. Each pair of functionally adjacent areas is connected by reciprocal bottom-up and top-down projections. We picked out two neighboring areas at different hierarchical levels (area A and B in Fig. 1A) and implemented them in a simplified model (Fig. 1B). Each of the two simulated areas is composed of an array of excitatory and inhibitory neurons. Each inhibitory neuron receives input from a related excitatory neuron. Inhibitory neurons in one area divergently project to excitatory neurons within the same area. Excitatory neurons in area A project to excitatory neurons in area B in a convergent way leading to larger and overlapping receptive fields of area B excitatory neurons. These projections establish the bottom-up pathway between the two investigated areas. The top-down pathway is implemented as projections from area B excitatory neurons to area A excitatory neurons. The connectivity of these projections is divergent and reciprocal to the bottom-up projections. However, the postsynaptic effects of these connections differ from those of the bottom-up pathway (see below and Appendix for a detailed description).

The investigated system receives two external inputs. Bottom-up signals to area A provide information about the actual stimulus from lower areas. External signals to area B represent top-down information from higher cortical areas mediating hypotheses or attentional signals. These two external inputs are provided as Poisson spike trains via excitatory synapses to excitatory neurons in area A and B.

Each neuron is simulated as a conductance-based model. Active sodium and potassium conductances are implemented for spike generation. Synaptic conductances are implemented for glutamatergic and gabaergic transmission. Two kinds of inhibitory conductances with different thresholding behavior and time constants are implemented to discriminate the effects of colocalized GABA-A and GABA-B receptors.

The neuronal model captures recently discovered physiological properties in a simplified implementation. On the one hand, it has been shown that somatic

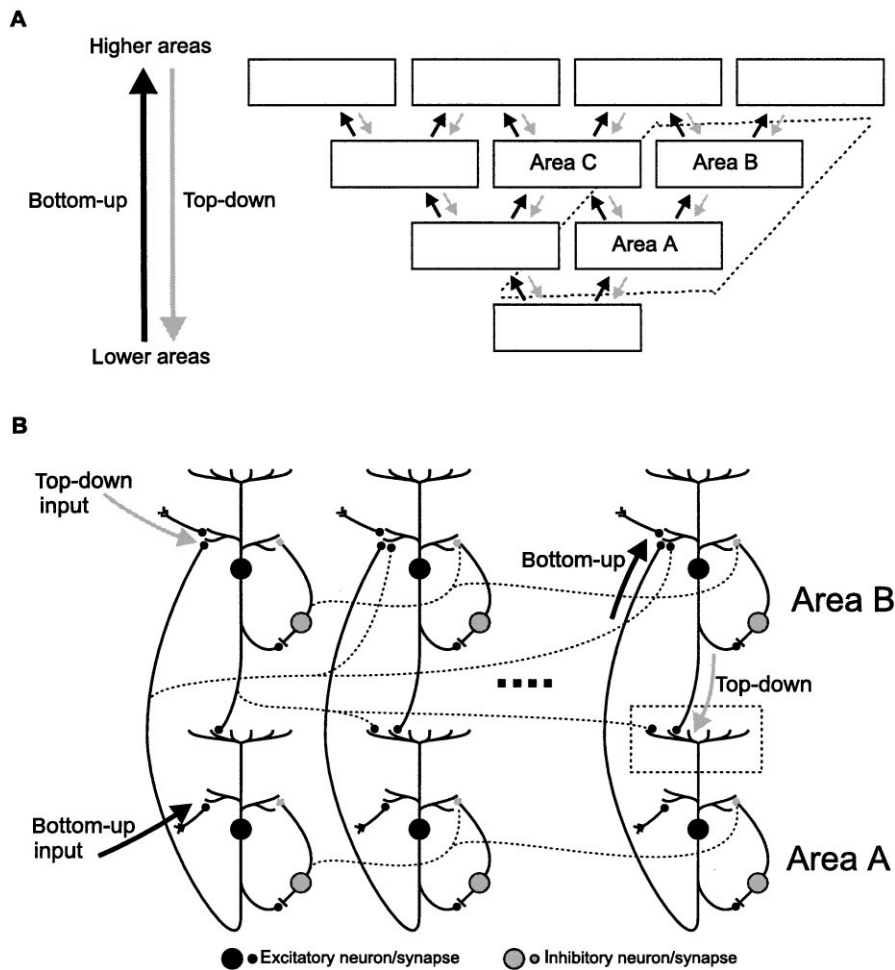


Figure 1. The investigated model. **A:** A network of functionally specialized areas that are ordered in multiple hierarchical pathways. Areas at different hierarchical levels are reciprocally connected by feedforward and feedback projections leading to two opposite directions of information flow. **B:** Two areas simulated at different hierarchical levels. Each area consists of excitatory and inhibitory neurons. Inhibitory neurons project to all excitatory neurons within one area. Excitatory neurons between both areas are connected reciprocally forming the bottom-up and top-down pathway. Two external inputs are provided: bottom-up information to area A and top-down information to area B. The full connectivity is not shown in this picture.

action potentials can actively propagate back into the apical dendrite, where most feedback projections terminate (Felleman and van Essen, 1991; Stuart and Sakmann, 1994; Stuart et al., 1997a, 1997b; Buzsaki and Kandel, 1998). On the other, it has been demonstrated that voltage-dependent calcium conductances can initiate slow dendritic calcium spikes inducing bursting behavior of the cell (Schiller et al., 1997; Stuart et al., 1997b). Recently it has been shown that these two effects interact leading to a drastically lowered threshold for generation of a burst if the excitatory input at the apical dendrite is paired with an action potential of

the postsynaptic neuron (Larkum et al., 1999). These results suggest that the apical dendrite receiving input of feedback projections serves as a relatively independent site of synaptic integration. Its contribution to the axonal spiking activity of the neuron is highly dependent on the presence of somatic sodium spikes back-propagating into the apical dendrite. In the presence of a backpropagating action potential, the subthreshold synaptic input at the apical dendrite can trigger a dendritic calcium spike leading to a burst of axonal action potentials (see Fig. 2). As the present study focuses on the functional implications of these somato-dendritic

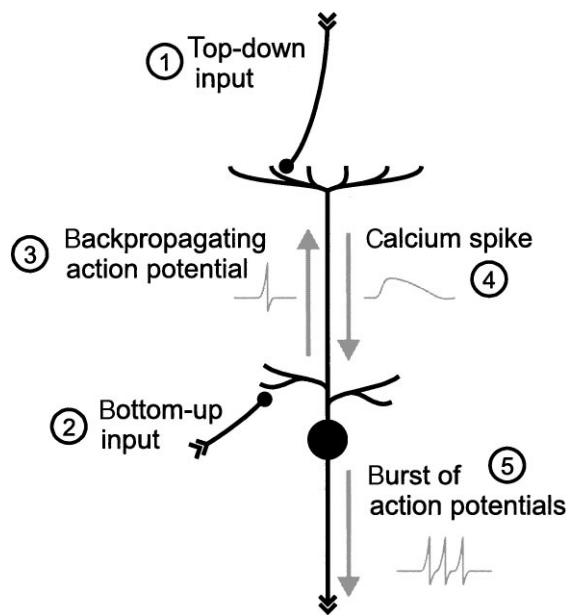


Figure 2. Somato-dendritic interaction and burst generation. If the excitatory input of top-down projections (1) is strong enough and bottom-up input (2) initiates an action potential that propagates back into the apical dendrite (3), a dendritic calcium spike is triggered (4). This calcium spike in turn initiates a burst of action potentials (5). A functionally equivalent mechanism is implemented in the model (see text and Appendix for details).

interactions on the network level rather than on the level of the underlying cellular mechanisms, a corresponding mechanism is implemented in the model in a simplified form. The excitatory synaptic input of top-down projections from area B to area A is integrated separately from bottom-up input, following the notion of the apical dendrite as a relatively independent site of synaptic integration. If the excitatory input at this “virtual” apical dendrite exceeds a certain threshold and a postsynaptic action potential occurs, a slow depolarizing conductance is opened leading to a stereotype burst of action potentials. This implementation captures the characteristic features of the physiological results in a computationally efficient form.

3. Results

To characterize the properties of the introduced model we applied various combinations of input stimuli to area A and top-down signals to area B. Three different interesting features of the network can be demonstrated: a cooperative computation, the effects of ad-

ditional top-down signals, and a specific effect on the temporal dynamics.

3.1. Cooperative Computation

First we compared the network behavior for enabled versus disabled top-down projections between the two areas. An input stimulus with varying amount of noise was presented to area A whereas area B received no external signals. We considered total spike numbers as well as burst numbers to analyze the signal/noise-behavior under the two described conditions.

When the network is operated with disabled feedback projections between the two areas, noise in the bottom-up input is somewhat reduced due to the threshold process of action potential initiation. However, this reduction is local to each neuron and unspecific. Therefore, the amount of noise in the activity of neurons in area A under this condition of disabled top-down projections was taken as a baseline for the further experiments.

Enabling of top-down projections leads to a slight decrease of noise in the signals conveyed by the total number of action potentials of neurons in both areas (spike signal, Fig. 3). This effect is mediated by the reciprocal top-down connections and thus exploits receptive field properties of neurons in area B. In that sense, it is more specific than the local threshold effect described above. Physiological experiments found rather subtle effects of higher cortical areas on the mean firing rate of neurons in lower areas. This implies that the noise reduction in the spike signal has to be limited, which is captured by the simulation results.

In contrast, if bursts are considered as a signal, this effect is much more pronounced (burst signal, Fig. 3). Even with a high proportion of noise in the input, the burst signal of neurons in area A is virtually noise free. The burst signal does not only reflect the properties of the bottom-up input to area A but also depends on the processing of this input performed by the higher area B. It can be seen as a qualitative signal confirming the match of bottom-up and top-down information by computation of an AND-like logical operation (Koch and Poggio, 1992). Furthermore, the properties of the burst signal are in accordance with recent physiological studies (Livingstone et al., 1996; Victor et al., 1998). Investigating stimulus-related activity in primary visual cortex, they show that bursts are a distinct signal and more reliable than the total number of spikes (Lisman, 1997).

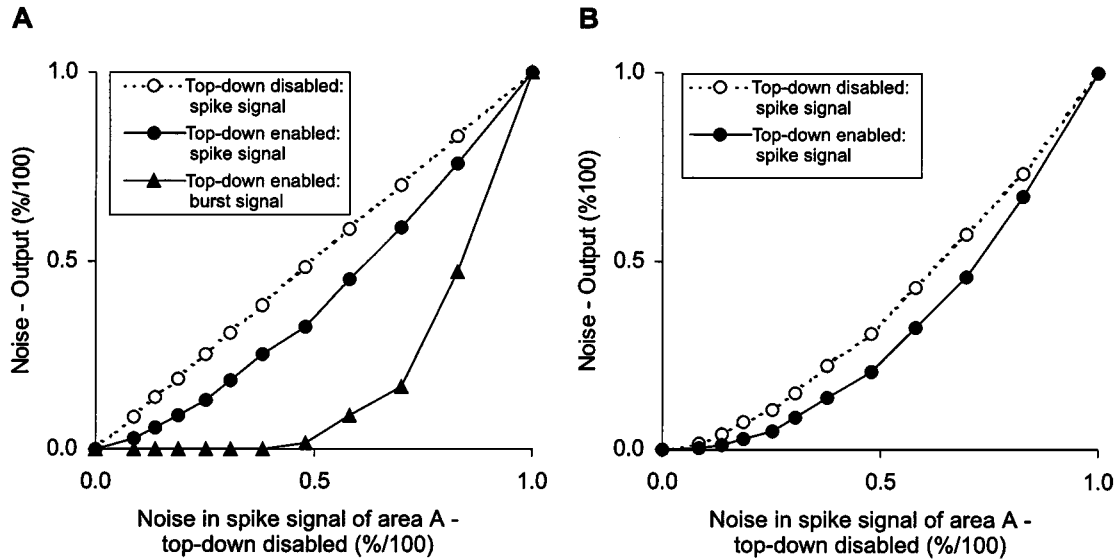


Figure 3. Cooperative computation and burst signal. An input stimulus with varying amount of noise is presented to area A and no external input is provided to area B. The abscissa refers to the noise in the spike signal of area A for disabled top-down projections. **A:** Noise in spike signals of area A for enabled and disabled top-down projections. For enabled top-down projections bursts are considered to be a unique signal. **B:** Noise in spike signals of area B for enabled and disabled top-down projections.

It is important to notice that the information from area B propagates back to area A and is available there as the burst signal. Thus, it can influence any other area (e.g., area C in Fig. 1) that is also driven by area A. The cooperative computation between two areas (areas A and B) in one pathway can therefore also enhance processing in a parallel pathway (areas A and C).

3.2. Additional Top-Down Signals

So far the top-down signals to area A do not convey any external top-down information provided to the system but are solely based on the stimulus interpretation performed by area B. To investigate the influence of additional top-down information, we also provided external signals to area B. They might convey hypotheses about the actual stimulus or attentional signals. As one might expect, these additional top-down signals lead to effects that are in psychological terms described as *priming*. Priming an interpretation of the actual stimulus by additional input to area B leads to faster and more reliable recognition and biases the processing if multiple stimuli are presented.

A stimulus with a constant amount of noise was presented as bottom-up input to area A, while this stimulus

was primed by providing corresponding top-down signals to area B with varying strength. Figure 4 shows that with increasing strength of additional top-down signals the processing becomes faster (Fig. 4A) as well as more reliable (Fig. 4B). The latter effect is most prominent for the burst signal of area A and rather limited for the spike signal of area A. These results are in line with physiological findings demonstrating rather modulatory effects of top-down signals on spiking activity (e.g., in the primary visual cortex).

If multiple stimuli are presented, additional external top-down signals bias processing toward one stimulus (Fig. 4C). A bottom-up input to area A is provided that is composed equally of two stimuli. One of these stimuli is primed by corresponding top-down input to area B with varying strength. The processing is biased toward the primed stimulus—what can be seen in the relative strength of the signals of the primed versus unprimed stimulus. While this effect is relatively weak considering the spike signal in area A, it is much more pronounced for the burst signal. We also varied the ratio of the two presented stimuli in the bottom-up input and analyzed the network response as a function of both: actual stimulus composition and strength of additional top-down signals (Fig. 4D). The network behavior depends on bottom-up information about the actual

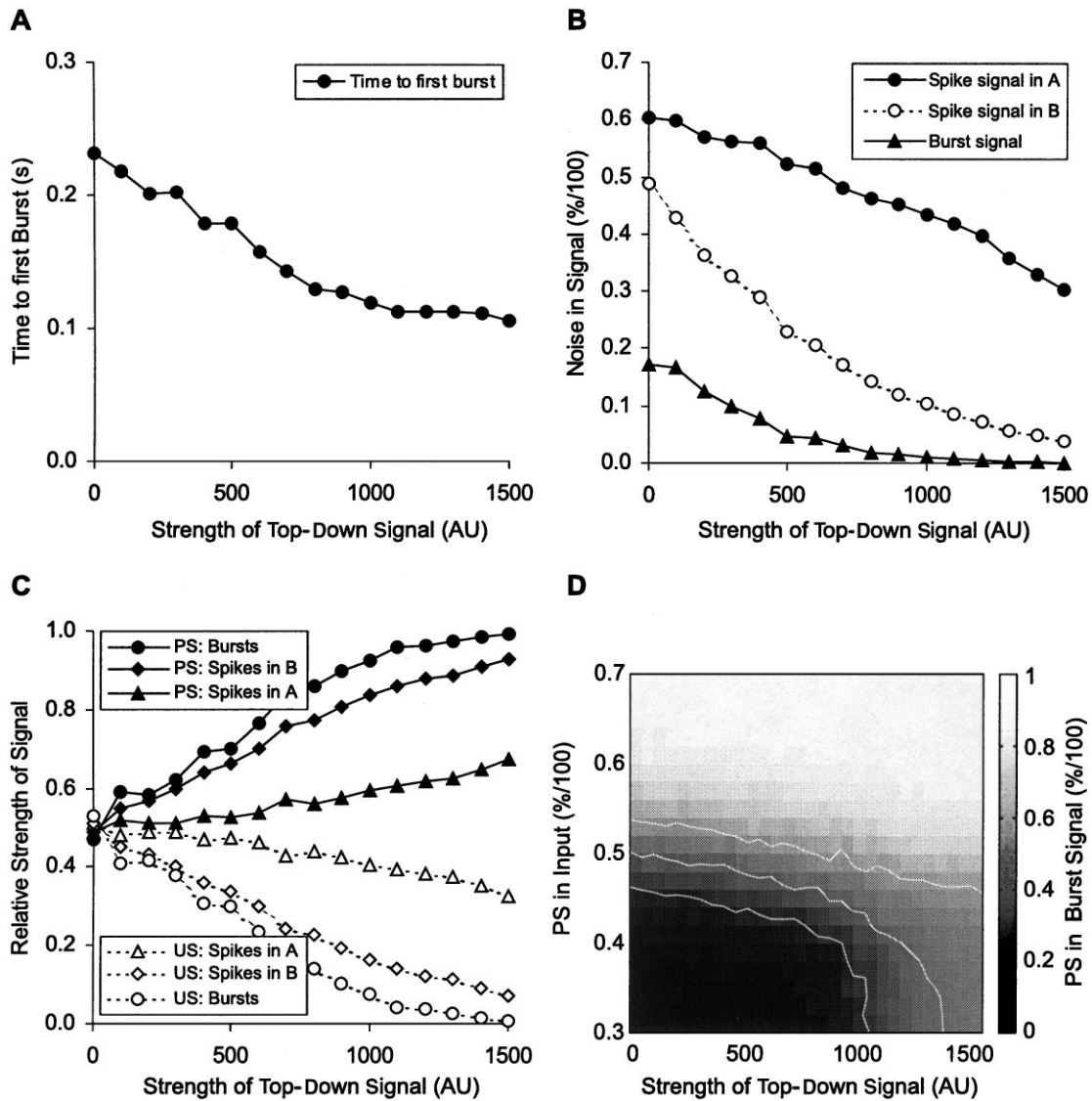


Figure 4. Additional top-down signals. If additional top-down input to area B is provided, priming-like effects can be demonstrated. **A:** A stimulus containing 70% noise is presented to area A. Top-down signals to corresponding neurons in area B are provided with varying strength leading to faster processing (time to first burst). **B:** The external inputs are the same as in Fig. 4A. Stronger top-down signals lead to more reliable processing (noise in burst-signal as well as in absolute spike signals for area A and B). The relation of the relative reliability of the three kinds of signals is, however, maintained over the full range of additional top-down signals. **C:** If multiple stimuli are presented, top-down signals bias processing toward one stimulus. An input stimulus composed equally of two distinct stimuli is presented. One of these is primed (PS) by corresponding top-down signals to area B, whereas the other stimulus is not (US). Strengthening the top-down signal of primed stimulus biases the processing toward primed stimulus in relation to unprimed stimulus. **D:** The relative strength of primed stimulus in the burst signal is plotted as a function of the strength of primed stimulus top-down signals and of the percentage of primed stimulus in the input stimulus. Isocontour lines for 0.25, 0.5, and 0.75 are plotted as white lines.

stimulus as well as on top-down signals. While the top-down signal has a rather modulatory effect on the spike signal in area A (data not shown), the effect of additional top-down information is prominent for the burst

signal. The demonstrated effects of additional top-down signals are not solely due to facilitating neurons in area B but are a result of integrating the two streams of information directed bottom-up and top-down.

3.3. Temporal Dynamics

Recent experiments in awake behaving cats focused on top-down effects on the correlation of oscillatory activity in different cortical areas (von Stein et al., 1998). Therefore, we studied the temporal dynamics of network activity in the context of top-down directed signals. Analogous to the analysis of the experimental data, we computed the power spectra of the population activity of each area (Fig. 5). Without additional top-down signals the activity evolves prominently in a low- (0 to 20 Hz) and high- (20 to 80 Hz) frequency range. These two oscillatory phenomena are due to the inhibitory conductances implemented in the model. A fast GABA-A inhibition is already activated at low levels of excitatory activity and tends to synchronize oscillatory activity in the high-frequency range. A slower inhibition mediated by GABA-B receptors is induced if excitatory activity is getting high due to bursting and

positive feedback between areas A and B (Connors, 1992; Kim et al., 1997). Without this slow GABA-B inhibition the network could lock in a loop of positive feedback between the two areas. The GABA-B inhibition prevents this locking by resetting the network to a lower level of activity. Thus the slow GABA-B inhibition leads to oscillations of the network activity in the low-frequency range.

If additional top-down signals are provided, these oscillations are characteristically modulated. The peak in the high-frequency range is reduced, and power is distributed over a broader range of high frequencies. On the other hand, the peak in the low-frequency range is increased. This is accompanied by an overall increase of power in the low-frequency domain. To quantify these effects integrals of the power spectra for the low- (0 to 20 Hz) and high- (20 to 80 Hz) frequency range were computed (Fig. 5C,D). Additional top-down signals enhance the signal in the low-frequency range by

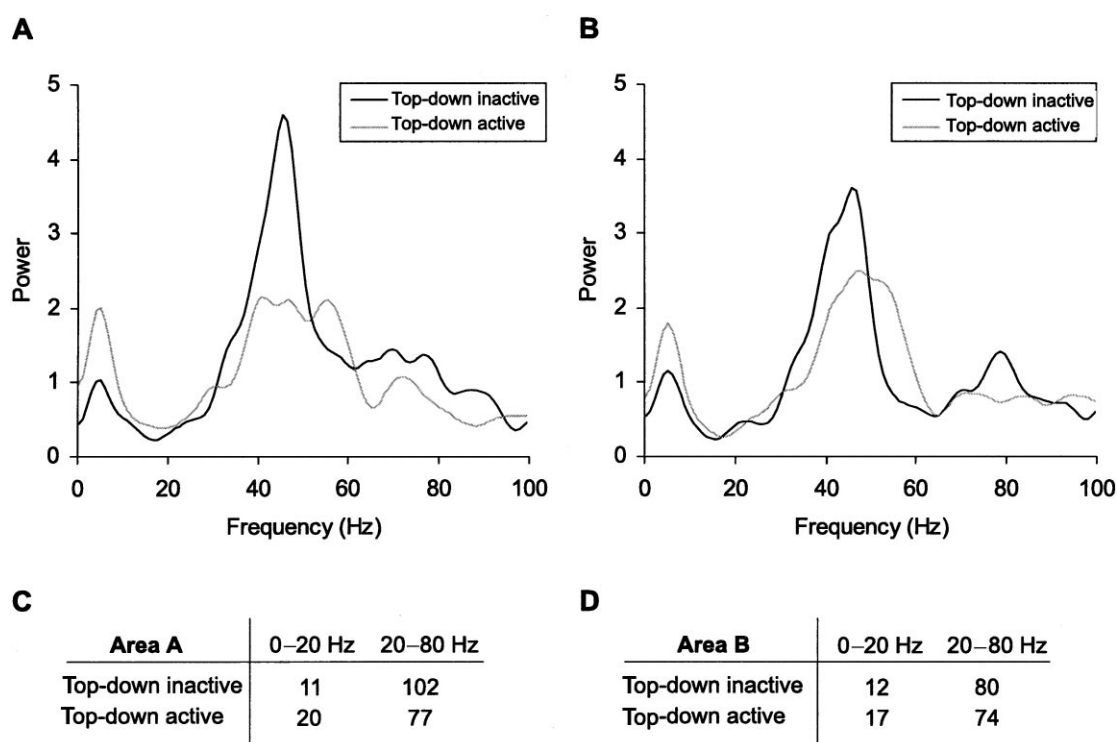


Figure 5. Intraareal coupling. Power spectra of the excitatory spiking activity for both simulated areas were computed under conditions with and without additional top-down signals. The two peaks in the low- (0 to 20 Hz) and high- (20 to 80 Hz) frequency range are due to the two types of inhibitory conductances implemented to differentiate between GABA-A and GABA-B receptors. **A:** Power spectra for spiking activity of area A excitatory neurons. **B:** Power spectra for spiking activity of area B excitatory neurons. **C:** Integral of the power spectra for the high- and low-frequency range of area A. Additional top-down signals prominently enhance power in the 0 to 20 Hz range while reducing power in the 20 to 80 Hz range. **D:** Corresponding values for area B.

$\sim 80\%$ (area A) and $\sim 40\%$ (area B). The effect is due to lower variation in the period length and a steeper rise of activity at the beginning of low-frequency cycles. In contrast, the signal in the high-frequency range is reduced by $\sim 25\%$ (area A) and $\sim 8\%$ (area B). Thus, additional top-down signals lead to a shift of oscillatory activity toward the low-frequency range.

These effects of additional top-down signals on the temporal dynamics are reflected in the interareal coupling as well (Fig. 6). The interareal coupling was computed by calculating the cross-correlation between excitatory neurons spiking activity of areas A and B. Without additional top-down signals strong oscillatory correlation in the high-frequency range and weaker in the low-frequency range is observed. The correlation in the low-frequency range is prominently enhanced if additional top-down signals to area B are provided. To quantify these effects data were filtered in the low- (0 to 20 Hz) and high- (20 to 80 Hz) frequency range, and the heights of central peaks in the cross-correlograms of these filtered data were mea-

sured (Fig. 6C). Additional top-down signals enhance interareal coupling in low-frequency ranges by $\sim 60\%$ while coupling in high-frequency ranges is reduced by $\sim 25\%$.

These effects may be compared to recent physiological experiments, which investigated the neuronal activity and interactions of several visual areas (von Stein et al., 1998). On presentation of trained stimuli an increase of the activity and the interareal coupling in the θ and α frequency ranges (4–12 Hz) was found. In contrast, a novel, surprising stimulus led to a strong decline of the low-frequency coupling and a slight increase in the high-frequency interactions. The internal state of the animal expecting a trained stimulus might be compared to the situation in the simulations with additional top-down signals. The surprising stimulus might correspond to the processing of bottom-up input without a matching top-down signal. Under these assumptions the presented model reproduces well the differential effect of top-down signals on interareal coupling in low- and high-frequency ranges.

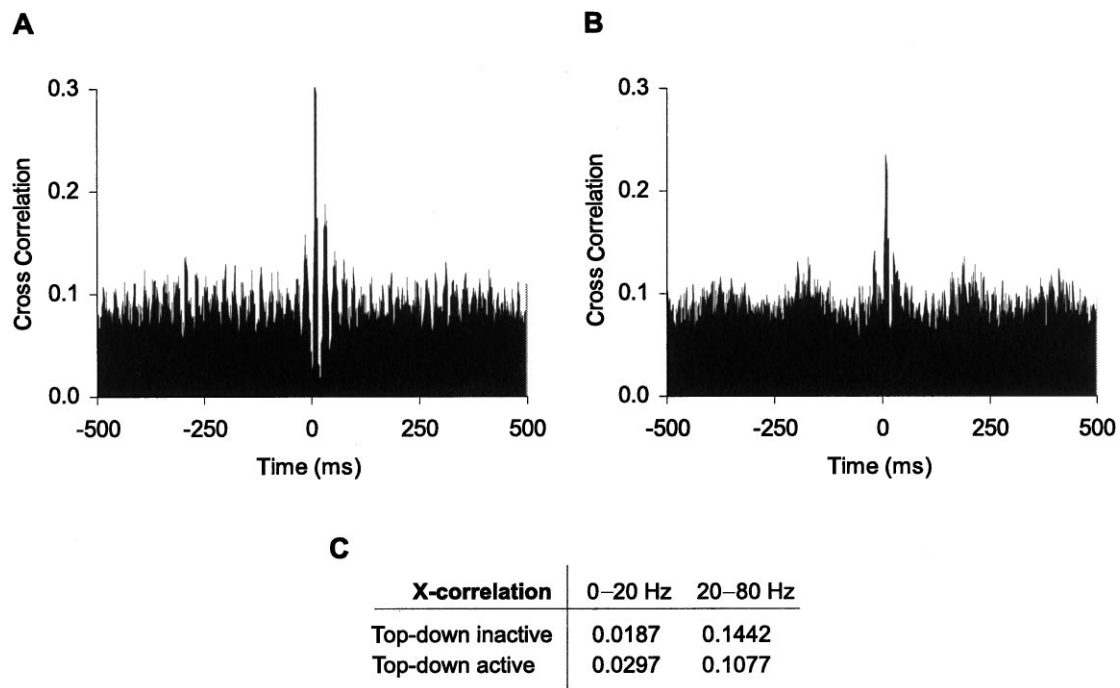


Figure 6. Interareal coupling. To depict the interareal coupling cross-correlations between the excitatory activity of both areas were computed. In the absence of additional top-down signals, strong coupling is found in the γ -range and weaker in the θ/α -range. This interareal coupling in the low-frequency range is prominently enhanced if top-down influence is increased while coupling in the high-frequency range is relatively reduced. **A:** Interareal cross-correlation of excitatory activity in the absence of additional top-down signals. **B:** Interareal cross-correlation of excitatory activity if additional top-down signals are provided. **C:** To quantify the effect cross-correlograms were filtered for the low- (0 to 20 Hz) and high- (20 to 80 Hz) frequency range and the height of the central peak in the cross-correlation of filtered data was measured.

4. Discussion

The anatomical connectivity of cortical areas reveals two conspicuous features. On one hand, most areas are reciprocally connected, while on the other, feedforward and feedback projections terminate in different laminae within each area. Combining these anatomical findings and recent experimental results on the computational properties of active dendrites and somatodendritic interactions, the model presented here accounts for the functional asymmetry of bottom-up and top-down pathways. In accordance with physiological results, the bottom-up input mainly drives activity in a cortical area, whereas feedback projections have rather modulatory effects on total spike counts. Nevertheless, the integration of top-down and bottom-up information leads to a robust burst signal.

4.1. What Are Top-Down Interactions Good For?

In the hierarchy of areas in the visual system, neurons have increasingly complex receptive fields. These reflect interpretations of activity patterns at lower levels that are “known” to the system. In that sense, receptive field properties establish an elementary form of “knowledge.” During the cooperative computation of hierarchically coupled areas, this information is propagated from higher to lower areas. Here this information is integrated with the bottom-up information and represented by bursting of neurons. Thus even if the system receives no additional external top-down signals, the reciprocal connectivity leads to top-down signals based on the “knowledge” of higher areas.

Furthermore, in the process of feature extraction and creation of invariance properties, some information about the stimulus is lost. Most notably, the generation of translational invariant responses implies that the precise spatial location of a stimulus is represented at lower but not at higher levels. To act on a stimulus, however, the system is required to fall back on information absent at higher cortical levels. Therefore, it seems to be an efficient solution to integrate high- and low-level information in bursting pattern of neurons, where it is available to any other area receiving projections from these neurons.

4.2. Assumptions and Simplifications of the Present Model

The present study assumes that action potentials propagate retrogradely into the dendritic tree and lead to the

described interactions with synaptic input at the apical dendrite. Such processes have been observed in slice preparations, where they are sensitive to inhibitory or modulatory activity. Furthermore, recent experiments show that action potentials do backpropagate in the somatosensory cortex of adult and awake rats (Buzsáki and Kandel, 1998). Whether the described somatodendritic interactions leading to bursting behavior occur in the adult cortex under physiological conditions is, however, presently unresolved.

In the present implementation the model obviously simplifies several physiological aspects. The complex nonlinear dendritic properties have been reduced to a threshold mechanism triggering bursting behavior of the neuron. Unless bursts are triggered, the current flow from the apical dendrite to the soma is neglected. Including such a current could result in a new class of interesting phenomena. Top-down signals could not only make a spiking cell burst but directly induce activity. Thus priming could be passed down the hierarchy over several stages independent of bottom-up activity. Because of this effect the system would be able to generate activity at lower levels without bottom-up input. Such a phenomenon might be called *network hallucination* and deserves to be analyzed in a more detailed investigation.

For the sake of clarity several anatomical assumptions had to be made. First, tangential projections between excitatory neurons within an area were omitted. These connections could be used for signal enhancement as well. Second, inhibitory projections were chosen to be global and uniform. More localized connections would lead to shorter spatial range of synchronization within an area. However, this would not qualitatively affect the network performance. Third, the interareal connectivity is chosen to be reciprocal. Although this is not shown directly by available anatomical data, there is also no direct evidence to the contrary. In summary, exploring the implications of more elaborated models seems to raise interesting questions that are beyond the scope of the present study.

4.3. Relation to Other Studies

The notion of bidirectional processing of sensory information has been previously addressed by several other authors.

Finkel and Edelman (1989) investigate a system of multiple, functionally segregated areas interacting by feedforward, tangential, and feedback connections.

Visual stimuli including illusory contours, defined in different feature domains, are processed in a cooperative way. Neurons in the network have specialized response properties (sensitivity to oriented lines, line terminators, occlusions, direction of motion, etc.) based on a specific wiring diagram. The top-down connections act mainly in an inhibitory manner and are of particular importance to resolve conflicts between different interpretations. When the feedback connections are disabled, aberrant activity appears in the network due to the loss of inhibition. In this system, the interaction of parallel pathways leads to a coherent interpretation of visual stimuli. In contrast to this work, in the model presented here the top-down interactions are excitatory. Furthermore, we made a deliberate attempt to avoid specialized circuitry and investigate a generic scheme of top-down interactions.

The adaptive resonance theory (ART) of Grossberg (Grossberg, 1980; Carpenter and Grossberg, 1987) proposes how interactions among areas at different hierarchical levels can lead to efficient representations of sensory information. A sophisticated pattern-matching algorithm leads to stable and efficient pattern classification. A mismatch signal at the lower level defines whether a new template has to be learned.

Mumford (1992) gives a comprehensive discussion of the problems raised by the integration of information on different levels of abstraction. A scheme is proposed where top-down and bottom-up pathways carry information regarding parts of the stimulus “explained” by the activity at the higher level and the residual still to be interpreted. This approach has been extended in the statistical theory of Kalman filtering and is applied to the problem of receptive field development (Rao and Ballard, 1997; Rao, 1999). Thus, the functional effect of top-down interactions is inhibitory and complementary to the interactions proposed here.

Ullman (1995) proposes a model of bidirectional information flow in which top-down and bottom-up pathways explore in parallel multiple interpretations of the sensory information and internal models. This leads to fast and flexible processing of input stimuli. The interaction between bottom-up and top-down signals rests on a priming influence among the two pathways. The two pathways are structurally separated and identified with neurons in different cortical laminae. Thus, the two types of signals used in the present model are mapped on separate but interacting neuronal populations.

A common feature of the above investigations is the use of an abstract level of analysis. Either the unit of the model network has continuous output, representing the mean firing rate of a group of neurons, or the dynamic of the model is implemented algorithmically. In the work presented here, we investigate properties of top-down interactions in a physiologically more detailed model. In particular, the temporal structure of neuronal activity is represented adequately using a spiking model neuron. This allows investigating the generation of bursting activity and synchronization phenomena. Furthermore, it facilitates the comparison with experimental results and the generation of experimentally approachable predictions (see below).

4.4. *Experimental Predictions*

The proposed model describes the interaction of bottom-up and top-down signals on a cellular level, leading to several experimental predictions. First, cooling or lesions of higher areas significantly reduce the frequency of bursting activity in lower areas by decreasing the amount of top-down mediated signals available. As these top-down mediated signals act on a spatial scale given by the receptive field size of the neurons in a higher area, the loss of top-down signals should appear as a reduction of nonclassical receptive field effects. In particular, this effect should be most pronounced for stimuli matching receptive field properties of neurons in the higher cortical areas. Second, direct interference with the burst-generating mechanism should have a particularly by strong effect on top-down mediated signals and also affect receptive field properties in the described way. Slice recordings show that the backpropagation of action potentials into the apical dendrite depends on muscarinic input, inhibitory input, and the firing rate (Buzsaki et al., 1996; Tsubokawa and Ross, 1997). Furthermore, it has been demonstrated that the triggering of bursts by correlated synaptic input at the apical dendrite and backpropagating action potentials is highly sensitive to inhibitory input (Larkum et al., 1999). These findings suggest that altering the activity of inhibitory or modulatory systems could be a suitable way to interfere with the burst-generating mechanism. These experiments seem to be demanding but within the reach of state of the art techniques.

Concluding, the model takes into account present physiological evidences on cortical top-down processing and demonstrates how computational properties of

somato-dendritic interactions could play an important role in the integration of bottom-up and top-down processing.

Appendix

The network was implemented in GENESIS and all simulations were performed with the same set of parameters. Area A consisted of 51 pairs of excitatory and inhibitory neurons in three rows of 17 pairs. Area B consists of 45 pairs in three rows of 15 pairs. Neurons at corresponding positions in different rows have same properties and receptive fields except excitatory weights at excitatory neurons. These weights are graded over rows to allow effects of population coding. To discriminate between GABA-A and GABA-B receptor kinetics, two different populations of inhibitory neurons were simulated with different afferent weights and kinetics of conductances at target neurons. Altogether 288 neurons were simulated. Three excitatory neurons of area A project to one excitatory neuron in area B. The projections from area B to area A are reciprocal. Corresponding to the receptive field structure of area B, bottom-up stimuli to area A consist of three-neuron-wide patches of excitatory input.

The membrane potential of a neuron is calculated according to Eq. (1):

$$C_m \frac{dV_m}{dt} = \frac{(E_m - V_m)}{R_m} + \sum_k [(E_k - V_m)G_k]. \quad (1)$$

E_m is the resting potential, V_m the membrane potential, C_m the membrane capacitance, and R_m the resistance of the membrane. The sum over k represents a sum over the different types of ionic channels in the compartment with reversal potentials E_k and conductances G_k . Parameters for all neurons are $E_m = -70$ mV, $C_m \approx 1.0$ $\mu\text{F}/\text{cm}^2$, $R_m \approx 4.0$ $\text{k}\Omega\text{cm}^2$, $A_{\text{membrane}} = 0.12566$ μm^2 . Synaptic conductances are described by a generalized form of a classical *alpha function* according to Eq. (2):

$$g_{\text{syn}}(t) = W \frac{Ag_{\text{max}}}{\tau_1 - \tau_2} (e^{-t/\tau_1} - e^{-t/\tau_2}), \quad \text{for } \tau_1 > \tau_2, \quad (2)$$

where W is the weight of the synapse, A is a normalization constant, g_{max} the peak conductance, and τ_1 and τ_2 are the time constants of the synaptic conductance. Parameters for excitatory synaptic conduc-

tances are $g_{\text{max}} \approx 0.3096$ nS, $E_k = 55$ mV, $\tau_1 = 10$ ms, $\tau_2 = 2$ ms.

Parameters for GABA-A like inhibitory conductances are $g_{\text{max}} \approx 0.516$ nS, $E_k = -90$ mV, $\tau_1 = 2$ ms, $\tau_2 = 2$ ms. Parameters for GABA-B like inhibitory conductances are $g_{\text{max}} \approx 0.0516$ nS, $E_k = -90$ mV, $\tau_1 = 20$ ms, $\tau_2 = 20$ ms. Top-down input from area B to area A is integrated with the following conductance: $g_{\text{max}} \approx 0.3096$ nS, $E_k = 55$ mV, $\tau_1 = 50$ ms, $\tau_2 = 2$ ms. This conductance does not affect the membrane potential of the postsynaptic neuron and is used to integrate the top-down input at a “virtual” apical dendrite separately. If g_{syn} is above a certain threshold (8 nS) and the postsynaptic neuron spikes, a slow depolarizing conductance is opened that triggers the generation of a stereotypic burst. In its simplified form this implementation neglects the complex properties and morphology of dendrites. However, it is qualitatively sufficient to capture the computational feature of the apical dendrite as an independent site of synaptic integration and the impact of regenerative dendritic calcium spikes on the bursting behavior of the neuron.

Parameters for the burst triggering conductance are $g_{\text{max}} \approx 0.3096$ nS, $E_k = 55$ mV, $\tau_1 = 5$ ms, $\tau_2 = 5$ ms. Detailed dynamics of the spike generating mechanism were neglected for reasons of computational efficiency. Simple voltage-dependent non-Hodgkin-Huxley-like sodium and potassium conductances are implemented for stereotypic action potential initiation (threshold = -40 mV). Parameters for depolarizing conductance are $g_{\text{max}} = 6$ mS, $E_k = 55$ mV, $\tau_1 = 0.4$ ms, $\tau_2 = 0.4$ ms. Parameters for hyperpolarizing conductance are $g_{\text{max}} = 0.7$ mS, $E_k = -90$ mV, $\tau_1 = 4$ ms, $\tau_2 = 0.2$ ms.

Weights and delays of synaptic conductances: Area A excitatory neurons to area A inhibitory neurons (GABA-A population): $W = 10$, $\Delta t = 2$ ms. Area A excitatory neurons to area A inhibitory neurons (GABA-B population): $W = 2$, $\Delta t = 2$ ms. Area A inhibitory neurons to area A excitatory neurons (GABA-A population): $W = 8$, $\Delta t = 2$ ms. Area A inhibitory neurons to area A excitatory neurons (GABA-B population): $W = 14$, $\Delta t = 2$ ms. Area A excitatory neurons to area B excitatory neurons (graded for different rows): $W_1 = 2.3$, $W_2 = 1.415$, $W_3 = 0.53$, $\Delta t = 5$ ms. Area B excitatory neurons to area B inhibitory neurons (GABA-A population): $W = 10$, $\Delta t = 2$ ms. Area B excitatory neurons to area B inhibitory neurons (GABA-B population):

$W = 2$, $\Delta t = 2$ ms. Area B inhibitory neurons to area B excitatory neurons (GABA-A population): $W = 5$, $\Delta t = 2$ ms. Area B inhibitory neurons to area B excitatory neurons (GABA-B population): $W = 14$, $\Delta t = 2$ ms. Area B excitatory neurons to area A excitatory neurons (graded for different rows): $W_1 = 2.8$, $W_2 = 1.723$, $W_3 = 0.646$, $\Delta t = 5$ ms. External inputs to area A and area B are provided as Poisson spike trains at excitatory synapses of excitatory neurons.

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Note

1. The terms *top-down* and *bottom-up* commonly refer to the direction of a process, such as differentiating the interpretation of a stimulus starting from simple features versus actively using high-level concepts for guiding or narrowing down the range of possible interpretations. In contrast, the terms *feedforward* and *feedback* are often used to describe anatomical projections in a hierarchy of cortical areas. Given the level of abstraction of the model presented here, we denote the pathways as well as signals and projections as *top-down* or *bottom-up* for clarity.

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