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A model of computation in neocortical architecture

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Abstract

We propose that the specific architecture of the neocortex reflects the organization principles of neocortical computation. In this paper, we place the anatomically defined concept of columns into a functional context. It is provided by a large-scale computational hypothesis on visual recognition, which includes both, rapid parallel forward recognition, independent of any feedback prediction, and a feedback controlled refinement system. Short epochs of periodic clocking define a global reference time and introduce a discrete time for cortical processing which enables the combination of parallel categorization and sequential refinement. The presented model differs significantly from conventional neural network architectures and suggests a novel interpretation of the role of gamma oscillations and cognitive binding. © 1999 Elsevier Science Ltd. All rights reserved.

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1. Introduction

The aim of this study is to elucidate some essential characteristics of neocortical processing by placing them into the context of a large-scale computational model, which incorporates available experimental data. The purpose of the model is to broaden our understanding of how the cortex works, by predicting data and phenomena, which can then be verified experimentally. We develop our computational conception, using the example of object recognition in the primate ventral visual pathway.

Animals at the phylogenetic level of amphibia do not yet have a developed cortex; they select behavioral output from a limited number of alternatives by evaluating a small number of trigger features from their environment. Feedforward networks that model this type of behavior use a similar strategy, namely, they use a priori knowledge to limit the number of alternatives to be dealt with (Brunelli & Poggio, 1993; Pentland, Moghaddam & Starner, 1994; Wiskott & von der Malsburg, 1995). The advent of the cortex in phylogenetic development is linked to the emerging capability of an increasingly deeper analysis of sensory input.

Finding structure and regularity in the barrage of afferent signals, and giving meaning to the flow of sensory events is

a task the neocortex performs better than any other brain structure. We argue that the specific architecture of the neocortex reflects the organization principles of neocortical computation.

Sensory stimuli regularly include complex and ambiguous scenes. For a brain with a cortex, the evaluation of the sensory situation is more difficult, due to the combinatorial explosion of possible alternatives for the interpretation of the input, in comparison to the simple detection of a few trigger features. The widely accepted assumption is that top-down prediction must be utilized, in order to manage the tremendous complexity of such decision processes. Moreover, experimental evidence suggests that recognition in the visual cortex of mammals is a bidirectional process, in which partial results of bottom-up processes trigger higher-level object representations, which then in turn guide the segmentation process (Vecera & Farah, 1997).

Models of bidirectional neocortical processing focus on the iterative refinement of recognition by means of top-down prediction. A plausible mechanism of how prediction could speed up the interpretation of a scene is the removal of already recognized parts from the input. Interpretation may then proceed with the residual part (Barlow, 1994; Mumford, 1994). Some recent models of bidirectional processing in the ventral visual pathway follow this philosophy by linearly subtracting the top-down prediction from the sensory input (Körner, Tsujino & Masutani, 1997; Rao & Ballard, 1999). From a computational point of view, the

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removal of correlated parts corresponds to a *whitening* of the input signal, which supports the discrimination of increasingly fine details. Even though these models were able to explain a number of experimentally observed phenomena, they fail to explain a number of phenomena on the psychophysiological and the single-neuron level:

1. A correct and sufficiently detailed initial hypothesis is generated at the inferotemporal cortex (IT) by the very first spikes signaling the respective sensory event (Oram & Perrett, 1992; Thorpe, Fize & Marlot, 1996). Existing models on bidirectional processing do not provide a reasonable explanation for this capability.
2. At least for the ventral visual pathway, many neurons continuously respond to an object while the stimulus is present (e.g. Kobatake, Wang, & Tanaka, 1998; Logothetis, Pauls & Poggio, 1995). This should not be the case if the recognized part had been removed from the input.

Iterative refinement may support discrimination within a recognized category. Since refinement takes time, the cortex should not need refinement in order to decide on the category. Thus, an initial hypothesis must be precise enough to grasp the essential semantics of a scene. At the same time, it must be rapidly available to initiate the proper type of behavior. We will show that rapid recognition and refinement require specific mechanisms and specific types of representation, which differ from conventional neural network models. Consequently, a model of processing in the ventral visual pathway should include both a rapid parallel forward recognition, independent of any feedback prediction, and a refinement system controlled by feedback.

The modeling of such complex systems and phenomena has to be carried out concurrently at three different levels: behavior, network, and the single neuron level. The best way to start a model of neocortical computation seems to be its architecture, the anatomically defined regularities of the neuronal system. It should be regarded as a graphical notation of the class of algorithms which the respective network can perform.

We propose that the columnar architecture, which can be found abundantly across cortical areas, reflects a *meta-algorithm* for the computation performed by these (columnar) modules. It represents a functional structure of the neocortical architecture and allows for a description of the neocortex as an almost homogeneous network of functional modules. Thus, we propose that the column serves as the elementary computational module of the neocortex.

The spiking property of cortical neurons imposes specific constraints on the way information is processed by columnar modules. These columnar modules embed two anatomically homogeneous processing systems: The first one is a purely forward driven parallel categorization system, while the second is a sequential refinement system, which contributes to the internal description of sensory input when it is enabled by a top–down prediction.

We propose a novel ensemble temporal encoding scheme that supports fast and reliable recognition in our model architecture. The combination of parallel categorization and sequential refinement requires short epochs of periodic clocking, which define a global reference time and introduce a discrete time for cortical processing. The resulting behavior of the system differs significantly from that of conventional neural network architectures and suggests a novel interpretation of the role of gamma oscillations.

In Section 2, we describe the overall conception of the model. There we will define the constraints of our approach. In Section 3, the conception is implemented as a model neocortical architecture. The resulting dynamics for both feedforward and bidirectional processing are evaluated in the context of experimental data. Finally, in Section 4, we will discuss the new concept that top–down prediction relaxes the constraints on both recognition and representation. Moreover, based on our model architecture, we offer a new interpretation of cognitive binding.

2. A conception of neocortical computation

2.1. Basic assumptions

Our proposed conception of sensory processing in the neocortex is based on several assumptions, which result from biological findings. The main assumptions are as follows:

Internal representation. Experimental evidence suggests that, at least in awake subjects, there exists an internal representation of the external world. This representation determines how cortical processing of incoming stimuli is organized. An internal representation, which we shall call *hypothesis*, is generated from the sensory input and guides the subsequent processing of sensory data by adding semantic value to the raw input. If a major variation of the sensory situation occurs the currently valid hypothesis is modified or even replaced.

Columnar architecture. The columnar architecture appears to be a property of many cortical areas (Britten, 1998; Hickmott & Merzenich, 1998), including the entire ventral visual pathway of primates (Tanaka, 1997). In our model, we regard the neocortex as a homogeneous network of complex computational modules and assume that the *columnar* organization of the neocortex reflects the *modular* organization of cortical information processing. Neocortical processing can be described and understood at the level of elementary computational modules: the *minicolumn*. The architecture of minicolumns is roughly the same in different cortical areas, regardless of the type of the represented information. The minicolumn is a discrete module at the layers IV, II, and VI, but blends smoothly with other minicolumns for most neurons of layer III.

Our model constitutes a hierarchy of processing which proceeds from V1 via V2 to V4 and finally to the

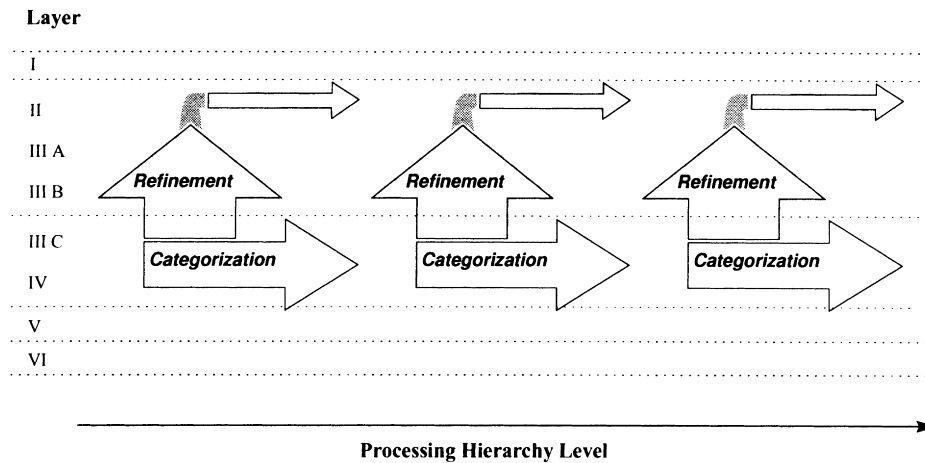


Fig. 1. Categorization and Refinement. The assignment of the two principal operations of intra-columnar processing, categorization and refinement, to the layers found in the neocortex is shown in this figure. Categorization is a feedforward process performed by layer IV and partially by layer IIIC. Layer II and other sub-layers in III are involved in the refinement process. Output to the next hierarchic level originates from layers II and IIIC.

inferotemporal cortex. At each topographically organized level in the hierarchy, a *macrocolumn* is defined as the set of minicolumns that share the same receptive field. At non-topographic representation levels, a macrocolumn may encompass all descriptions related to one object (Wang, Tanaka & Tanifuji, 1996).

Response characteristics of neurons. Our model employs spiking neurons, which operate as *feature detectors* in the following sense. The better the current stimulus matches the preferred feature of the neuron, the faster it will respond. If the deviation from the preferred feature is too large, there will be no response at all. In other words, the degree of match between the stimulus and the preferred feature is encoded in the latency of the response onset. Examples for features are oriented lines in V1 or faces in IT.

While the generation of this latency code results from the biophysical principles of the neuronal spike-generation process, its evaluation requires the neurons to operate as *coincidence detectors*. Indeed it has been argued that cortical neurons effectively operate as coincidence detectors (Abeles, 1982b; König, Engel & Singer, 1996) which estimate the instantaneous rate of large neuronal ensembles over a small integration interval. Here, an ensemble is to be understood as the set of inputs that define the tuning characteristics of a neuron.

This type of latency code proposed here, is supported by recent work of Celebrini, Thorpe and Trotter (1993) for oriented bars in V1, and has been confirmed for low contrast stimuli (which dominate natural pictures) by Gawne, Kjaer and Richmond (1996).

Rhythmic modulation. In our model, information processing is under the influence of a rhythmic modulatory input. This oscillatory input provides coherent processing intervals, which provide the global temporal reference for the proposed latency code. The assumed common source of the modulatory input to the cortex is the thalamic complex of intralaminar nuclei (ILN), which is likely to project to all

areas of the neocortex (Steriade, 1997). The ILN are thought to play a role in attentive and discriminative functions (Macchi, 1990) and its activation increases cortical responsiveness to sensory stimulation (Raos, Dermon & Savaki, 1995).

Stimulation of ILN neurons may result in gamma oscillations in cortical areas (Barth & MacDonald, 1996). ILN cells respond with high frequency burst activity in the gamma range to depolarizing currents (Glenn & Steriade, 1982). ILN neurons may be activated by unspecific stimulation of the brain-stem reticular formation (Groenewegen & Berendse, 1994) or by specific sensory inputs; thus signaling the occurrence or the fast change of a sensory stimulus in their large receptive fields (Schlag & Schlag-Rey, 1984). Whereas most ILN projections modulate the membrane potential of cortical cells (in layers I–III) in an excitatory way (Olausson, Shyu & Rydenhag, 1989), recently ILN induced inhibition in layer IV of the visual cortex was described by Schiff, Purpura, Kalik and Victor (1998).

2.2. Forward categorization

In the ventral visual pathway objects are recognized during the first 100–190 ms after the onset of stimulus (Oram & Perrett, 1992; Schendan, Ganis & Kutas, 1998; Thorpe et al., 1996). The onset of first responses in the inferotemporal cortex barely exceeds the time that is necessary to transmit a signal from the retina through several levels of processing to the IT cortex. As has been pointed out before (Körner et al., 1997), the first response to a visual input can be regarded as a rough categorization of the afferent input and is exclusively defined by a forward filtering process. This *initial hypothesis* initiates top-down feedback, which then enables the subsequent refinement of the representation (Lamme, Super & Spekreijse, 1998a; Ringach, Hawken & Shapley, 1997; Sugase, Yamane, Kawano & Ueno, 1998). The refinement, in turn, results

in an increasingly elaborated hypothesis. Additionally, each level in the processing hierarchy propagates its hypothesis to the next level. Thus, at each level of the hierarchy, a hypothesis is generated. This is illustrated in Fig. 1. Those neurons at the highest level of the ventral visual processing hierarchy (inferotemporal cortex) which are activated first encode the initial hypothesis and keep their activity throughout the subsequent period of refinement (Oram & Perrett, 1992; Sugase et al., 1998). This suggests that the initial hypothesis has a high probability of being correct despite the rapid forward processing.

2.2.1. Selection of the initial hypothesis

If all possible responses of a feature detector were to be considered for the decision about the first hypothesis, the system would face a combinatorial explosion of decision alternatives. This suggests that only reliable information, i.e. optimal responses, should be transmitted in order to activate an initial hypothesis at the subsequent processing level. The signaling of sub-optimal responses, i.e. partial matches, should be delayed long enough, until a hypothesis has been generated at the next level to provide the context for their evaluation.

2.2.2. Encoding the initial hypothesis

The discrimination between perfect and partial matches cannot be carried out on the basis of firing rates, because the low firing frequencies for natural stimuli (Abeles, Vaadia & Bergman, 1990) require too long integration times for a fast categorization. The selection of perfect matches must be achieved by the latency of firing relative to some reference. However, the temporal separation of the various degrees of match of a feature detector is not good enough to allow for a reliable selection of the best matches. Thus, the threshold of these neurons must be high enough in order to ensure the transmission of only the best matches.

We propose that each hierarchy level signals its perfect matches as a coherent spike wave front to the next level. The partial matches follow as a spatio-temporal distribution of spikes in the order of their degree of match. As we proceed higher in the processing hierarchy, the afferent signal is increasingly reduced, until only the representation of a few salient features triggers the initial hypothesis at IT.

This coding scheme has two main drawbacks:

1. A code based on latencies requires a global reference point in time. The units at each level can only decode spike time latencies if they refer to a common reference time.
2. Employing feature-detector type neurons, as described above, all but the best matches are lost, due to the limited integration interval of the neurons. Hence, the coding capacity of a relative latency code is rather low. As a result, a significant amount of information, transmitted by partial matches, would be lost. However, the information submitted by partial matches is needed in two ways: Partial matches should contribute to the subsequent

refinement, and learning of new objects always starts from partial matches of already acquired representations.

These two drawbacks of coding by latency are overcome in our model in the following way: the need for a common reference time can be fulfilled by introducing a global *clocking mechanism* that is related to the decision process. This clocking imposes coherent intervals during which decisions at each level may take place. The information supplied by partial matches will be utilized in a separate forward-processing system that enables the subsequent refinement of representations.

2.3. Refinement of recognition

Partial matches, having a large relative latency, are not transmitted and cannot be analyzed by the fast forward categorization system. A second forward processing system provides the extra capacity that is required for analysis of partial matches.

In our model we assume, that partial matches require context information, provided by feedback from the next higher level, in order to allow for their correct interpretation. The activation of an initial hypothesis at each level in the processing hierarchy provides this context, by defining the activation state for the subsequently arriving partial matches. These can then be correctly evaluated as *attributes* (but not as alternatives) to the description, provided by the best matches. The appropriate timing between the initial hypothesis and its subsequent refinement can be ensured by a rhythmic clocking of the system.

2.3.1. The refinement system

There must be a system that has the capability of recalling the partial matches and ranking them according to their degree of match. Moreover, it must be able to evaluate their temporal sequence. The process is sequential and should be started by the coherent wave of best matches with a fixed phase-relation. Partial matches are suppressed by the high threshold of their respective feature detector and are represented by a sub-threshold activation. A monotonically increasing depolarization of the membrane potential would facilitate the recall of these partial matches and their distribution over a certain time interval according to their degree of match (Hopfield, 1995). We propose that the refinement is carried out by the same columnar module from which the respective best match of the categorization originated, but at different cortical layers. Before partial matches can be transmitted from level n to $n + 1$, the units at level $n + 1$ must provide a top-down prediction to the preceding level.

2.3.2. Rhythmic clocking of processing

A reference time, coherent across the processing system, enables the separation of best from partial matches by relative latency of spiking. It also provides the timing for start and termination of the refined description. Furthermore, it

ensures that the spatio-temporal ensemble of spikes, created by the recall of partial matches, is properly attached to the immediately preceding coherent spike wave of best matches.

The process of categorization and subsequent refinement should be repeated several times, as it is unlikely that with the first sweep of forward processing, the results are correct at every macrocolumn of the system. Repeated decisions under increasingly strong supervision of top–down feedback, result in a smooth convergence of the decision process. These epochs of coherent decisions define a discrete internal time scale for the evaluation of the continuous afferent signals.

We propose that a periodic modulation of the respective membrane potentials, generated by a common external source, controls this repetition of the decision process. Moreover, it defines a coherent time interval for the description of an *internal cortical event*. This *decision interval* begins with the arrival of the first coherent wave of spikes, the best matches, and ends after the subsequent wave of partial matches has contributed its part to the description. The onset of this internal event defines the reference time for the employed latency code. As partial matches can only be added to the description if they are supported by feedback and modulation, the duration of the coherent interval defines the time window for the refinement.

2.3.3. Emergence of a global hypothesis

The first cycle of rhythmic modulation resets the system and defines the phase position for subsequent cycles. With any further cycle, the local decision processes are repeated under the successively increasing influence of the feedback that is caused by the emerging hypothesis at the succeeding processing level. During the first cycle, the feedback is limited to the prediction, supplied by the immediately succeeding level. Subsequent cycles then provide the chance to adjust the local decision according to increasingly global predictions from higher processing levels.

2.4. Two modes of clocking

We propose that there are two modes for synchronizing decision intervals. They utilize the same basic mechanisms, but differ in their driving sources and their characteristics.

2.4.1. Stimulus locked bottom–up synchronization

In case of a sudden change of the sensory situation, the currently activated global hypothesis has to be replaced immediately by a better one. This can be carried out by shifting the phase of the modulation, thereby removing the coherence between the decision interval and the previous hypothesis. This *reset* of decision intervals (for categorization and subsequently for the refinement) has to be stimulus locked in order to allow for a global interpretation of locally distributed features (forward grouping): temporal correlation is the only immediately available information,

describing that features at different local sites may belong to the same entity. Additionally, sub-threshold fluctuations of the membrane potential of the categorizing neurons must be suppressed beforehand to prevent a corruption of the forward grouping by their differences in excitability. We call this a non-specific bottom–up stimulus-locked synchronization. After the global hypothesis has been established, the bottom–up synchronization is no longer needed.

2.4.2. Stimulus-induced top–down synchronization

Once an initial hypothesis has been established and refined, it needs to be stabilized and maintained. This should be carried out by a second, weaker mode of clocking which can still be reset by the bottom–up clocking described above. This top–down clocking must support only those macrocolumns that are part of the hypothesis. Hence, it must be induced by the hypothesis. The modulation is focused to a specific set of macrocolumns, which may, however, be widely distributed over the system. Since the time needed to reach a fully entrained state of a global hypothesis depends on the respective situation, there is no strict locking to the stimulus onset, the synchronization is merely *stimulus induced*.

The global hypothesis is composed of local hypotheses that are synchronously active during a decision interval. The synchronous activity of the global hypothesis could be interpreted as a top–down/bottom–up reverberation within the system. However, we argue that this coherent cortical activation is not the result of an autonomous synchronization process within the cortical network. Rather, it is externally driven by local oscillations, induced by the ILN and triggered by predictive feedback. If predictive feedback, by itself, would be strong enough to initiate a strong top–down/bottom–up reverberation within the signal pathway, it would not only mask the sensory input, but would also lock the system into the first activated state (Crick & Koch, 1998).

For spiking neurons, the top–down activation is represented as a flash of sparsely distributed spikes. Spike events, which are fed back, will usually not arrive synchronously with the afferent spikes. Moreover, they might not be available at every decision interval. Thus, some mechanism is required to maintain the predictive feedback over several decision intervals (i.e. gamma cycles).

We propose that there exists a kind of buffer mechanism that maintains the effect of predictive feedback sufficiently long to bridge more than one decision interval. This buffer mechanism might be implemented by the exceptionally long excitatory post-synaptic potentials (more than 50 ms), generated by the cortical top–down feedback contacts at synapses at apical dendrites of pyramidal cells in layer I (Cauller & Connors, 1994).

2.5. Relation between clocking and gamma activity

2.5.1. The role of gamma activity

The functional requirements derived from our conception

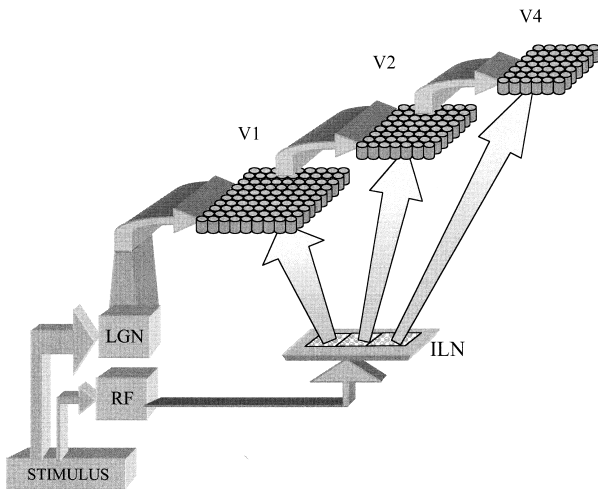


Fig. 2. Feedforward processing in the neocortical architecture with bottom-up ILN modulation. Feedforward processing is started with the arrival of a stimulus at the retina. Through fast connections via the reticular formation (RF) of brain-stem, the ILN are broadly activated. Gamma modulation is now evoked and can affect the different processing levels before the main body of information that has to pass through the LGN, arrives. In this figure, only three cortical processing levels (V1, V2 and V4) are shown. This figure illustrates stimulus-locked and bottom-up ILN modulation. Modulation affects every minicolumn at every level, allowing all neurons with proper input to participate in the decision process.

of neocortical computation are in good agreement with the experimentally observed phenomenon of cortical oscillations in the 40–60 Hz band. There are two different kinds of so-called gamma activity:

Stimulus-locked gamma activity with very short latencies (called *evoked* gamma activity) can be recorded in the cortex (Bertrand & Pantev, 1994). This low-amplitude EEG oscillation consist of 5–7 gamma waves which start some milliseconds before the sensory signal can activate the first cortical neuron.

Long latency gamma activity (called *induced* gamma activity) develops 200–300 ms after stimulus onset without strong time locking to the stimulus (Livingstone, 1996). In contrast to the short-latency gamma activity, the induced gamma oscillation depends on the properties of the sensory input (Singer & Gray, 1995).

These findings suggest that the required stimulus locked bottom-up synchronization corresponds to the observed

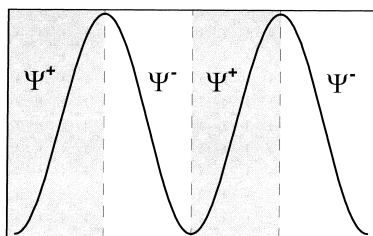


Fig. 3. Different phases of gamma modulation. Gamma oscillations have two functionally different time intervals: The phase of rising amplitude Ψ^+ and the declining phase Ψ^- . ILN modulation is effective only during Ψ^+ .

evoked gamma oscillations, while the top-down synchronization corresponds to induced gamma oscillations. The model of gamma activity proposed here is consistent with concepts put forward by Llinas and Pare (1996), Llinas and Ribary (1993) and Steriade, Contreras, Amzica and Timofeev (1996). By contrast, most authors interpret gamma activity as a phenomenon that is driven by and is restricted to neocortical processing (see Ritz & Sejnowski, 1997, for an overview).

In our model, the intralaminar thalamic nuclei (ILN) play a key role for rhythmic control of the otherwise asynchronous neocortical processing. However, we do not regard the ILN as the exclusive source of gamma activity. The origin of cortical oscillations is quite complex and probably involves the influence of cortico-cortical connectivity (Singer & Gray, 1995) and of inhibitory networks (Traub, Whittington, Stanford & Jefferys, 1996).

2.5.2. Evoked gamma activity and bottom-up synchronization

For bottom-up synchronization, the onset of visual input after a saccade is proposed to result in a fast, diffuse activation of the ILN via the reticular formation of the brain stem (Fig. 2). The emerging ILN gamma bursts start to modulate the excitability of the neurons of the columnar units during the first 150 ms after stimulus onset.

This influence is proposed to consist of:

- an excitatory modulation of the pyramidal cells in cortical layers II, III, and V, which extend their apical dendrites to layer I;
- an inhibitory modulation of the spiny stellate neurons in layer IV via collaterals of ILN axons to the mutually interconnected network of inhibitory interneurons in layer IV/lower layer III.

The activation of inhibitory neurons in layer IV is assumed to result in a synchronization of the sub-threshold membrane potential fluctuations in the spiny stellate cells. The inhibitory modulation of these spiny stellate cells is phase locked to the excitatory modulation of the pyramidal cells of the upper layers. The network of the inhibitory cells may, thus, stabilize the phase-locking between the categorization system (which is not subject to depolarizing modulation) and the refinement system. Hence, it may define a coherent decision interval for the repeated analysis of afferent input. The refinement starts with the rising phase of an ILN gamma cycle and stops at its maximum (see Fig. 3).

2.5.3. Induced gamma activity and top-down synchronization

We propose that top-down synchronization is confined to those columnar units that receive predictive feedback and locally activate the ILN–cortex modulation loop via pyramidal cells in lower cortical layers. Indeed, it was observed that cortically activated ILN gamma activity is

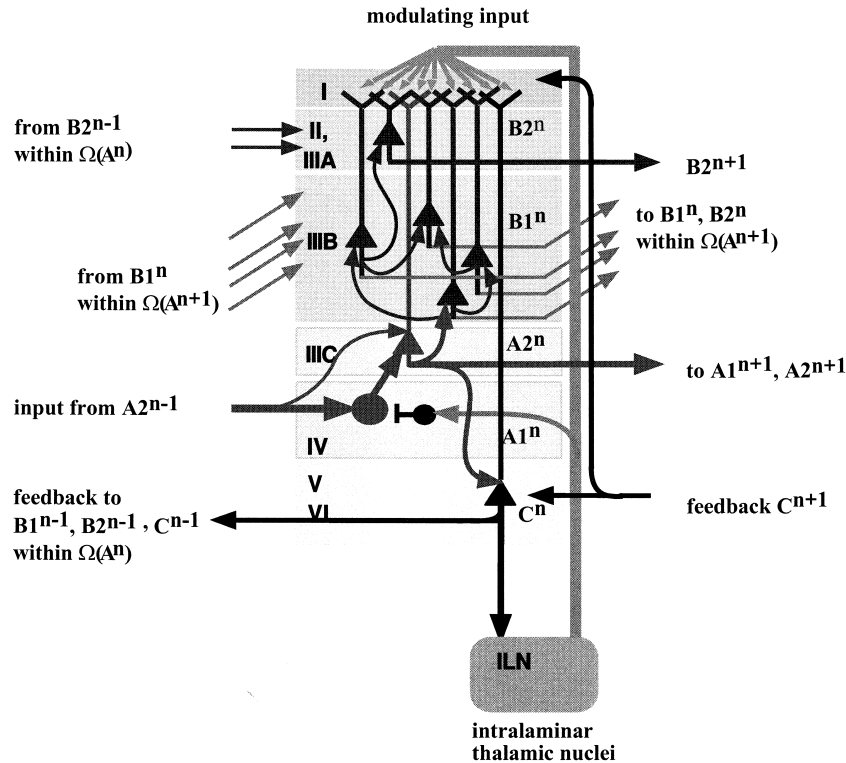


Fig. 4. Proposed architecture of a minicolumn. Arrows indicate connections. Rotated arrows (45°) indicate horizontal connections of the $B1$ system within the same processing level. Roman numbers on the left-hand side give the biological notation for the different layers. The corresponding terminology in our model is given on the right hand side. The index n refers to the processing level within the hierarchy. Solid triangles indicate pyramidal neurons, large solid circles correspond to spiny stellate (SS4) neurons. Small circles represent a local inhibitory network. At the bottom of the picture the activation of ILN by the reticular formation of brain-stem is depicted. A columnar module is divided into three functional subsystems, the forward processing system A , the context analyzer B and the prediction system C . Within a minicolumn information travels from A to C . Subsystem A is divided into a categorizer $A1$ and a category ranking system $A2$. $A1$ neurons act as *feature detectors* and drive corresponding $A2$ neurons. Subsystem B is divided in $B1$ and $B2$. System $B1$ is not localized to a column but extends over the entire processing level. $B2$ follows a columnar organization. $B2$ transmits the categorization of the characteristic dynamic state in $B1$ to the feedback system C and the B system of the next level. C provides feedback to selected minicolumns in the preceding processing level, contacting all subsystems except $A1$. All subsystems in a minicolumn, except for the spiny stellate cells in layer IV are modulated by feedback and ILN induced gamma oscillations. In layer IV, inhibitory networks are proposed to mediate the synchronization of membrane potential fluctuations of the spiny stellate cells. All other inhibitory networks are omitted for simplicity.

sharply localized and may last for several hundred milliseconds (Barth, pers. comm.)

ILN activation should result in sub-threshold oscillations of the membrane potential of neurons at the columnar units, even if no spikes can be observed. However, any spike that is triggered will occur with high probability at the apex of a gamma cycle. This type of *silent synchronization* is supported by a number of recent findings. High coherence of activity has been observed between sparsely distributed neocortical sites during feature integration processes (Arieli, Sterkin, Grinvald & Aertsen, 1996; Eckhorn et al., 1988; Frien, Eckhorn, Bauer, Woelbern & Kehr, 1994). Connections between laterally displaced pyramidal neurons are by itself not reliable enough to produce time-locked responses (Thomson & Deuchars, 1994). Thus, we propose additional rhythmic modulation via ILN.

Here, we assume that a bottom-up driven global synchronization of decision intervals is later replaced by top-down induced specific modulation, which is supported by the findings mentioned above. This long-latency

synchronization is based on the coherent top-down activation of the respective modules and is supported by rhythmic modulation via ILN. It can be recorded as induced gamma activity, starting about 200 ms after stimulus onset.

3. A model of neocortical computation

We will now formalize the computational hypothesis, presented so far, to an abstract structure-model. A simplified version of the model is currently being implemented.

3.1. Basic framework

3.1.1. Main concepts

The model architecture is a hierarchical system with several processing levels. The network structure is homogeneous and activation is sparse. The proposed basic computational modules are minicolumns. These are comprised of subsystems, which are modeled as coincidence detector neurons. Spike time latencies encode the

reliability of information. A first hypothesis is generated through fast feedforward processing. The current hypothesis is represented by feedback activity. The initial hypothesis is refined by incorporating local context, feedforward and feedback processing. The ILN synchronize decision processes by means of gamma modulation.

Processing levels are composed of macrocolumns, with each macrocolumn having its own receptive field. A macrocolumn at processing level n is denoted as M^n . The set of minicolumns with a common receptive field forms a macrocolumn. Every minicolumn in the system has the same architecture and performs the same basic operations using specialized subsystems. Each minicolumn represents a specific feature. We also define $\Omega(X^n)$ as the receptive field of subsystem X at level n .

We use spiking model neurons that act as coincidence detectors. The architecture of a model minicolumn and connections to other minicolumns are illustrated in Fig. 4.

3.1.2. Subsystems

A minicolumn consists of three subsystems:

Subsystem A. This is the principal processing unit for feedforward input. It operates as *categorizer*. The afferent input is compared to the preferred feature of the minicolumn. A is comprised of two separate subsystems—A1 and A2. Both have the same receptive field and are tuned to the same feature. In A1 only internal processing operations are performed, while A2 sends output to other minicolumns.

1. A1 receives only feedforward input. It separates best from partial matches. The latter are suppressed by inhibition.
2. A2 receives the same feedforward input as A1. It relays A1 activity to other subsystems. With support from ILN modulation and under the constraints set by feedback it can add partial matches to the description of the input.

Subsystem B. This subsystem analyses the output of A2 from neighboring macrocolumns. It also consists of two subsystems—the internal processing system B1 and the output system B2.

1. B1 encodes the output of A2 as a *spatio-temporal activation pattern*. It is similar in structure and dynamics to a synfire chain (Abeles, 1982a, 1991) and is not localized to a minicolumnar structure, rather it is distributed over the whole processing level.
2. B2 analyzes the activation pattern in B1 and outputs its decision to the prediction system C and to the next processing level.

Subsystem C. This subsystem signals the decision of a minicolumn to sub-cortical neurons and sends predictive feedback to the previous processing level.

3.1.3. Connections to other minicolumns

There are feedforward connections from $A2^{n-1}$ to $A1^n$ and $A2^n$ up to the highest level. This constitutes the fast

forward processing system described above. Additional feedforward connections exist from $B2^n$ to $B2^{n+1}$. Feedback connections originate from subsystem C and contact A2, B1, B2 and C at the previous level. Additionally, these subsystems are modulated by ILN.

3.1.4. Modulatory control

As described in Section 2, global synchronization of bottom-up and top-down processing is ensured by ILN enforced gamma modulation. The ILN have a rhythmic activity pattern, thus, the modulation strength changes periodically. The interval during which it is monotonically increasing is called Ψ^+ (see Fig. 3). For a specified set of neurons, the modulation can shift the membrane potential towards the threshold. This can effectively reduce the amount of input (feedforward or feedback) that is necessary to trigger this neuron (or subsystem). Thus, during the Ψ^+ gamma phase, ILN modulation disables activity in A1 and enables processing in the subsystems A2, B and C.

3.2. Structure of the model neocortical computational modules

All subsystems, except B1, are localized to a minicolumn. A minicolumn can be characterized by the feature represented in its subsystem A.

3.2.1. Subsystem A

Both A1 and A2 obtain feedforward input from their receptive field. The size of the receptive field is approximately the same for all minicolumns within a processing level. Recall that all minicolumns within the same macrocolumn have the same receptive field.

From a computational point of view, every minicolumn stores a specific template in its A system. Feature detection is performed by matching the stored template with the afferent input. The system is sensitive to the temporal fine structure of the input spike trains.

Categorizer A1. Activation of an A1 in M^n indicates that the corresponding feature is present in its receptive field.

Within a macrocolumn, the various A1 systems act like *standard feature detectors* with a Winner-Takes-All (WTA) characteristic. To find the best fitting feature we make use of the fact that best matches fire first. Fast forward inhibition then blocks all additional firing in the macrocolumn. Thus, there will be only one active A1, which represents the feature that best describes the input to the macrocolumn.

As mentioned above, activity in A1 can be controlled by the ILN. Output from A1 is relayed to the next processing level via A2.

Category Ranking System A2. It receives the same feedforward connections as A1. However, they are weaker and are not strong enough to trigger A2. Activity in A2 is only possible with a combination of feedforward- and feedback-inputs plus ILN modulation. Direct input from A1 is merely relayed to the next processing level. Thus, A2 represents the

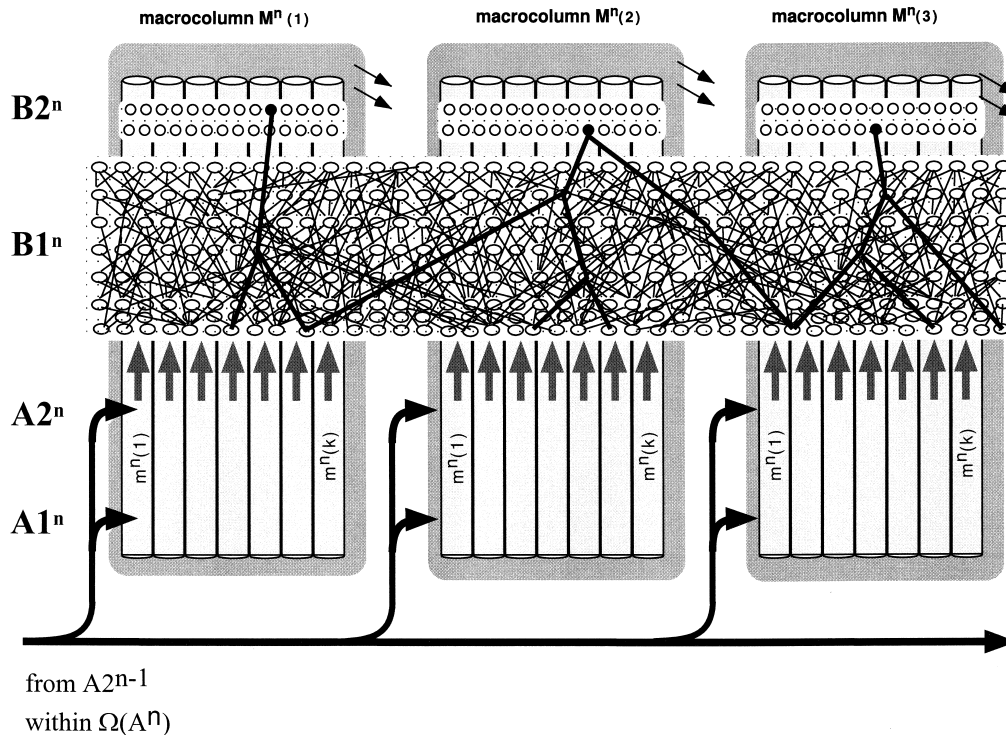


Fig. 5. Example macrocolumns of processing level n . Every macrocolumn consists of k minicolumns. The prediction system C^n has been omitted for simplicity. In every minicolumn, contacts from $A2^{n-1}$ enter $A1^n$ and $A2^n$. Output from $A2^n$ enters $B1^n$. The subsystem $B1$ is not restricted to one mini- or macrocolumn, but extends over the entire processing level. System $B2$ again follows the general columnar structure. Thin lines represent diverging forward connections of $B1$. Thick lines illustrate possible activation trajectories. Here, only a few contacts are shown, but a large number of active contacts is necessary to trigger a spike within $B1$. $A2$ neurons from different macrocolumns can contribute to the activation of a $B1$ neuron (convergent connectivity). Additionally, the same neuron in $B1$ can be part of several trajectories. Trajectories in $B1$ that finally reach $B2$ trigger specific neurons within a minicolumn. These neurons represent variations of the basic prototype feature encoded in A .

same features as $A1$, but with different activation constraints.

The combined input may result in a membrane potential, which is considerably larger than the threshold and allows even partial matches to trigger a spike. Consequently, while gamma modulation is in its Ψ^+ phase, several $A2$ within a macrocolumn may fire. Those $A2$, which represent partial matches, are incorporated in the local description of the input. Thus, the description of the input at $A2$ is much more refined than at $A1$.

The combined output of the $A2$ systems of a macrocolumn is a temporal sequence of spikes, representing the ranked matches. This is in effect a description in similarity space (Poggio & Edelman, 1990).

$A2^n$ has feedforward connections to $A1^{n+1}$ and $A2^{n+1}$ of the next processing level. In addition, $A2^n$ sends input to the system C^n , which, in turn, feeds the *decision* of its minicolumn back to the previous level.

$A2^n$ also connects to the $B1^n$ system. The processing path $A2^n \rightarrow B1^n \rightarrow B2^n$ performs a refined and detailed analysis of the output of all A subsystems in the macrocolumn and even in its wider vicinity (see below).

3.2.2. Subsystem B

Subsystem B is composed of two parts: $B1$ and $B2$. Unlike

all other systems, $B1$ is not confined to one minicolumn, but stretches over the entire processing level (Fig. 5). System $B2$, however, shares the same columnar organization as the other systems (A and C). The information flows from $A2$ through $B1$ to $B2$.

Context encoder $B1$. The output of all $A2$ systems of the respective processing level enters $B1$. $B1$ is assumed to integrate this information within a certain *neighborhood*. This neighborhood includes minicolumns of several macrocolumns. Thus, subsystem $B1$ combines local context information ($A2$ activity) from different macrocolumns.

$B1$ has a divergent/convergent connectivity pattern that is strictly feedforward, i.e. each neuron receives inputs from a large number of neurons and projects to a large number of other neurons. These contacts are generally weak. This network structure resembles a large number of overlapping synfire chains and is well suited to analyze the spatio-temporal spike sequences, which are generated by the various $A2$ systems of a processing level. These sequences result in specific *activation trajectories*, which originate at the input layer of $B1$ and terminate at specific $B2$ neurons. The propagation of activity is modulated by feedback activity from the respective higher level and the ILN.

Context descriptor $B2$. The different neurons of subsystem $B2$ describe variations of the basic features, represented

by subsystem A. Consequently, the number of neurons in $B2$ has to be larger than in A.

Processing in $B2$ is strongly modulated by the ILN. It gets feedforward input from the $B2$ system of the previous processing level and feedback input from system C of the succeeding processing level. Without ILN modulation and feedback, $B2$ cannot contribute to the forward processing. Output of $B2^n$ is sent to $B2^{n+1}$ and to C^n .

3.2.3. Prediction system C

The local hypothesis of the macrocolumn is transmitted from $A2^n$ and $B2^n$ to subsystem C^n . It represents all features stored in $B2^n$ that can be activated as a pool (by $A2^n$) or individually (by $B2^n$).

Subsystem C^n contacts specific minicolumns at the previous level. Within these minicolumns all subsystems, except for A1, receive feedback.

3.3. Dynamics

Processing is both parallel and sequential. Activity travels within the hierarchy from level to level (feedforward and feedback processing) and from layer to layer within a minicolumn (refinement). In this processing, the precise timing of activation between different parts of the system is crucial.

3.3.1. Feedforward processing and hypothesis generation

Without prior knowledge about the input (e.g. a new image is presented), a coarse initial hypothesis has to be generated. As described in the previous sections, the first global hypothesis is triggered at the highest level by feedforward activation only. Irrespective of the state of the remaining system, forward processing in A1 is exclusively input-driven. Supported by the ILN, subsystem $A2^n$ adds partial matches to the forward description, provided they are supported by feedback from higher levels. The forward contacts from $B2$ play only a minor role and will not be considered here.

To illustrate the dynamics of this processing scheme, we present a step by step description (see also Fig. 2). We shall discuss the processing across an entire processing level. Consider that a new image is presented and that neither inhibition nor feedback is active.

1. The ILN are activated by the stimulus and synchronize the system.
2. Feedforward input from the previous processing level arrives at level n . The best matching inputs trigger a limited number of $A1^n$ neurons.
3. Fast forward inhibition blocks further $A1^n$ activity in all macrocolumns that have just fired. Activity travels from $A1^n$ to the corresponding $A2^n$ systems.
4. Those $A2^n$, which were activated by $A1^n$, send their spikes to the refinement system B^n , the prediction system C^n , and to the next processing level ($A1^{n+1}$ and $A2^{n+1}$). Now the ILN block all further activity in $A1^n$.
5. Refinement in $A2^n$ and B^n is enabled by the ILN.

However, without predictive feedback, no additional $A2^n$ systems are activated. Moreover, there is no processing in B^n .

6. The negative gamma-phase Ψ^- at level n disables processing in $A2^n$, B^n and C^n .
7. The spike wave of best matches propagates through all levels. With every level the number of generated spikes is reduced until only a few active macrocolumns emerge at the highest level.
8. The first global hypothesis is generated at the highest level and fed back as prediction to the lower processing levels.

3.3.2. Refinement and feedback

For a minicolumn at level n refinement is only possible after a hypothesis has been generated at level $n + 1$, as feedback is needed for refinement in A2 and B. We now consider the dynamics of the refinement process at level n . We assume that feedback from C^{n+1} is present. The sequence of events proceeds as follows:

1. The input triggers $A1^n$ which, in turn, activates the corresponding $A2^n$ systems. Then the ILN suppress $A1^n$ and enable processing of partial matches in $A2^n$.
2. Supported by feedback and ILN modulation, several additional $A2^n$ systems are activated. These represent good partial matches that are consistent with the local hypothesis (feedback).
3. $A2^n$ activates the prediction system C^n which sends unspecific feedback to all minicolumns at level $n - 1$ which provide input to the corresponding A^n system.
4. The ILN activate system B^n and the spatio-temporal sequences of spikes from all $A2^n$ of level n enter $B1^n$.
5. Depending on the $A2^n$ activity and the feedback from higher level C^{n+1} , a specific sequence of $B1^n$ neurons is activated.
6. A number of $B2$ neurons is triggered, indicating that specific variants of basic features have been recognized.
7. Output from $B2^n$ enters C^n . Feedforward input from $B2^n$ is sent to $B2^{n+1}$.

3.4. Reference to experimental data

3.4.1. Embedding of the model in neocortical architecture
Categorization system A. We propose the neocortical layer IV as the essential part of the categorization module A1 and the lower layer III pyramids (layer IIIC) to embody A2.

The principal neurons of this structure, the spiny stellate neurons (SS4) receive the main afferent input (and inputs from other SS4 of its surrounding). The number of GABA-ergic synapses in layer IV is twice as high as in other layers (Micheva & Beaulieu, 1995). Forward inhibition of spiny stellate neurons, produced by afferent inputs to local inhibitory neurons is very fast and powerful (Freund, Martin &

Whitteridge, 1985), and may implement the proposed winner-takes-all characteristics.

The supragranular pyramids that obtain direct input from spiny stellate cells in layer IV are assumed to elicit a spike immediately because of their unique multi-synaptic connectivity pattern (Szentagothai, 1978, 1983). Spiny stellate neurons of layer IV restrict their layer II/III projection to the lower third of layer III (Callaway & Wiser, 1996; Fitzpatrick, Lund & Blasdel, 1985; Lachica, Beck & Casagrande, 1992). In addition to the massive afferent input to layer IV, a more diffuse termination of afferent inputs is found especially in lower layer III. Some complex cells in lower layer III of V1 share geniculate inputs with simple cells and show correlated firing (Alonso & Martinez, 1998). This completely meets our requirements, formulated for the functional architecture of the *A* subsystem.

The inhibitory neurons in layer IV have been shown to have sub-threshold oscillations and fire in gamma range if depolarized. Their axons ramify extensively in layers IV and III (Llinas, Grace & Yarom, 1991). Once triggered, they could serve to stabilize the hyperpolarizing gamma modulation of *SS4* and lower layer III pyramids at a fixed phase relation to the depolarizing gamma modulation at apical dendrites of pyramids, as proposed in Section 2.

Refinement system B. The pyramids in layers II and III show abundant mutual connectivity by ascending axon collaterals. These collaterals make sparse en-passant type contacts with many other pyramids in their vicinity, but never more than one or a few contacts to the same individual neuron. It is very likely that those pyramids can only fire if they receive a coherent activation by a large number of different pyramids in their surrounding, in addition to a modulation by cortico-cortical feedback and ILN (Section 3.2.2).

These mentioned collaterals travel upward to upper layer II, while extending up to 6 mm laterally (Gilbert and Wiesel, 1989; Rockland, 1985). With a macrocolumn measuring about 300 μm in diameter in layer V1, this is an exchange of local processing results over a wide neighborhood. Context over a wide environment could be evaluated by such a collateral system, as proposed in Section 3.2.2.

Latencies of responses to afferent stimulation in the upper part of layer II of the primary visual cortex of monkey are roughly 12–15 ms longer than in layer IV (Maunsell and Gibson, 1992; Nowak, Munk, Girard & Bullier, 1995; Schroeder, Mehta & Givre, 1998). In the context of our model, this reflects the interval for the description of an internal event clocked by gamma modulation.

Feedback system C. In our model, the infragranular layers are assumed to provide feedback as submodule *C*. Any columnar unit that sends its output to a target unit at a higher hierarchic level gets a recurrent feedback from that unit (Felleman & Van Essen, 1991) and influences both recall and learning. Feedback to lower hierarchic levels, targets mainly apical dendrites of pyramids at neocortical layer I.

In the ventral visual pathway, feedback from later stages of processing to V1, V2 and V4 is of point-to-patch rather than point to point characteristic, targeting a local spot of macrocolumnar width (Rockland & Van Hoesen, 1994). Multiple feedback from different levels of the processing hierarchy seems to be a general feature of sensory processing at higher levels, too (Rockland & Van Hoesen, 1994; Saleem & Hashikawa, 1998).

In our model, we simplify considerably to provide an instructive visualization of the framework of the neocortical columnar organization. For instance, in the real cortex, the source of forward and feedback connections is not exclusively confined to supragranular or infragranular layers as implemented in our model (Felleman & Van Essen, 1991). As we do not consider the sub-cortical outputs of columnar units, submodule *C* is not divided, although there is clear evidence for functionally separate output systems.

3.4.2. Neurophysiological support and predictions

Parallel-sequential processing. Much processing begins simultaneously in V1 and V2. Latencies in V1 are on the average 10 ms shorter than in V2, but there is an overlapping of distribution of latencies (Nowak et al., 1995). This suggests that the first processing results get rapidly transmitted to V2, though processing continues in V1. The same is true for the visual system of cats (Dinse & Krüger, 1994). Latencies of neurons in layers II and III are at least 10 ms longer than latencies at layer IV. They fit directly into the proposed gamma modulation scheme. A smaller percentage of upper layer neurons have very large latencies, covering several gamma periods. For these neurons, we predict that feedback is necessary to have a chance for activation. Note that this effect is major: 65% of V1 infragranular neurons were less responsive to visual stimulation while V2 was inactivated (Sandell & Schiller, 1982). Moreover, recent evidence shows that cortical feedback improves figure—background discrimination by V1, V2, and V3 neurons, having the strongest effect for stimuli of low saliency (Hupé, James, Payne, Lomber, Girard & Bullier, 1998) just as predicted by our model.

Stabilization of prediction. As proposed in Section 2, predictive feedback should sustain its support even longer than one decision interval, to stabilize the recognition process. Spikes transmitting the top-down prediction must be turned into a long-lasting sub-threshold modulation of the membrane potential of neurons in subsystems *A2*, *B* and *C* (but not in *A1*), in order to refine and stabilize the activated hypothesis. Apically generated EPSPs, released from cortico-cortical connections, have a strong and long lasting effect (more than 50 ms) on the respective pyramids (Cauler & Connors, 1994). We predict that in layer I top-down feedback contacts are of NMDA type (long EPSPs) and may undergo learning, while the synaptic contacts by modulatory connections from ILN in layer I should be of AMPA type. This would be in agreement with results of Thomson and Deuchars (1994). ILN modulation works in the gamma

frequency range, hence, the EPSPs, elicited by ILN synapses at apical dendrites should last not longer than 9–15 ms, and there should be no learning at all in this ILN modulation control circuit.

Tuning characteristics. Neurons in layer IV of V1, which receive direct input from thalamus, show a single orientation preference that remains unchanged throughout the response period. However, they are more broadly tuned than the neurons in the output layers (Ringach et al., 1997). The preferred orientation of pyramids in layers II, III, V and VI, which receive top-down feedback, usually changes with time. In many cases, orientation tuning has more than one peak (Celebrini et al., 1993; Ringach et al., 1997; Shevelev, Sharaev, Lazareva, Novikova & Tikhomirov, 1993). These data are in support of the proposed system architecture of a forward-only categorization system (in layer IV) in parallel to a second forward processing system that is supervised by top-down prediction. Category activation at subsystem A should be immediate, and should not change its tuning, while the response of neurons in subsystem B should be delayed and refined by prediction. It is observed, that the initial responses of neurons in V1 are typical filter responses to local features, while later responses (80–200 ms) depend on context information (Lee, Mumford, Romero & Lamme, 1998).

Modulation by top-down prediction. The context modulation of V1 neurons in awake monkeys unfolds spatially and temporally with a characteristic latency of 80–100 ms (Zipser, Lamme & Schiller, 1996) and resembles the figure/ground percept. However, recordings from anesthetized animals showed a selective suppression of figure/ground related modulatory activity (Lamme, Zipser & Spekreijse, 1998b). Note that anesthesia inhibits the reticular formation of the brain-stem, and thus reduces the ILN activation. Hence, ILN modulation may indeed be a necessary condition for a refinement at subsystem B.

V1 neurons can be modulated by feature-specific attention (Knierim & van Essen, 1992; Motter, 1994). This modulation must be a top-down process, as deactivating V2 (James, Hupe, Lomber, Payne, Girard & Bullier, 1995), or lesioning extrastriate areas beyond V2 (Lamme et al., 1998a), eliminate context-sensitive surround effects in the response characteristics of neurons in V1. Our model predicts that only those local spots of columnar modules which are part of the global hypothesis have a better chance to contribute a more detailed description of the input to subsystem B. This difference in activation should be observable—as it is indeed the case at an early level of visual processing (Roelfsema, Lamme & Spekreijse, 1998).

Functional interpretation of classical and non-classical receptive fields. Neurons of the category subsystem A define features of the classical receptive field of a macrocolumn, while the refinement subsystem B evaluates the activated features in a wider vicinity. Since in V1 several aspects of the stimulus are being analyzed in parallel, the categories in A1 and A2 (SS4 and pyramids in layer IIIC) are expected to

be specific for orientation, disparity, color and movement. Yet, description at B2 should combine all of them. The characteristics of our B subsystem predicts, that the closer the position of a supragranular neuron to the pial surface is, the wider its RF should be (where the response could be modulated by inputs in a lateral distance). Hence, the more complex its response characteristics should be.

Characteristics of layer III originated feedback connections. In subsystem A category features are encoded. Being activated by A2 output, the predictive feedback from C also represents the category. By contrast, refinement in B selects a specific instantiation of this category, depending on the local context and the feedback.

If there is feedback from upper layers, it is from layer IIIA (Lachica et al., 1992), which refers to our system B2. At the level of the first sensory areas, say V1, the number of specifically memorized feature/context combinations may be lower than at higher levels of representation. At least for higher levels of processing, not only features, but also very specific instantiations of them should be predictable (e.g. for imaging). Hence, we predict that: (i) At higher levels of the hierarchy, the feedback from pyramids of layer IIIA is more frequent for subsequent levels of the hierarchy than at lower levels. (ii) Feedback from pyramids of layer IIIA is more divergent at the respective lower level, compared to that of pyramids of layers V and VI.

4. Discussion

We have presented a model that integrates cortical morphology and physiology into a consistent computational hypothesis on coding, rapid and robust recognition, and predictive control of processing in neocortical architectures. It provides a novel interpretation of gamma oscillations, which is plausible from the biological as well as from the computational point of view.

4.1. Coherent decision intervals and rhythmic modulation

The clocking of cortical computation by intrinsic rhythmic processes is a concept which is still under controversial debate, regarding both its origin and its underlying biological mechanisms (see Phillips & Singer, 1997; Ritz & Sejnowski, 1997, for a recent review). Our approach offers a new interpretation of rhythmic cortical activity, which differs in several important aspects from most existing theories: We propose that the main purpose of rhythmic activity is not the synchronization of spikes, but rather that of decision intervals. Oscillatory activity provides a coherent, temporal organization of cortical processing, which otherwise runs in an asynchronous mode. Thereby, it provides a coherent temporal framework during which decisions may take place. Thus, in our model rhythmic activity reflects *control information* rather than a direct description of stimulus features, as was proposed by other authors (see e.g. Aertsen & Arndt, 1993; Singer, 1993). This

control information allows the definition of globally coherent *internal events*. It is related to the idea that time is discontinuously processed in the neocortex in order to establish a globally coherent internal description of behaviorally relevant aspects of the current situation (Körner, Tsujino, Körner, Masutani & Nagai, 1995; Körner et al., 1997; Pöppel, 1970).

The definition of a discrete time window is an important step towards a model of the brain as an active system in the process of sensory recognition. Apart from simple template matching, the introduction of a globally coherent decision interval provides the system with the capability to actively compose an internal event out of the steady stream of sensory signals, increasingly guided by its acquired and hierarchically structured knowledge. This interactive process of knowledge based decomposition of the sensory signal flow and the composition of an internal semantic description, supported by temporary clocking of cortical processing, also provides a plausible scheme for cognitive binding. A wealth of experimental evidence is available for local field potential oscillations in the gamma range (see Gray, 1994, for a review) as well as for precise spatio-temporal spike patterns (Abeles, Bergman, Margalit & Vaadia, 1993a) and zero-phase synchronous spike discharges (Vaadia et al., 1995). It appears that not the phenomena themselves, but rather their underlying mechanisms are at the focus of the controversial debate on the functional relevance of synchrony.

One approach to cognitive binding, the *active feature linking hypothesis* uses temporal synchrony, e.g. synchronization of spikes, in order to *bind* perceptual elements (Singer, 1993, 1994; von der Malsburg, 1995). The model presented here, offers a more plausible interpretation of the experimental findings. As the essential steps for recognition are already carried out within the first 150 ms, stable induced gamma oscillations, which are observed more than 200 ms after stimulus onset, cannot represent forward segmentation by lateral interactions. During the first 200 ms after stimulus onset, only sub-threshold oscillations can be observed and only with stimulus-triggered averaging methods (Bertrand & Pantev, 1994). This absence of spike synchronization is consistent with our model, as all response spikes are still distributed over an entire decision interval by the stimulus-locked, bottom-up modulation.

Synchrony, enforced by top-down feedback of an activated globally consistent hypothesis, is expected to resemble more closely the coherent firing of sparse local spots, frequently observed later than 200 ms after stimulus onset. In addition, our model ensures synchronization of decision intervals despite the typically low cortical firing rates. It does not require actual cortico-cortical connectivity, in order to *bind* activated neurons into a description of an internal event. In our model, zero-phase synchronization is a natural result of the bottom-up and top-down synchronization by active processing-state-dependent global clocking.

This mechanism for organizing cortical computation is

not limited to cortico-cortical interactions as in the *feature-linking theory*. Instead we place the temporal control of processing into the context of interactions between the cortex and the ILN.

4.2. Two separate but functionally complementary forward processing systems

The introduction of subsystems of columnar modules provides the capability to define two separate, functionally complementary forward processing systems. One for rapid forward categorization to obtain a first impression of the sensory input, and the other for the refinement of the internal world model guided by prediction (top-down feedback). In most cases, forward categorization, by itself, may supply sufficient information, especially if an internal representation of the interaction between the subject and its environment has already been established. As long as there is no critical inconsistency between categorization input and internal representation, sensory stimuli might not even leave any traces in cortical activity. A coordinated function of both forward systems is only expected if a changed environment enforces the composition of an internal representation, or if a refinement of recognition is required for specific behavioral needs. As long as the categorization system is sufficient to refresh and update the current internal representation, we should observe the silent synchronization of sparsely distributed active spots at the cortex while supra-granular activity is at a very low level.

4.3. Feedback prediction makes the world appear more regular

Top-down prediction modulates the conditions for refinement in system B^n , in order to *abstract* from fluctuations in the afferent input. The feedback signal generates a sub-threshold depolarization of pyramidal neurons in the columns of its receptive field at the lower level $n - 1$. If they are supported by predictive feedback, partial matches at the lower level $n - 1$ may be regarded as more reliable. As a result, the latency representation of a feature, recognized as partial match in the first decision cycles, moves closer to that of a reliably recognized category during the subsequent decision cycles. In effect, its relevance is upgraded by predictive feedback from attribute to category. Thus, the input to subsequent processing levels is cleaned from fluctuations that were already identified as *noise* in the course of the recognition process. This process results in some kind of *unconscious abstraction* that considerably reduces the required coding space from one level of the representational hierarchy to the next. Thus, the description of the world gets more *prototypical* with each additional level of processing. This process makes the world *appear* more regular than it actually is.

4.4. Temporal ensemble code

We propose that relative latency with respect to a global clock provides a very important control information to all neurons, which are involved in recognition. With the definition of a time window for internal events, each spike carries information on the reliability of its signaled recognition result by its temporal position within the decision interval. Spikes arriving at the beginning of a decision interval provide information for profound category decisions. The later the spike appears in the decision interval, the less reliable is the information. It is then used as attribute to refine the category. There is no need for a central-management system that would define the most reliable analysis out of a number of possible ones. Each feature detector itself attaches a label of the degree of reliability of its decision onto the spikes sent to the next processing instance by its relative latency. This temporal code is universal and can be decoded by any neuron as long as the clocking of neocortical processing guarantees a proper reference time.

It has to be noted, that, currently, experimental evidence for this type of temporal coding is weak. This is mainly due to the fact that most electrophysiological work is based on a rate code assumption. However, we want to emphasize that the latency code, presented here, is a direct consequence of the biophysical mechanisms, underlying the neuronal spike generation.

The ILN complex could support a proper clocking of the cortex. It is located at the center of the brain and has about the same distance to all cortical areas. This is a prerequisite in order to avoid de-synchronization of the clocking signal, caused by different conduction times (conduction is extremely fast from ILN to cortex, but slow for cortico-cortical connections). At the sensory periphery of the neural system, matters are different: Here, distances are large and may vary considerably. Thus, it seems impossible to synchronize all peripheral-processing levels by a globally consistent clock. Rate coding does not need any clocking and might be the best compromise for coding signals at the periphery. As a consequence, one expects that at primary sensory cortices the neural activity contains temporal structure, superimposed by residuals of rate coding from the periphery. The more we move upwards in the hierarchy of sensory processing, the more we expect the response properties of cortical neurons to reflect the sparse, low frequency firing characteristic for the temporal ensemble code. Indeed, this has been observed by Abeles et al. (1990) and Abeles, Prut, Bergman, Vaadia and Aertsen (1993b).

4.5. Processing with single spikes. What about bursts?

In our model we assume that during each decision interval each neuron releases either one spike or none at all. This simplification is probably valid for most operation conditions of cortical neurons, except during the first few tens of milliseconds after stimulus onset. During this short interval,

the initial response transient of most neurons relaxes to a steady low level of firing (mostly below 40 Hz). Excitation in the cortex usually goes along with rapid forward inhibition that prevents re-excitation (Douglas & Martin, 1991). This may explain the rather low cortical firing rates for natural stimuli. Average responses of cat V1 neurons to natural scenes are at about 4–9 Hz (Baddeley et al., 1997).

Even if more than one spike per neuron is released during a decision interval, e.g. spike doublets or bursts after stimulus onset, processing in our model would not be impaired. For the categorization in system A, bursts pose no problem, for only the first activated category is transmitted by its winner-takes-all mechanism. According to our model, bursts may *ensure* that synaptic transmission is effective (Lisman, 1997). Moreover, the coincidence interval, during which perfect matches could be detected, would be increased. This may even increase the chance of transmitting sufficiently complete object descriptions to higher levels of processing.

Repetitive spiking is more critical for the refinement system B; here, bursts reduce resolution. However, right after stimulus onset, when bursting occurs, categorization takes place. The detailed analysis in the refinement system requires support by top down prediction and, thus, follows about 80–100 ms after stimulus onset (Lamme et al., 1998b; Lee et al., 1998). At this time, the system has already relaxed to a steady level of low firing. Hence, low resolution of refinement, during the first two gamma cycles, does not really pose a problem to the quality of processing.

For the feedback prediction, matters are different: A neuron in C^n provides predictive feedback to many pyramidal cells in its receptive field at $A2^{n-1}$, $B1^{n-1}$, $B2^{n-1}$, and C^{n-1} . Here, bursting behavior is needed in order to ensure the efficient activation of a sufficiently large EPSP. Therefore, we predict that neurons of layers V and VI which feed their activity back to the lower level, should regularly fire in burst mode to ensure the efficiency of transmission at its synapses to the recipient neurons. Indeed, many pyramids in layer V are burst-generating neurons. In this scenario, firing rates do not carry information (except a coarse measure of the degree of match at the onset of the response), but they represent a control measure to cope with the probabilistic characteristics of synaptic transmission (Markram & Tsodyks, 1996).

5. Conclusions

The main focus of our approach is to broaden our understanding of how the computation is organized in the brain. A large-scale computational concept is proposed by deduction of possible meta-algorithms from neocortical architecture, using the constraints of a properly defined cognitive task to be performed by this modular architecture composed of spiking neurons of distinct characteristics. It is the implementation of the concept into a detailed model description

that enables very specific and testable predictions. On the one hand, our approach provides a biologically and computationally plausible model for high-level computational processes, whose possible mechanisms are still under controversial discussion, e.g. cognitive binding and unconscious abstraction. On the other hand, it offers reasonable explanations for the functional role of a number of details of cortical architecture that has been elusive so far.

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