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The Control of Low-Level Information Flow in the Visual System

Katrin Suder and Florentin Wörgötter

Institute of Physiology, Department of Neurophysiology, Ruhr-University, Bochum, Germany

SYNOPSIS

Visual information processing needs to be error free and efficient. Our visual system tries to achieve the first goal by accommodating a wide variety of visual algorithms for the extraction of the relevant features in the scene, while at the same time the second goal is addressed by controlling the amount of visual information flow in the network employing selective attention. Attentional or pre-attentional mechanisms are found throughout many visual areas and these processes may start as early as in the visual thalamus (lateral geniculate nucleus, LGN). In this review we pay particular attention to experimental and theoretical findings which indicate that even low-level structures, such as LGN and V1, can play a major role in the flow-control of visual information.

KEY WORDS

attention, computational models, thalamus, dynamic receptive field restructuring, visual cortex, EEG, brainstem

1. INTRODUCTION

The surrounding world provides us with far more input than we can process simultaneously due to the limited capacity of the brain. To be able to deal with the huge amount of information bombarding us, a selection process has to be carried out. The necessity of such a process has been

shown by psychophysical experiments /26,86 (and references therein)/ and also by theoretical considerations, proving that a so-called general-purpose vision would not be possible without a reduction of the input to be processed /106,111/. This is exactly where *attention* comes in as the process that selects a particular piece of information or, for the visual system, a spatial area out of the whole sensory pattern for further processing. But how can attention be defined?

In 1890, for William James in his *Principles of Psychology*, a definition was obvious and without any doubt: 'Everyone knows what attention is. It is the taking possession by the mind [...] of one out of several simultaneously possible objects of trains of thought.' But throughout later research it has turned out that dealing with attention is not as easy as James thought. Attention has many different facets and components and it has been studied by all the different disciplines trying to understand the brain: psychology /38,94/, psychophysics /33/, neurology /26/, neuroimaging /37/, neurophysiology /22,27, 33/ and computational neuroscience /72,79,107/. Most of the disciplines have their own focus and their own definition of attention.

In the context of this review we can give an operational definition: Exposed to a number of stimuli, that are equal in their physical appearance, both animals and humans can respond to certain stimuli while disregarding others (without the need for saccadic eye movements). This internal, covert focus, this selection of (spatial) items is the basic operation of spatial selective attention. By selecting information which is to be gated to higher regions for further processing, attention will modulate the signal on its way through the brain. Thereby, a second major problem of cortical information processing is solved: the binding problem /33,112/. Attention links (or binds) information together which is distributed over the different parallel pathways, i.e. the ventral and the dorsal stream /103/.

Reprint address:

Florentin Wörgötter

Institute of Psychology

University of Stirling

Stirling FK9 4LA, Scotland, UK

e-mail: worgott@neurop.ruhr-uni-bochum.de

Attention can be classified in several ways, e.g. by its different procedural components (engage, disengage, move) /86/ or by the different regions involved. Posner and coworkers suggested differentiation between two subsystems: the posterior and the anterior attentional systems /85/. The former - consisting of subcortical areas such as the thalamus and the superior colliculus - seems to be involved in directing attention. The latter involves the anterior cingulate cortex and portions of the basal ganglia. This anterior or executive system has been suggested to be responsible for actions and for ideas.

Preattention vs. attention

From a computational point of view, a different classification might be useful, namely one due to the two major functional mechanisms used by attention: bottom-up vs. top-down processing /12, 13,22,33,72,74,79,94,115/ (Table 1).

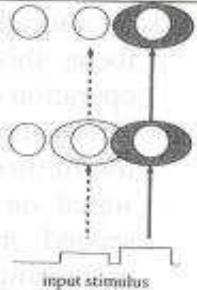
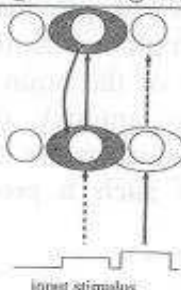
Bottom-up (pre-)attention is data-driven and involuntary. Any kind of new or salient stimulus

will automatically attract our attention, e.g. the random flight of a large fly or the newly red-dyed hair of our partner. Bottom-up attention accounts for pre-attentive effects, i.e. the well-known pop-out phenomenon. These effects are transient (0-300 ms), since the saliency of a new object quickly decays with time, and they are fast, to enable us to react adequately to new situations. The speed can be ensured by low-level implementation, therefore bottom-up attention should also show effects in the early visual system (V1 or even subcortical, see Section 2).

In contrast, top-down attention acts on a different, longer time-scale (up to several seconds). We all know from experience that we can voluntarily direct attention to a specific region of interest, e.g. while searching for a certain object. This task-driven form of attention must involve high-level regions, i.e. those responsible for cognitive functions. Top-down attention is what James described in his definition and it is part of conscious processing /4/.

TABLE 1

Bottom-up vs. top-down attention

| | preattentive processing | attentive processing |
|-------------------|---|---|
| data flow | bottom-up | top-down |
| driven by | input data | task data (memory) |
| controlled by | unconscious, involuntary | conscious, voluntary |
| processed where | low-level regions | high-level regions |
| time-scale | transient (0-300 ms) | sustained (100 ms - seconds) |
| responsible for | pop-out effects | searching and highlighting |
| connection schema |  |  |

The figures at the bottom show that top-down influences (right) can actually overrule bottom-up attention (left), i.e. although the stimulus presented to the right neurons is more salient, the left location can 'win' if additional top-down excitation is on.

Psychological models

Early evidence for the existence of covert visual attention came from psychophysical reaction time studies (see /84,102,115/ for reviews). Subjects are asked to find target objects in a visual display. It has been shown that in trials where a valid cue was given before the target presentation, reaction times were significantly reduced.

The results of several years of research led to the formulation of many different models and hypotheses as to how the search experiments could be explained, e.g. Treisman's *feature integration theory* /103/ or Julesz's *texton theory* /58/. Many of the proposed models share the same basic idea, which is probably the most prominent and also most accepted psychological model: the *spot- or searchlight paradigm* /15,28,75/. It has two stages. First, as soon as a new stimulus is presented, the whole visual field is processed in parallel during the pre-attentive mode. For many tasks (especially for pop-out effects) this mode alone is sufficient. For more complex tasks (conjunctive search), a different, second strategy is needed, i.e. the attentive mode described by the spotlight metaphor. Only a limited area is highlighted and analyzed in detail, whereas the rest is in the dark. In a serial process the whole field is scanned. The enhancement of a specific region has different effects characteristic for the processing of attended stimuli: reaction times are reduced, discrimination thresholds are lowered and neural activity is increased /86,94 (and references therein)/.

Since not all search experiments could be explained by the purely bottom-up approach of the searchlight hypothesis, top-down components were added to the model. In his *guided search* model Wolfe proposed that top-down processes favor features belonging to the target object /115/.

A different view emphasizes the idea that attention always works as a parallel process /17,33/. In the framework of this *biased competition* model /33/, attention is not a fast, serial scanning mechanism, but a slow, competing interaction of all neurons. It can be biased by bottom-up mechanisms such as figure-background stimuli or by top-down mechanisms that select certain behaviorally relevant objects.

Over the years many hybrid models have been developed which integrate serial, parallel, bottom-up and top-down processing (e.g. /50/). It has furthermore been proposed that the notion of serial vs. parallel search should be omitted altogether, since there is no significant experimental evidence for this kind of dichotomy /115/ (for a discussion of the two processing strategies from a computational point of view see /79/).

Computational models

The dichotomy between bottom-up and top-down processing is a dominant category for most computational models trying to simulate selective attention or its effects. These models deal with the problem of how a focus of attention can be selected and how its information can be routed through the network. They are included in one class of models, i.e. *selection and routing models* (see Fig. 2). A second class of model deals with another dimension of how to implement selective attention. The aim is to find answers to the question of how the firing of neurons inside the spotlight of attention might be modulated, i.e. how the selected neurons differ in their behavior from neighboring neurons (*tagging models*).

In Section 2, we review the most important experimental results which form the basis for computational models. After reviewing the selection and tagging models in Section 3, we introduce a third kind of models, i.e. models of low-level (pre-)attention which try to build biologically plausible implementations and focus especially on the role of the thalamus for (pre-)attention. These models are discussed in detail in Section 4.

2. EXPERIMENTAL BASIS

Attention has been studied by the various disciplines in neuroscience: by lesion studies and functional mapping /27,85/, by behavioral and psychophysical methods /37,38/, by pharmacological studies /27/ and also by single unit recordings /22,33/. In this review, we concentrate only on summarizing the most important results relevant for the modeling of visual attention.

One of the first cellular studies of selective attention was made by Wurtz and coworkers /120/. Experiments were carried out in awake primates while recording neurons from the superior colliculus (SC), striate cortex (V1) and posterior parietal cortex (PP). The basic finding was that cells in V1 and in SC responded with a higher firing rate when the animal oriented to an attracting spot *with* a saccade, while there was no change in response when the animal maintained fixation at a central spot and only shifted its attention covertly. PP neurons, in contrast, also show an activity enhancement due to covert shifts of attention. Since then, many studies examining the neural basis of overt and covert attentional shifts have been carried out. Thereby, researchers explored most of the different brain regions looking for their role in attentional processing (Fig. 1).

Moran and Desimone extended the first app-

roach by showing that also neurons from the inferior temporal cortex (IT) and from V4 behave differently depending on the attentional task /69/. In the experimental setup, two objects were placed inside the receptive field of an IT neuron, one being an effective stimulus for that neuron and the other ineffective. If attention was focused on the ineffective stimulus, the activity of the neuron decreased, while it increased if attention was on the effective stimulus. It seems as if the receptive field shrinks around the attended object.

Similar attentional modulations have been found in other areas and with other techniques, e.g. Büchel and Friston /16/ showed an attentional modulation of V5 and PP measured with fMRI, Connor *et al.* /24/ concentrated on the spatial relationship between stimulus and attention in V4, and others looked at orientation tuning curves /67,104/.

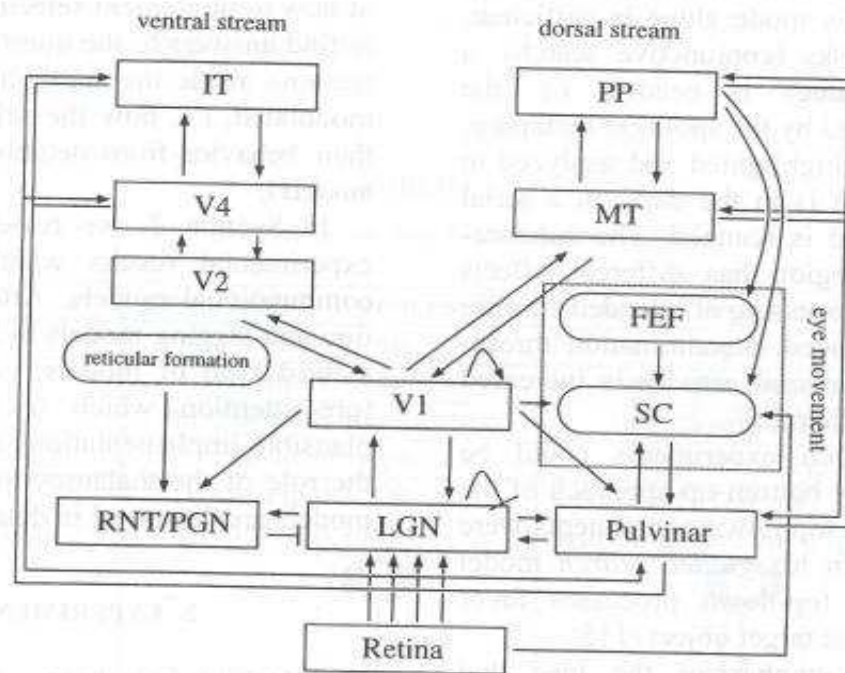


Fig. 1: Simplified schema of the visual processing system. Only the areas and connections relevant for the purpose of this review are included. The fact that covert attention influences neural firing in high regions of the processing stream [such as the posterior parietal (PP) or the inferior temporal cortex (IT)] seems to be indisputable today, but whether, or under which conditions, it also influences low-level structures (such as V1) is still a debated issue (e.g. /64/). Evidence has also been provided for an attentional modulation of V4 and the medio-temporal cortex (MT) /23,66/. The frontal eye field (FEF) and the superior colliculus (SC) are mainly involved in overt shifts of attention, i.e. in eye movements /86,119/. Subcortical structures, especially the different thalamic nuclei - the reticular nucleus (RNT) with its substructure the perigeniculate nucleus (PGN) which is inhibitory connected to the lateral geniculate nucleus (LGN) and the pulvinar - are also supposed to play an important role in (pre-)attentional processing (see text).

The most debated question is whether the influence of attention starts as early as the striate cortex. V1 poses a problem because receptive fields are so small that even small eye movements may destroy the measurement of attentional effects. Furthermore, it is extremely difficult or even impossible to place competing stimuli - an important condition for attentional experiments /64/ - inside these small receptive fields.

Moran and Desimone /69/ did not see any modulation of V1, V2 or V3 neurons. Luck *et al.* /63,64/ also reported no attentional modulation of ERP signals or firing rates for V1 cells. In contrast, other studies did indeed find an attentional influence on the early visual system. For example, Motter /70/ found significant attentional effects in V1, V2 and V4. These early results have been confirmed by more recent publications: Using fMRI signals, Martinez *et al.* /65/ found that not only the extrastriate but also the striate cortex is involved in spatial attention. V1 exhibited a later attention dependent response component than the extrastriate cortex, which could be seen as a delayed, re-entrant feedback component. Using fMRI Brefczynski and DeYoe also reported a modulation of V1 and the extrastriate cortex by a shifting focus of attention /14/.

Taking the studies together, the picture arises that attentional modulation is most prominent in

higher cortical areas, where receptive fields are wide and where several objects can compete inside a single receptive field. In V1 attentional effects seem to be existent and measurable, but less strong, and may be related to specific experimental setups /64/.

However, not only cortical areas are influenced by attention. The different thalamic nuclei in particular seem to play an important role in visual attention /22,27,28,93/. The specific connection structure - not only receiving input from the retina, but also from the brainstem and from higher cortical areas - supports this. There seems to be convincing evidence that the pulvinar is directly involved in attention. Single cell recordings showed an attention-dependent enhancement of the firing rate, and pulvinar lesions led to an impairment in the ability of engaging attention /86,90/. The possible role of other thalamic nuclei is discussed in Section 4.

3. COMPUTATIONAL MODELS OF SELECTIVE ATTENTION

Apart from the neurophysiological implementation (discussed in Section 4), modeling selective attention has two major and independent problems which need to be solved (Fig. 2): One concerns the question of how to select and implement the focus

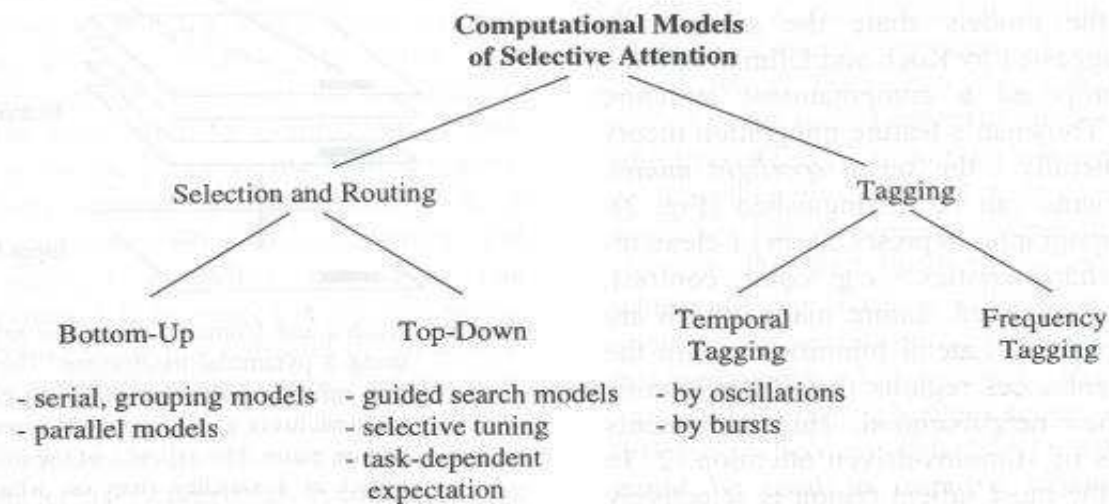


Fig. 2: Schema showing the main model classes. A third group of models - those concentrating on the role of the thalamo-cortical circuit in attention - is not included in the schema. They are discussed in more detail in Section 4. (For alternative classifications see /72,79/.)

of attention (Section 3.1), and the other provides solutions to the question of how to mark or modulate the neurons which are in the focus of attention (Section 3.2).

3.1 Selecting and routing the focus of attention

Most of the models dealing with attention propose answers to the question of how to select the focus of attention and how to route the information from the focus of attention through the various stages of the network. Due to the close relationship to search processes, the number of models increases even further, especially since search procedures are also of technical importance, i.e. in robotics /7,40, 56/ or hardware implementation /54/. Again, it is necessary to differentiate between purely bottom-up models and those including task-dependent top-down components.

3.1.1 Bottom-up models

In bottom-up (pre-)attentional models it is assumed that different regions of the input field differ in their information content, e.g. in contrast distribution. This difference of a specific region from its surroundings is sufficient to assure that this region will be preferentially processed further up in the system. Two major subclasses can be differentiated (see Table 1): those regarding attention as a serial operation and those regarding it as a parallel operation.

Most of the models share the same basic elements as suggested by Koch and Ullman in 1985 /60/. They proposed a computational structure implementing Treisman's feature integration theory or - more generally - the *serial spotlight model*. Different elements can be distinguished (Fig. 3): 1. An early, topographic representation of elementary stimulus characteristics - e.g. color, contrast, orientation - in so-called feature maps, which are computed in parallel. Lateral inhibition within the feature maps enhances regions that differ significantly from their neighborhood. This implements pop-out effects of stimulus-driven attention. 2. In the next step, the most salient region is selectively mapped to a higher non-topographic representation for further analysis, e.g. object recognition. 3. The selection process is implemented via a so-called

saliency map, which combines the information of the individual feature maps into one global representation. The saliency map can also be seen as an interface between pre-attentive bottom-up and attentive top-down mechanisms (for a more detailed discussion of the saliency map see /79/). A winner-takes-all (WTA) network filters out the most salient region to be mapped into the central representation. In order to achieve a convergence of the WTA algorithm, Koch and Ullman proposed a pyramidal strategy. The algorithm itself has been the topic of several further investigations, e.g. /62,107/. 4. Finally, delayed inhibition of the currently selected region will enable a shift of the processing focus to another location.

The first implementation of the Koch and Ullman model was supplied in 1990 by Chapman /20/ showing that the proposed structure is actually able to select locations of interest, which can be

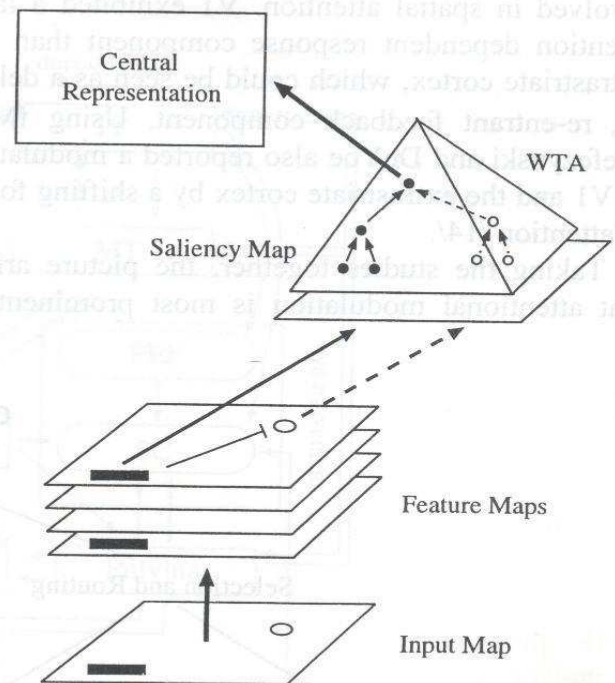


Fig. 3: Koch's and Ullman's model for selective attention using a pyramidal mechanism. The visual input is first split in parallel into different characteristics of the stimulus (e.g. contrast), which are represented in feature maps. The saliency of the different stimuli is coded in a saliency map on which a pyramidal winner-takes-all mechanism looks for the most salient region. Only information from this region is routed to a central representation. (Adapted from /60/.)

used as starting points for further processing, e.g. for motor routines. However, the pyramidal network used has several drawbacks, e.g. the fixed size of the focus of attention or the slowness of the algorithm (see /1,107/).

In their *shifter circuit* model, Anderson and van Essen focus less on the saliency mechanism, than on how the focus of attention is shifted and how the containing information is routed from the retina to a central representation /3/. The original idea was further elaborated by Olshausen *et al.* /81/. The main achievement of the shifter circuit model is a successive, object-centered representation of different salient inputs. The sophisticated representation algorithm furthermore provides position- and scale-invariance, which dramatically eases object recognition, since different sizes and retinal positions are coded in one single representation (for a more detailed discussion of the preservation of spatial relations see /79/). This is achieved by a dynamic routing mechanism which modifies the synaptic weights in such a way that only certain regions are routed (mapped) to the top of the processing stream. Spatial relationships inside the routed region are preserved throughout all mapping stages, thus the name shifter circuits. This is accomplished by a connection structure inspired from biology, in which the distance between neighboring neurons increases systematically while the topography is preserved. The mechanism that selects regions of interest is purely bottom-up. The input image is low-pass filtered so that the input objects (letters were used in /81/) are blurred into blobs. The brightest or largest blob is selected and this information builds the basic input for control units which are responsible for the gating of the desired region. These inhibitory control neurons function as a WTA mechanism based on local competition and selectively suppress ascending pathways. The 'surviving' region will be routed to the top where object recognition takes place. Based on an associative memory mechanism, the content of the high resolution attentional window will be compared to the memory content. In the case of a good agreement, the object is counted as recognized, the corresponding input area is inhibited, and the next region is then analyzed. One interesting aspect is the use of control units, which allow a dynamic

modification of the synaptic weights on a short time scale.

Other models followed those first proposals (e.g. /87/). Mozer /71/ introduced a different strategy to find the focus of attention. Instead of a pyramidal structure, he favors an iterative relaxation mechanism, in which the activity of different neurons (or processing units) is compared to the surrounding activity and locally adjusted at each time step. This will finally lead to a "winning" region of maximal activity, with the advantage that this region is not fixed in size. However, Mozer's model does not provide an explicit integration of top-down information.

Recently, it was shown that the original Koch and Ullman /60/ proposal can be extended and implemented in such a way that it can be used for a rapid scene analysis of different real world input images, i.e. to detect traffic signs /56,77/. To achieve a robust and computationally efficient algorithm, the model is more abstract and only the basic features are biologically plausible.

In contrast to the serial models, a number of proposals have been made for the implementation of the *biased competition* idea /33,89/. In this framework, objects are supposed to be processed in parallel and attentional selection is made of those objects that 'win' a competition. Consequently, a representation in the form of a saliency map is not necessary.

In a series of papers Bundesen and coworkers developed a computational theory of attention based on stochastic processes /17,18 (and references therein)/. The basic idea - which is closely related to the biased competition model - is that the selection of targets from multi-element displays can be described by so-called *race models*. Elements compete for processing capacities and those elements that first finish the processing - i.e. the winner of the race - will be in the focus of attention. It has indeed been shown that responses to objects with a low contrast - that would not be very salient - have a longer latency, and that latency differences between objects with different contrast could be used to improve object segmentation /116/. In general, these race models are very similar to the described WTA networks, with the difference that Bundesen *et al.* do not use the connec-

tionist framework. Since the model is mathematically treatable the interplay between serial and parallel processes can be studied in detail. Also, different experimental data can be explained. On the other hand, the model is still mainly phenomenological and Bundesen *et al.* have just started to analyze possible microscopic or neurophysiological implementations and/or consequences of their mathematical theory /19/.

The biased competition idea has also been carried out with the help of a more biological implementation, introduced by Reynolds *et al.* /89/. Data from experimental recordings (from V2 and V4) are in accordance with the results from a model simulation with a simple feedforward competitive neural network.

The notion that attention modulates local competition is also used in a recent model study by Lee *et al.* /62/. In their model, attention changes the lateral inhibition between filters and thereby modulates the winner-takes-all competition. Among other things, the model can explain threshold changes for discrimination tasks.

Using a neural network approach, Wu and Guo /118/ also showed that a parallel competition mechanism - in contrast to the serial searchlight mechanism - can successfully carry out attentional processing. They introduced a computational model based on a two-layered network (hippocampus and cortex) with phase oscillators showing that attention can be seen as an emergent property of the dynamic cell assemblies.

3.1.2 Top-down models

Since the initial selective routing models were purely bottom-up, they cannot account for more complex phenomena, e.g. those occurring during visual search for specific objects (see /1,115/). In addition, computational complexity arguments have shown that a purely feedforward and parallel network is not sufficient to provide solutions to general search problems /106/. Therefore, it has been suggested to add a feedback control to the basic feedforward model structure (see Table 1). Top-down information can be used for grouping or weighting of selected features or to favor a specific region, and may even overrule bottom-up attention. Consequently some sort of memory or learning

algorithm is necessary which matches the data from the focus of attention with the stored target information /6,108,109/.

In the implementation of his *guided search model*, Wolfe /114/ suggested that top-down feedback from higher visual areas weights or biases the importance of different features. Only those regions with additional weighting are further processed.

Several models including top-down feedback and/or improving the basic structure proposed by Koch and Ullman have been published over the years /2,6,50,53,72,107,109/.

Apart from including top-down information, Tsotsos /106,107/ furthermore proposed a way to integrate the control process, which was suggested within the scope of the shifter circuit model, in the processing stream in his *selective tuning model*. Thereby, he proposed that there is not one single saliency map, but that each processing layer has its own representation of what is salient. At each level a winning unit exists which inhibits its neighborhood. This has been described as an attentional beam shining through the network.

Another very interesting approach is provided by Rao /88/. He suggests viewing attention as an emergent property of a distributed network of neurons whose primary goal is visual recognition. The simulations are based on a *predictive filtering model* (Kalman filter), in which bottom-up signals of presented objects interact with top-down expectations due to learned and stored object patterns. Given multiple objects or conflicting stimuli, the responses of feedforward, feedback and predictive neurons are modulated as if certain objects were being attended to, although attention is nowhere explicitly used in the model.

A model implementing the idea of competition as the basic attentional driving mechanism in a search task has also been proposed by Usher and Niebur /108/. As is typical for competition models, a saliency map is not needed. The competition is implemented with an inhibitory cell pool via which all parallel maps - representing the visual input - interact. Top-down influence is assumed to come in via weak excitatory projections from a higher, working-memory level. In this way, searching for a specific target will interact with bottom-up signals. Simulated cell activities are in good agreement with

experimental data from IT cells recorded by Chelazzi and coworkers /21/.

Major attempts towards understanding attentional processing and its computational modeling have been provided by Grossberg and coworkers (see /47,48,50,51/ and references therein). Their aim is to find a basic and unifying framework which can explain as many experiments as possible. We selectively discuss here two important papers, one providing a solution of how to model search processes including top-down and bottom-up mechanisms, and one suggesting a detailed physiological basis of attentional priming.

In 1994, Grossberg *et al.* published a paper /50/ in which a neural theory of attentive visual search was suggested. Their (computational) model provides an alternative to Treisman's feature integration theory /103/ and to Wolfe's guided search model /115/ insofar that not only bottom-up and top-down mechanisms are implemented but that, furthermore, spatial grouping and object recognition are included. The visual input is first analyzed in parallel by preattentive processes, which filter out basic stimulus features. In a second step these extracted features support boundary segmentation and surface formation - thus achieving grouping. In the next step, a candidate region is selected for further analysis. Finally, object recognition takes place by matching objects from the selected region with stored targets. The different steps are compared to results from earlier models, which simulated single facets of the problem, e.g. the boundary contour system (BCS), which is used to find boundary segmentations. All processing steps are mapped to neurobiological circuits. The final simulations, though, are carried out using a more abstract model to describe reaction times in search experiments as a result of processing times in the single steps. Good agreement with several different search experiments has been achieved.

Physiological implementation is the main topic of another, more recent paper entitled 'How does the cerebral cortex work?' /49/. Grossberg suggests 'how bottom-up, top-down and horizontal interactions are organized within visual cortical areas V1 and V2' and how these connections might implement learning, attention and grouping. Special emphasis is put on the laminar circuits, i.e. on the

interplay between layers 2/3, 4 and 6. One main hypothesis is that via feedback from layer 6 to 4 the preattentive perceptual grouping - e.g. that responsible for illusory contours - serves as its own attentional primer; thus the priming mechanism can also work at regions which do not receive direct bottom-up input. For the matching process between bottom-up and top-down signals, Grossberg reuses his ART (Adaptive Resonance Theory) /45,46/ but now with a detailed physiological implementation. Simulations are not provided, but several interesting predictions arise from this model.

Although at a macroscopic level there seem to be many similarities between biology and the individual models introduced in this section, many of the selective routing models still fail to provide any explanation of how their algorithmic features could be implemented in the real brain.

3.2 Tagging the selected focus of attention

After a region of interest is selected the question arises of how this region differs from other regions. Higher processing areas have to be able to detect regions of interest out of the whole incoming data stream, i.e. the neurons currently in the focus of attention have to be tagged in some way. Two major strategies can be differentiated: temporal tagging and rate modulation.

3.2.1 Temporal tagging

Crick and Koch /29/ hypothesized that cell assemblies - which are made up of those neurons currently in the focus of attention - are glued together by a specific temporal firing pattern. In particular, they proposed that this is done 'in a coherent semi-oscillatory way, probably in the 40-70 Hz range'. This first proposal of temporal tagging as a way to mark neurons in the focus of attention also solves the binding problem /112/ in an elegant way (for the connection between binding and attention, see /64,103/). The idea was computationally carried out by Niebur and coworkers /80/. Attentional modulation was added to the output of the cells of the primary visual cortex and was supposed to affect only the temporal structure of neural firing. V1 cells project to V4, where frequency-selective interneurons are supposed to exist

and to block out all non-frequency modulated signals, i.e. the activity of neurons not currently in the focus of attention.

Following this first paper, several other mechanisms have been proposed implementing the *temporal tagging* hypothesis. Niebur and Koch /78/ suggested that temporal tagging does not necessarily have to be oscillatory but might be in the form of a non-homogeneous Poisson process. Kazanovich and Borisjuk implemented the idea of a central element (see /26/) which oscillates as soon as the attentional system is switched on /10,59/.

A more abstract, but nevertheless very interesting approach comes from non-linear system theory. Chaotic neural networks exhibit complex dynamics including unstable periodic orbits. These can be stabilized by small parameter changes via feedback control /35/. It has been proposed that a similar mechanism might underlie attention, i.e. specific oscillatory modes, which code behaviorally relevant stimuli, are linked by transient chaotic states /82,97/.

Carvalho *et al.* /32/ presented a biologically realistic model of the visual pathway from V1 to IT, based on a detailed description of ionic currents. The neurons have different firing modes, ranging from adaptation to bursting, depending on the calcium level. Attention is assumed to influence the conductance of calcium channels, thereby causing burst activity in V2. The pathway along which the *bursting* signals propagate wins the competition, i.e. is in the focus of attention. The physiological mechanism behind the model is not discussed. The idea that the attentional signal groups several spikes into bursts has also been adapted by Bosch *et al.* /11/. There, the burst activity is used to synchronize the neurons.

One general problem of the temporal tagging hypothesis is that the mechanisms which tag the attended neurons are quite artificial in most of the proposed models and have also not finally been proven to exist.

3.2.2 Rate modulation

Most of the models not explicitly dealing with temporal tagging use another strategy to mark the neurons belonging to the focus of attention, i.e. the regulation of the mean firing rate of neurons. In

accordance with experimental evidence (see Section 2), the activity of neurons in the focus is enhanced while it is inhibited outside (e.g. /81, 107/).

4. MODELING LOW-LEVEL (PRE-)ATTENTION WITH THALAMO-CORTICAL CIRCUITS

In Section 2 we mentioned that the thalamus has been suggested as an important structure for the gating of attentional processing. This idea has been elaborated by different authors, not only on an abstract level /26,28,55,73,76/ but also suggesting biologically plausible implementations /9,32,61, 99,100/. Those models concentrate mainly on stimulus-driven (pre-)attention and its interaction with the thalamo-cortical circuit.

4.1 The hypothesis

Our own hypothesis is that attentive processing can be explained by different spatial and temporal firing patterns of low-level visual structures (LGN and V1) which will lead to a dynamic adaptation of the temporal and spatial resolution in order to differentiate attentive and non-attentive regions of the primary visual pathway. This idea is based on experimental findings showing that receptive fields in V1 change their size as a function of different EEG states /99,117/. They are wider during synchronized than during non-synchronized EEG (see Fig. 4A and B). It has also been shown that the receptive fields restructure from wide to small *during* the non-synchronized state when a stimulus is left on (Fig. 4C).

The different EEG states are classified by their frequency components. We distinguish between a globally synchronized EEG (δ -waves) and a locally synchronized or non-synchronized EEG (α/β -waves) (Fig. 5 top). The states correspond to different levels of alertness, e.g. δ -wave activity usually occurs during deep sleep or sleepiness, whereas higher frequencies are dominant during drowsiness or alert wakefulness.

We suggest that the two main EEG classes distinguished in the experiment can be further subdivided, especially for the less synchronized EEG states (Fig. 5). In that framework attention can be

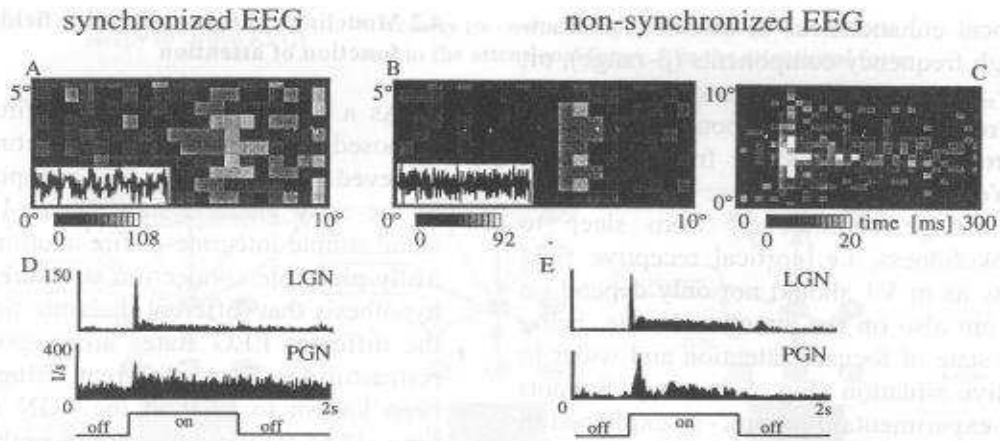


Fig. 4: Experimental data from an anesthetized cat showing spatio-temporal receptive field restructuring in the early visual system. Cortical receptive fields (V1) are wider during synchronized EEG (A) than during non-synchronized EEG (B). In addition they shrink over time (C). (Insets show the EEG traces. For details about the experimental setup see /99,117./) D and E show data from the thalamus, for which spatial characteristics are constant, whereas the temporal characteristics change. LGN cells are in a burst mode during the synchronized state and in a tonic firing mode in the non-synchronized state /41,68,93,95,117/. For PGN cells it is the other way round (see /44/).

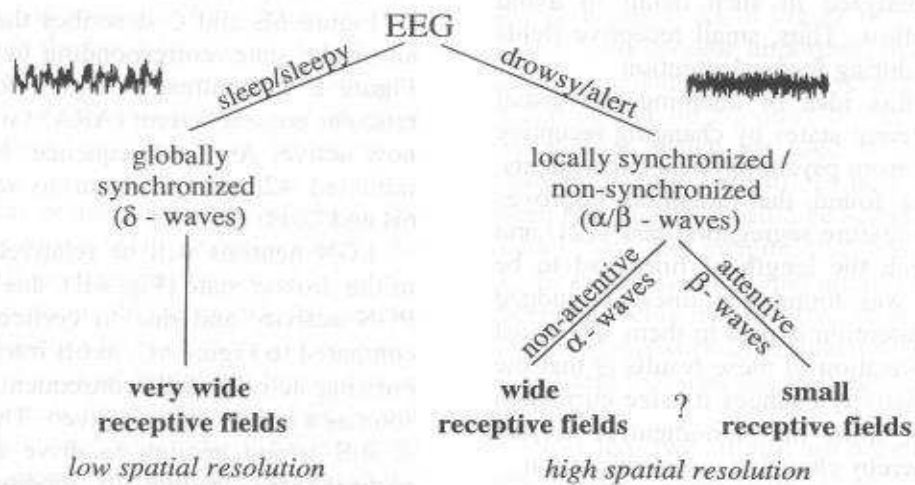


Fig. 5: Different EEG states - as characterized by waves in a certain frequency range (δ : 1-4 Hz, α : 8-13 Hz, and β : 14-30 Hz) - can be associated with different global states. Changing states are characterized by changing receptive field sizes and, thereby, by different spatial resolutions.

seen as a local enhancement of alertness characterized by high frequency components (β -range), or, alternatively, the non-attentive state as a more drowsy and relaxed mode (corresponding to a local EEG synchronization with lower frequencies, i.e. α -range). We furthermore propose that receptive field sizes change continuously from sleep to attentive wakefulness, i.e. cortical receptive field sizes as early as in V1 should not only depend on EEG states but also on the attentional state, being smaller in a state of focused attention and wider in a non-attentive situation (Fig. 5 bottom). Support comes from experimental findings - as explained in Section 2 - that receptive fields in V4 have been shown to shrink in size from the non-attentive to the attentive state /69/.

The question remains as to what would be the functional advantages of this kind of size change. Wide receptive fields only provide a low resolution picture of the environment, but they can integrate activity over a wide region, thus ensuring that any important stimulus is detected. Thus, wide receptive fields are suited to a non-attentive state. Furthermore, the information - that a relevant stimulus has occurred - has to be processed fast, since this kind of wake-up call should reach higher areas as quickly as possible. In contrast, small receptive fields provide a high resolution picture. But only the most salient regions of the visual scene can be analyzed in such detail to avoid information overflow. Thus, small receptive fields should dominate during focused attention.

Support for this idea of adapting the visual resolution to different states by changing receptive field sizes comes from psychophysical experiments, in which it was found that attention improves performance in a texture segregation task /121/ and in a task in which the length of lines had to be judged /105/. It was found that lines are judged longer when no attention is paid to them. The most reasonable interpretation of these results is that the point spread of activity changes its size correlated to the transition from the non-attentive to the attentive state, thereby changing visual resolution.

4.2 Modeling changing receptive field sizes as a function of attention

As a next step, we want to find out how the proposed receptive field restructuring could be achieved. With the help of a computational model of the early visual system (retina-LGN/PGN-V1), using simple integrate-&-fire neurons and a biologically plausible connection structure, we tested the hypothesis that different thalamic firing patterns in the different EEG states are responsible for this restructuring. These different firing patterns have been known to exist in the LGN for quite some time /41,68,93,95/, but were recently also found in the PGN (see Fig. 4 and /42,44/). The mechanism of the restructuring is illustrated in Figure 6. (For a detailed description of the model see /99/.) Figure 6A pictures the situation during a globally synchronized EEG, which is typical for sleepy states. Brainstem influence is low, therefore PGN neurons are highly active (see Fig. 4D, /44/), while LGN neurons are inhibited by PGN and brainstem activity /43/. LGN cells are, therefore, in a hyperpolarized state. If a stimulus is presented to the retina, they answer with a high-frequency burst response /52,57/. This strong signal is able to drive cortical cells also further away from the main projection column, resulting in a wide point spread function or - looking from top to bottom - in a wide cortical receptive field.

Figure 6B and C describes the network during an awake state, corresponding to the right part of Figure 5. In contrast to Figure 6A, the ascending reticular arousal system (ARAS) of the brainstem is now active. As a consequence, PGN neurons are inhibited /42/ and LGN neurons activated /39/ (Fig. 6B and C, cf. Fig. 4E).

LGN neurons will be relatively hyperpolarized in the drowsy state (Fig. 6B), due to the remaining PGN activity and due to cortico-fugal input. As compared to Figure 6C, in 6B intermediately strong bursting activity will, consequently, be elicited as soon as a retinal input is given. This activity profile is still strong enough to drive a relatively wide cortical area leading to medium-size receptive fields in V1.

The situation in Figure 6C - which corresponds to an alert state with focused attention - differs from B in that cortico-thalamic feedback becomes a

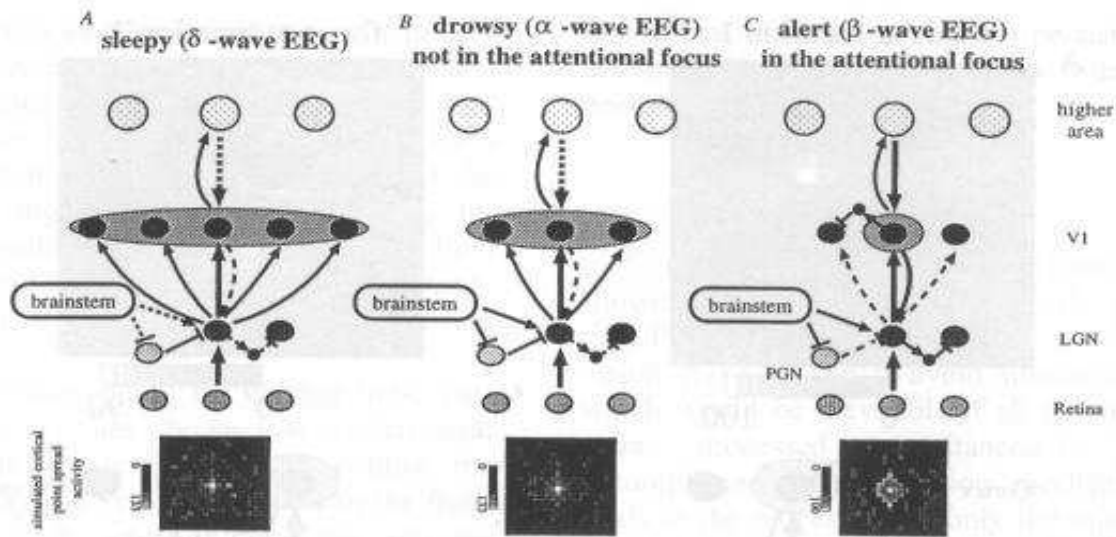


Fig. 6: Connection schema and model data of a generic and biologically plausible model of low-level preattentive processing (see Fig. 5). **A:** Situation during sleepiness, in which the brainstem influence is very low and consequently PGN activity is high, whereas LGN activity is low. In **B** and **C**, which correspond to an awake state, brainstem influence is highly active leading to a depolarized LGN state. In **C**, additionally, the cortico-fugal feedback is active. The lower part shows two-dimensional cortical point spread functions for a model simulation. The spike activity is grey-scale coded. Since orientation tuning was not included in the model, the activity fields are concentric. The point spread function - looking from top to bottom - of the receptive field shrinks continuously from left (sleepy state) to right (alert state).

dominant functional component. It is essential to keep the level of depolarization high at the central LGN cell to enable a switch to the tonic firing mode [30]. This tonic component is necessary to code specific information about the stimulus, e.g. contrast or color. But since this tonic firing activity is much lower than the burst activity in A and B, it cannot drive cortical cells lateral to the main projection column. As a consequence, the cortical point spread function (and, thus, also the receptive field) is narrow.

In summary, the brainstem and its effects on the thalamo-cortical pathway play a special role in the realization of different global states [83] in the context of our hypothesis. In the model, the general shift between different levels of alertness is mediated by different levels of brainstem activity and, consequently, different firing activities of PGN and LGN cells. The RNT (of which the PGN is a part) has already been shown to play a special role in the control of different sleep states [5,34,92,113] and, together with the cortex, it contributes to a widespread synchronization of low frequency oscillations [25,96].

4.3 Modeling bottom-up induced shifts of attention

In the next step, we want to extend our model to also allow for shifts *between* different locations of interest and not only between non-attentive and attentive states. As in Figure 6C, the cortico-fugal connections become important, since a specific and localized enhancement and restructuring is needed which cannot be provided by the diffuse thalamic connections which we used to implement global changes. Figure 7 illustrates how such a shift between two locations could be accomplished with our model. One can imagine that just before situation A, the model was in a non-attentive state with wide receptive fields everywhere, as in Figure 6B. The simulated network is similar to the one in Figure 6C, except that now the shift between two stimuli is analyzed.

Now that two stimuli are presented, LGN neurons of both regions switch to tonic firing. Stimulus 1 has a slightly higher contrast than stimulus 2, i.e. it is more salient, which leads to a slightly higher firing of neurons at location 1. This small difference is potentiated by cortico-fugal feedback and

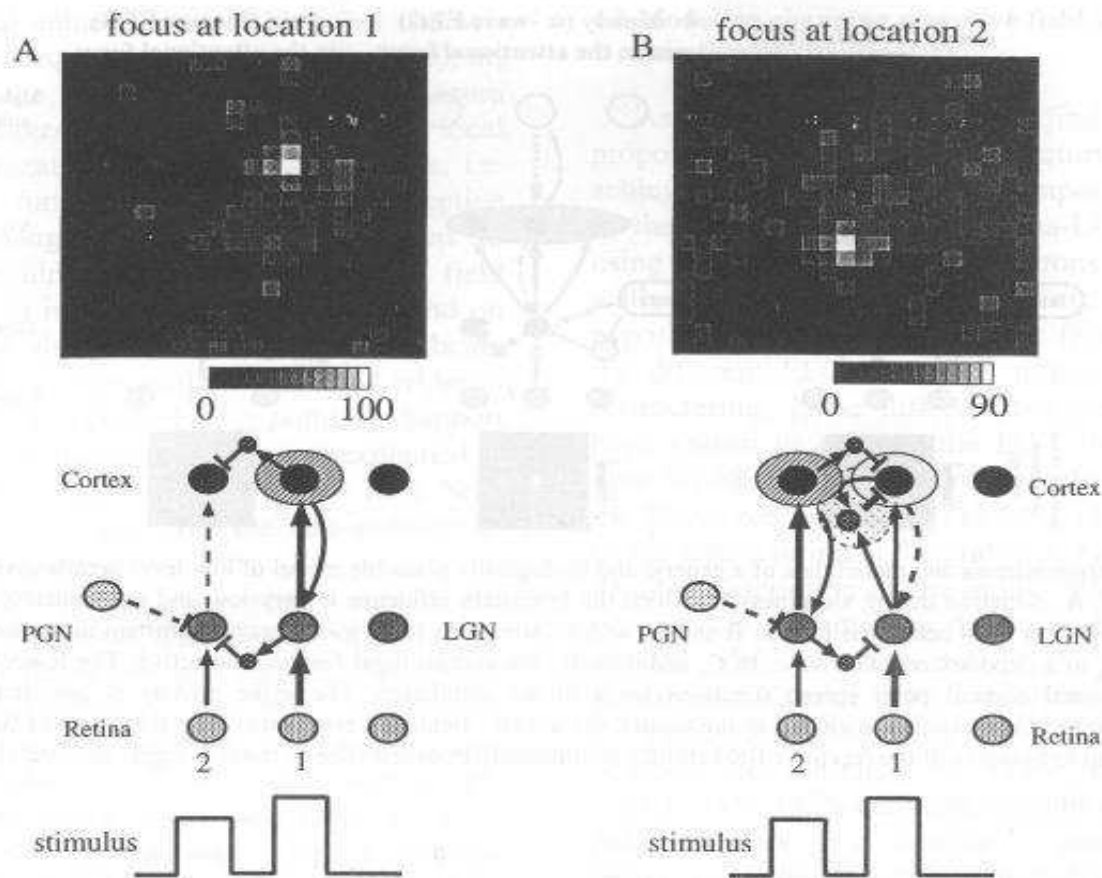


Fig. 7: Model simulation showing how the focus of attention shifts from one location to another. Two stimuli of almost similar contrast were presented. The shift between the two regions is mediated via cortico-fugal feedback and via delayed feedforward and intracortical inhibition. The plots show the firing activity in the cortical layer as a two-dimensional point spread function with grey-scale coded spike activity.

by lateral network effects, especially by the inhibitory connections inside the LGN and the cortical layers (WTA). Lateral connections are a necessary prerequisite for the implementation of a WTA mechanism, and the thalamus, supported by the cortex, is an ideal candidate for this /100/.

After a short time (approx. 50 ms) this data-driven restructuring leads to narrow cortical receptive fields at location 1, which are specific and which provide a high-resolution picture (Fig. 7A).

In order to work as an attentional scanning mechanism, the focus of attention must shift to analyze a second location. To achieve this, inhibition of the first selected region is necessary so that a new region has a chance to get into focus (see step 4 of the Koch and Ullman model explained in Section 3.1.1). Both LGN and cortical cells project excitatorily to interneurons, which in turn inhibit the cortical cells. This (recurrent) inhibition will

suppress the firing of those cells which initially fired strongly (Fig. 7B). It has been shown that the inhibition has its strongest influence after approximately 50 ms /8,36/, which is in accordance with the time scale of attentional shifts /38,91/. This (delayed) inhibition leads to a restructuring of the thalamic and cortical network with an increase of firing at location 2, i.e. this location is now in the focus of attention.

The question arises what happens if the two stimuli are equal in their saliency or if they are farther apart than the range of the inhibitory connections in the LGN and the cortex. In these cases a purely bottom-up (pre-)attentive mechanism is not able to account for a proper analysis of the input scene. Additional symmetry breaking is necessary. If it is not given by the initial conditions, a possible solution is that it is induced in a top-down manner. Still, totally equal stimuli are very

unlikely, and even small differences can be greatly amplified by cortical excitatory circuits, as has been shown by Douglas *et al.* /36,98/. In our model, top-down influences can be easily implemented by a pre-depolarization of a certain region in V1 by feedback from higher cortical areas (see Fig. 6). This region would then be processed first. In a similar way, top-down feedback can voluntarily direct attention to a weaker input or to a certain region.

In a model study based on varying ionic currents, Carvalho /31/ has shown that cortico-fugal activity can be efficiently used to control the thalamic gateway. He explicitly associates the feedback activity with attention marking relevant information. Still, local inhibitory circuits in the thalamus (RNT-dorsal thalamus) also play an important role for filtering the information.

Taken together, our simulations showed that the concept of changing receptive fields can be extended to implement shifts between different locations of interest. Until now, V1 and LGN have often been suggested to play a role mainly in the building of basic feature maps. But due to its specific connection structure with inhibitory circuits and recurrent connections to many different cortical and also subcortical regions, we in accordance with others /26,28,55,73,76,93/ suggest that effective attentional (pre-)processing and gating can be accomplished in the early visual pathway.

Different aspects of the thalamo-cortical circuitry and its relation to attention have already been examined by others. Especially due to its inhibitory connections and the fact that it receives input from very many different areas (including brainstem influences), the RNT has often been suggested to play a central role in the control of the information flow between the thalamus and the cortex /26,76/. In detailed model simulations of different pulvinar circuits, LaBerge *et al.* /61/ showed that lateral thalamic inhibition together with cortico-fugal feedback is able to effectively enhance small input differences and thus selectively process information from specific spatial locations, supporting our more generalized scheme. The possibility of bottom-up priming of certain information due to interactions between different thalamic and cortical neurons has also been tested by Bickle *et al.* /9/. They showed

that areas of stronger inputs persist while the activity of neurons activated by weaker stimuli declines.

5. DISCUSSION

Computational models and experiments have shown that attention is an essential operation not only for animals and humans but also for machine vision. It is necessary to avoid information overload which would be inevitable if all incoming stimuli were processed simultaneously. This is accomplished by a selection mechanism, which leads to the processing of only the most salient or relevant stimulus at any time. The relevance - or saliency - can depend on either bottom-up or top-down factors, i.e. it may be involuntary and data-driven, conscious and top-down induced, or a combination of both. From an information processing point of view, this means that symmetry breaking between different regions of the visual input has to be enhanced in a way that only one region wins and that only this region will be processed in detail. The determination of the saliency - and especially the physiological processes underlying this - is still one of the major unsolved problems in studying attention.

If a strong symmetry breaking is already contained in the input, e.g. in the form of a pop-out stimulus, attentive scanning can be carried out without any high-level processing, i.e. pre-attentive processing is sufficient and dominant. Bottom-up mechanisms are extremely fast and efficient. Both qualities are necessary to enable the system to react adequately to non-ambiguous and demanding situations. Consequently, pre-attentive, bottom-up mechanisms play an important role in the visual system.

Immediately the questions arise of which areas carry out this processing and which functional mechanisms underlie it. We suggest, conforming with other authors /26,28,55,73,76/, that the thalamo-cortical circuit mediates attentional pre-processing and that, therefore, low-level components are sufficient to implement these bottom-up mechanisms. The advantages of low-level implementation are speed and simplicity, which are necessary for stimulus-driven situations. Indeed, visual

processing can be very fast, as has been shown experimentally by Thorpe *et al.* /101/ showing that it is even possible to react to higher cognitive cues within 200 ms (for a model study based on the experimental findings see /110/).

The thalamus is ideally suited for implementing low-level information flow control, not only because of its connection structures but also by its ability to fire with different modes (burst vs. tonic). These modes can be additionally influenced by brainstem inputs which converge at the different thalamic nuclei. Furthermore, the thalamus is the first stage where lateral inhibition is efficiently able to implement a WTA mechanism. In addition to this, there are many cortico-fugal feedback connections, which can not only provide top-down influences but which could also be important to implement shifts between different attentional locations.

As a mechanism, we suggest that thalamic and cortical spatio-temporal receptive field properties change to control the information flow and that these properties are, therefore, an expression of different attentional states. This hypothesis is based on experimental data which show that thalamic neurons change their temporal firing pattern and that cortical receptive fields change their size as a function of changing EEG states which - in a non-anesthetized animal - correspond to changing levels of alertness (Fig. 4). Extending the experimental observations, we suggest that attention can be regarded as a locally enhanced level of alertness around the focus of interest (Fig. 5). Therefore, cortical receptive fields should also change their size in an attention-dependent way. The mechanism which changes the receptive field size, functions as an adjustment of spatial resolution to the demands of the situation and the task. Resolution should be fine in interesting parts of the visual scene and coarser everywhere else, thereby computational resources can be used efficiently (for a discussion of spatial resolution and attention see also /79/). With the help of a computational model we showed how receptive field changes can be implemented physiologically and how they could work as a data-driven pre-attentive process (Figs. 6, 7).

Reviewing the existing literature of computational models we have differentiated between

routing and tagging models. The former - to which our model belongs - provide mechanisms to select and route information of a specific region through the processing network, while the latter propose solutions to the question of how the information from one region differs in its firing pattern from other regions. Most existent models focus on one of these two questions. However, both problems are of equal importance and have to be solved simultaneously. One hypothesis is that first the most salient region is selected in the low-level structures of the dorsal stream - mainly, but not exclusively determined by a bottom-up mechanism - and that the contents of this spatial region are then routed to the ventral stream, where object recognition takes place and where objects in the focus of attention might be tagged /79/.

Apart from the interplay between the different classes of model, there is also no final answer to the question of which level of description should be chosen (for an extremely interesting discussion of computational models in the context of search experiments and attention see /72/). Phenomenological and mechanistic models coexist and both have provided important insights into understanding attentional processing. However, due to the lack of experimental results, it cannot be decided which model approach is most adequate or which best describes the experimental data. Part of the problem is that the mapping between psychophysical and physiological findings has still not been solved in a satisfactory way. The physiological substrate and even the level on which attentive processing takes place is still controversial. Nevertheless, computational models have provided fruitful insights into how attentional processing can work and how attention could be implemented in the brain.

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