ESANN'1995 proceedings - European Symposium on Artificial Neural Networks
Brussels (Belgium), 19-20-21 April 1995, D-Facto public., ISBN 2-9600049-3-0, pp. 205-210

LATENCY-REDUCTION IN ANTAGONISTIC VISUAL CHANNELS AS THE RESULT OF CORTICOFUGAL FEEDBACK

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Abstract

In this study we present a biologically realistic simulation of a part of the primary visual pathway including retina, lateral geniculate nucleus (LGN) and visual cortex (V1). Cells are simulated as improved integrate and fire neurons additionally including voltage gated (NMDA) mechanisms. Both, the ON- and the OFF- visual channels are implemented. We propose a novel type of excitatory feedback connection from the cortex back to the LGN. With this feedback the otherwise separated ON- and OFF-channels are directly connected by weak synaptic weights, which induce only subthreshold effects. For an alternating contrast stimulus only one of the channels (ON- or OFF-) is active at any one point in time and the feedback from this onto the other channel induces a subthreshold depolarization. As soon as a contrast reversal occurs this subthreshold depolarization leads to a reduction in the latency of the response in the now active opposite channel. This reduction can reach up to 10% of the total latency in the cortex and is strongest during the combined activation of voltage gated (NMDA) and voltage independent (AMPA) mechanisms.

1 Introduction

Observing normal visual scenes, bright and dark stimuli are changing often and in a quick sequence. Especially head- and eye movements lead to periods of time between two contrast changes of only a few hundred milliseconds. Given an intermediate background illumination and a stimulus with a strong contrast, then the probability of a contrast change in the opposite direction is higher then the probability for a change in the same direction. For example, the probability that a dark stimulus follows a bright stimulus is higher then the probability of a further increase in luminance. It would have advantages for a visual system, to use this situation to speed up reaction times. In the following sections we try to achieve a reduction of the reaction time to visual stimuli in a biological realistic simulation of a part of the visual pathway, using a novel type of corticofugal feedback connections, which utilizes active conductances, introduced by N-Methyl-D-Aspertate(NMDA)-channels.

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2 Simulator

First, we briefly present the biological realistic simulator, for a more detailed explanation we refer to [1]. The neuron-model of the simulator is an improved integrate-and-fire neuron, described by the following differential equation for the membrane potential:

$$C_i \frac{dV_i}{dt} = \sum_{j=1}^{k} g_{i,j,exc}(t)(E_{exc} - V_i) + \sum_{j=1}^{l} g_{i,j,inh}(t)(E_{inh} - V_i) + g_{leak}(E_{leak} - V_i) + g_{i,AHP}(t)(E_{AHP} - V_i) \quad (1)$$

C_i	membrane capacity of cell i
V_i	membrane potential of cell i
$g_{i,j,exc(inh)}$	conductance of an excitatory(inhibitory) channel from presynaptic cell j to postsynaptic cell i at time t
g_{leak}	leakage-conductance
$g_{i,AHP}$	conductance of the after-hyperpolarisation
$E_{exc(inh)}$	excitatory (inhibitory) reversal potential
E_{leak}	resting potential
E_{AHP}	reversal potential of the after-hyperpolarisation

The solution of this differential equation is calculated during the simulation using a (4th order) Runge-Kutta method. The time-course of the conductance of a not voltage-dependent AMPA[1]-channel is that of a simple alpha-function:

$$g_{AMPA} = \hat{g}_A \frac{e}{\tau} t e^{-\frac{t}{\tau}} \quad (2)$$

$\hat{g}_A$	peak-conductance of AMPA-channel
τ	time-constant of AMPA-channel (1 ms)

The time course used to simulate NMDA-Channels is described in equation (3)

$$g_{NMDA} = \hat{g}_N \frac{e^{-\frac{t}{\tau_1}} - e^{-\frac{t}{\tau_2}}}{1 + \eta[Mg^{2+}]e^{-(\gamma V_m)}} \quad (3)$$

$\hat{g}_N$	peak-conductance of NMDA-channel
τ_1, τ_2	first and second time-constant of AMPA-channel (80 ms, 0.66 ms)
$[Mg^{2+}]$	magnesium-concentration
γ	0.06/mV
V_m	membrane potential

All simulations are done with a time step of 0.1 ms and a fire threshold of -40mV.

The simulator exists in two versions, a massive parallel version with 16000 Neurons, running on a supercomputer (Connection Machine CM2), and a seriel version of a few hundred neurons running on a workstation. Both versions were used for these simulations.

[1] AMPA=Alpha-amino-3-hydroxy-5-methyl-4-isoxazole proprionic acid

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3 Visual pathways

The visual system is divided into ON- and OFF-channels, encoding positive or negative contrast changes, respectively. The ON-channel is active during stimulation with a bright stimulus, while the OFF-channel is silent, partly due to inhibition in LGN and cortex. The OFF-channel is active during a dark stimulus. The simultaneous activity of between 10 and 100 LGN-cells is necessary to drive a cortical neuron (see fig.1). Cortical cells usually consist of several ON and OFF subfields. For our purpose it is sufficient to simulate only two cortex cells and only one subfield per cell. The subfield of the one cortical neuron is driven by a group of ON-LGN-cells and that of the other cortical neuron by a group of OFF-LGN-cells. Both, the cortical and the LGN-cells mutual inhibit each other. The novel type of corticofugal feedback, we suggest, connects the ON-

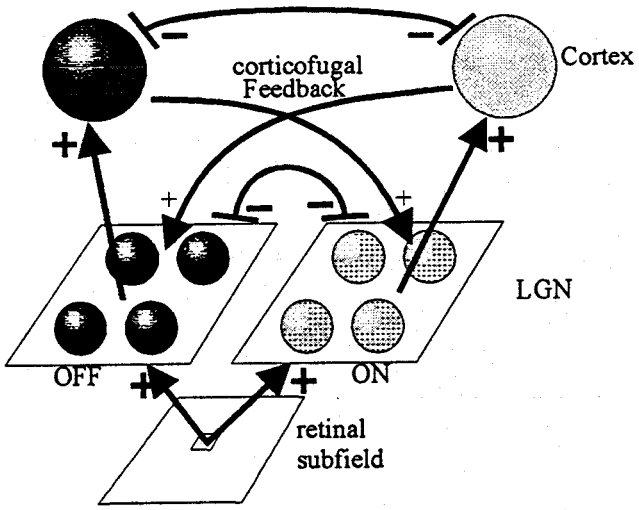

Figure 1: Wiring Diagram

and the OFF-pathways with a weak excitatory link. Because of the small weights of the feedback connections, the effect is a small subthreshold depolarisation in the silent channel. The feedback connections are implemented in four types to demonstrate the influence of different channel properties: No-feedback, AMPA-feedback, NMDA-feedback and combined AMPA/NMDA-feedback

4 Simulation with alternating contrast

For the simulation of input activity we used a poisson-distributed spike-train. Thus, the contrast information is only encoded in the firing rate and not in the

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temporal structure of the spiking pattern. Figure 2a shows the input contrast alternating between +100% and -100%. The PSTH of a LGN-ON-cell (Fig. 2b) shows that the activity of this cell is high between 500 ms and 1000 ms. When the LGN-ON-cell is silent (between 0 ms and 500 ms) the LGN-OFF-cell is active (not shown). Figure 2c,d present the interval histogram of an LGN- and a cortex-cell. They are poisson-distributed in both cases, with a peak at about 8 ms for the LGN-cell and about 20 ms for the cortex-cell. This is similar to experimental findings. The main result is shown in Figure 2e. It illustrates

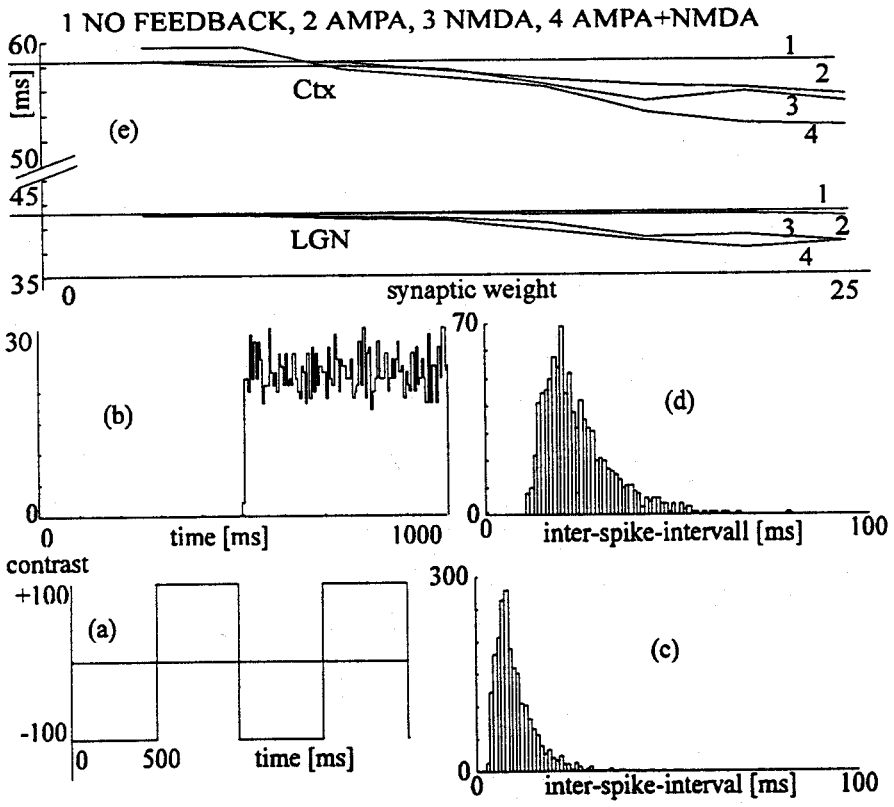

Figure 2: Alternating contrast

the latencies between the start of the stimulation and the first spike of the cell response. The lower part of the diagram shows the response of the LGN-cells. The latency without any feedback is about 41.4 ms. This is plotted as a straight

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line. The other results are plotted against the synaptic weight of the feedback-connections. Increasing the synaptic weights leads to a reduction of the latencies. The membrane potentials of the LGN-cells are more depolarised because of the incoming spikes from the opposite cortex cell and this reduces the distance from the threshold leading to a shorter reaction time. The reduction reaches up to 2.7 ms for AMPA- or combined AMPA/NMDA-channels. The pure NMDA-channel has little effect of up to 0.6 ms reduction. The reason for this is the voltage dependency of NMDA-channels in the LGN-cells and its blocking reaction due to hyperpolarisation caused by mutual inhibition between the LGN-cells. The upper part of the diagram shows the latencies of cortex cells. Without feedback it amounts to about 58.5 ms. It can be reduced with strong synaptic weights and a combined AMPA/NMDA-channel by up to 5.5 ms, equaling 10% reduction of the total latency from the retina to the cortex.

5 Alternating contrast with pauses

To more clearly show the effect of the NMDA-channels on the membrane potential another stimulus type with pauses between the ON- and the OFF-phases was used (Fig. 3a). The whole stimulus has now a total length of 1100 ms. After 500 ms with a contrast of 100% the background-contrast is presented for 50 ms. Then the opposite contrast is presented for 500 ms, with a second pause of 50 ms following. The 50 ms background-phases cause that both, the ON- and the OFF-pathways are silent. Figure 3b shows the accompanying PSTHs of a LGN-ON and a LGN-OFF-cell. The responses of both cell types are shown in one diagram. The effect of this new type of stimulus on the latencies is shown in Fig. 3c. Depending on the small time constant of AMPA-channels the pre-depolarization of the LGN cells is completely eliminated after 50 ms. On the other hand, the longer time constant of NMDA-channels leads to an elevated membrane potential at the end of the pause and to a latency-reduction up to 1.1 ms. This is demonstrated in figure 3d, showing the membrane potentials of an LGN-cell during the background-phase between 500 ms and 550 ms. The potential of an LGN-cell with AMPA-feedback is after 50 ms equally to the resting-potential at -71 mV, while the LGN-cell with NMDA-feedback, due to release of inhibition, still exceeds the resting-potential and repolarizes more slowly. Therefore, at the moment of the first incoming spike from the retina, the distance to the threshold is smaller than in the case of AMPA.

6 Conclusion

The simulations demonstrate the possibility of latency reduction in the visual pathway by means of corticofugal feedback. A comparison of both stimulation methods shows that a combination of AMPA- and NMDA-channels would have the strongest effect for the facilitation of fast contrast changings. It should be noted, that this antagonistic feedback mechanism induces a subthreshold-

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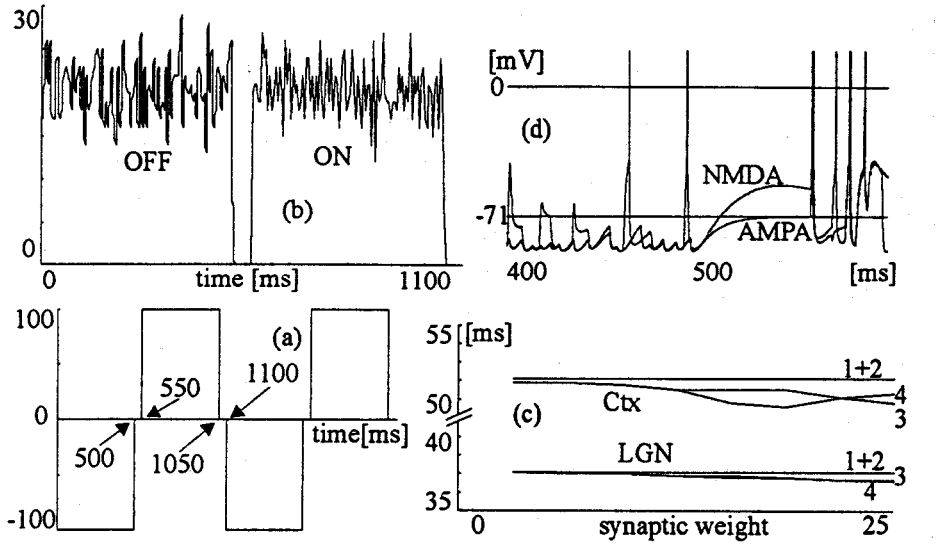

Figure 3: Interrupted contrast change

effect, which can only affect the transient phase of the response. It has no influence on the steady state responses and does not induce a reduction of the contrast enhancement observed in the LGN. In an experimental situation such a mechanism would be superimposed to the rebound responses elicited by the release from inhibition and intracellular recordings would be required to access such a possible antagonistic feedback experimentally.

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