Spike-latency codes and the effect of saccades

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Abstract

Input enters the visual system structured by saccades. The exact timing of spikes produced is believed to be interpreted in terms of latency or spike rank.

Spike-time based simulations often cover only a few spike waves. This disregards the continuous character of visual processing. We demonstrate that in an extended simulation, a spike latency code is lost after short time, and needs to be explicitly reestablished. We suggest and implement several biologically relevant strategies of how to do this. We conclude that relaxation of neurons is an effective way of setting temporal reference frames for spike-time processing.

Key words: spike-time, latency, spike rank, saccade, temporal reference frame

1 Introduction

Many models of visual processing start from the assumption, that an image or scene is analyzed as whole and that at the start of an analysis phase all neurons are essentially in the same state (e.g. [1,2]). However, at least in primates, this is not the case: here, the visual input is scanned during a series of fixations of 150 to 300 ms duration each, followed by a saccade to the next fixation point. Thus, after each saccade, the neurons are not in their resting state, but in a state which depends on the previous fixation point and whatever happened during the saccade. This dependence of the neural state on the previous fixation point is particularly devastating for models which rely on the precise timing of the initial spikes, like spike rank [1,3] or latency models [2]. Thus, these models need some form of *reset* in order to work properly after a saccade to a new fixation point.

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For the magno-cellular pathway, *saccadic suppression* has been demonstrated [4,5]. Also for the remaining pathways some form of saccadic mechanism may exist which brings the neurons into a well defined state. In this contribution we investigate a number of mechanisms which could account for a reset of the neuronal states during saccades.

2 Simulation and Methods

In the context of temporal spike codes, a reset mechanism must ensure that for a particular stimulus (a particular fixation point) the response is *independent of stimulus history* (i.e., the preceding points of fixation), as well as *reproducible*, meaning that spike times should be the same when fixating the same spot again. Only then can the network judge the current stimulus on the basis of spike times.

We investigate this criterion in a simple simulation of visual processing, exemplarily assuming saccades as points in time at which network function is reset. We focus on mechanisms, which could implement this reset, effectively creating a temporal reference signal for spike time processing.

Simulations are performed on a regular lattice of 100×100 fixed-threshold integrate-and-fire neurons with reset [6]. "Visual" stimulation is implemented via direct current injection into the neurons. Cells are thought of as being located in visual cortex, but results transfer to other areas. Any simulation of retina and LGN is skipped. Their properties are not in the focus of this examination, and are knowingly neglected for simplicity. Simulations were done using the *NEST Initiative* simulator [7], at a temporal resolution of 0.2 ms.

We select 100×100 pixel input patches from natural images, which we present to the lattice of neurons in a sequence, resembling those produced by natural saccades. The complete simulation contains 100 such presentations (*trials*). In each trial, the respective input patch is presented for 100 ms of simulated time, followed by a short period during which a *saccadic action* is performed on the network neurons (cf. fig. 1). Trials follow each other consecutively in a continuous simulation run.

We record the spike-times of all neurons in the network and compute the latency of the first spike *in each trial*. I.e., the time from the change of visual input until the immediate next spike a neuron fires – because this latency is expected to carry crucial information about the new input.

The input sequence was designed to contain one image patch that appears repeatedly, but with different predecessors (see fig. 1). We compute the mean and standard deviation of each neuron's first spike's latency, over all trials for this reappearing image patch. This way, we quantify the reproducibility of a possible latency code. For a complete simulation of a 100 trial sequence, the *saccadic action* is fixed. For brevity, we restrict ourself to the following sac-

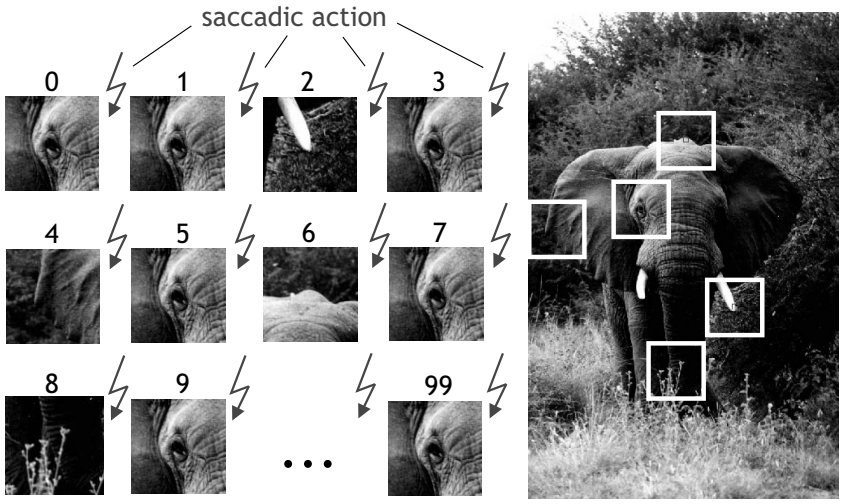

Figure 1. Stimulus sequence. Patches were derived from a set of natural images (example image shown on right). One patch appears repeatedly, with varying predecessors.

cadic actions: *no action*, *relaxation* and *suppression*. The full set of saccadic paradigms will be shown in the conference contribution.

No action. In this paradigm, no action is performed upon change of input. Image patches are presented one after the other, for 100 ms of simulated time each, without separation.

Relaxation. In this paradigm, each presentation period is followed by a 10 ms period of blank input, allowing the network neurons to relax towards their resting potentials.
In the visual system, input blanking for the time of the saccade could be caused by saccadic suppression of preceding network stages [4]. Saccadic effects very similar to input blanking could also be created by retinal "smear" of the visual stimulus, caused by the fast eye movement. The temporal variation of this input exceeds the temporal sensitivity of most cells, effectively shutting down spike transmission for the time of the saccade (cf. e.g. [8]).

Suppression. In this paradigm, each presentation period is followed by 10 ms of strong inhibitory bursts which are applied to the neurons. During this period, the visual stimulus is maintained.
This paradigm reflects the effect of saccadic suppression at the site of the processing neurons themselves. High-frequency inhibitory bursts with a great effect on the receiving neuron are fired by the perisomatic inhibitory cells (*basket* and *chandelier cells*) in cortex [9].

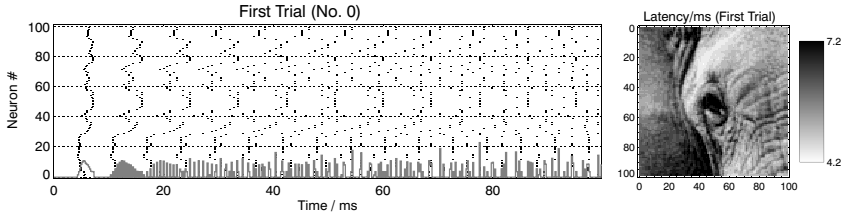

Figure 2. Spike trains of 100 selected neurons, for the first trial after simulation start. Bottom of panel: spike time histograms. Right panel: grey-coded first-spike latencies. Result is identical for all paradigms, as no saccadic action has been performed.

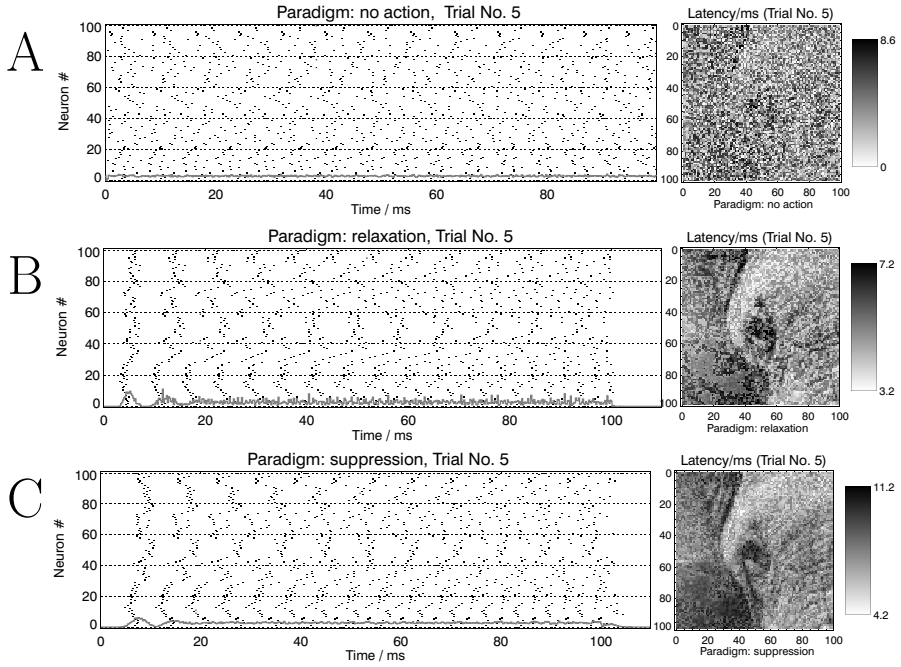

Figure 3. Same as fig. 2, but for trial no. 5. Results differ for the three paradigms: **A**: No saccadic action. **B**: Relaxation paradigm. **C**: Suppression paradigm. Note the different value ranges in the greylevel plots.

3 Results and Discussion

Figure 2 shows the spike trains of 100 selected neurons, for the first trial. Since no saccadic action has been performed yet, the response is identical for all paradigms. Since initially all neurons are in the same state, the first spikes form a distinct spike wave with individual latencies coding the stimulation strength. The grey-coded panel on the right demonstrates the good quality of the latency code: The stimulus can be reconstructed with high fidelity from the wave of first spikes which arrive during the first 10 ms. However, as time proceeds, the states of the neurons get increasingly different, and the spike waves dissolve.

Figure 3 shows the results for trial number five (cf. fig. 1). In this trial, the neurons are initially not in the same state. Their state is determined by the

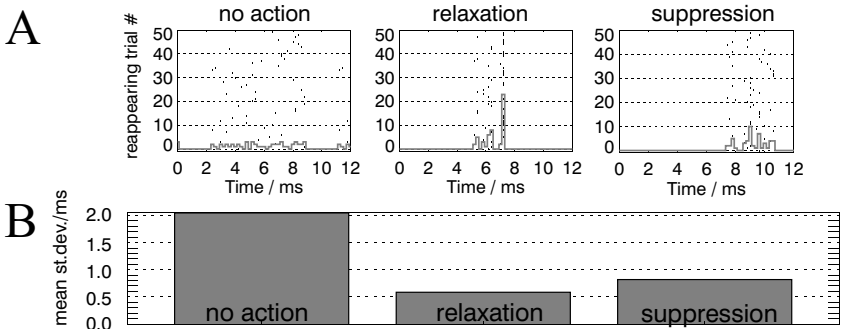

Figure 4. **A**: Distribution of the first response spike of one selected neuron over all trials containing the reappearing image patch. **B**: Standard deviations of first response spike distribution (A), averaged over all neurons.

stimulus history and the saccadic action. Panels A to C show the results for the different saccadic actions.
From fig. 3A, the *no action* paradigm, it is obvious that the spike latency code that was present in the first trial (fig. 2) has disappeared after five presentations. The temporal structure is regained when the saccadic actions are performed (panels B and C).

To further quantify the reproducibility of the latency code, we collected the first spike times from all trials that contained the reappearing image patch. A good latency code should depend only on the current stimulus and not on the stimulus history. Thus, spike latency should not vary across trials.
Figure 4A shows the first response spike of one selected neuron over all trials containing the reappearing image patch for the different saccadic paradigms. If no saccadic action is performed, the spike distribution is flat, resulting in a wide standard deviation of the response spike latency (left panel). For the *relaxation* and *suppression* paradigm, distributions are sharper, as the respective action has "reset" the neuron to a state which depends less on stimulus history (middle and right panel).
Figures 3 and 4 demonstrate the effect of the saccadic actions taken upon stimulus change: Both, the *relaxation* as well as the *inhibition* paradigm succeed partially at re-establishing the timeframe for latency coding that had been lost over time.
This is reached in very short time: 10 ms of relaxation or suppression is enough to reduce the standard deviation in spike timing considerably below the typical inter spike interval, separating the spikes into distinct waves (fig. 3). The relative latencies can easily be decoded by a next stage of neurons, e.g. using a mechanism of feedforward inhibition [3]. The temporal structure imposed on the firing sequence is also a good foundation for the spike-time based integration of feedback signals from higher processing areas [2].

Figure 4B shows the standard deviations of the first response spike distributions (panel A), averaged over all neurons. Most surprising is the fact that

10 ms of relaxation is an even more effective temporal reference than a strong inhibitory burst. For processing in the visual system this means that saccadic input blanking is an effective way of maintaining a proper latency code. The effect could either be produced by the fast saccadic input changes, exceeding the temporal characteristics of retinal neurons. It could also be produced by explicitly shutting down transmission to the cortex, e.g. at the LGN.

We conclude that (1) spike latency codes require some reset of the processing neurons performed upon stimulus change, i.e., at saccades. (2) Both relaxation and suppression can serve as appropriate reset signals. (3) Relaxation of neurons creates an even more effective temporal reference than suppression. This corresponds to a short period of input blanking during the saccade.
We expect these findings to be instructive for our further developing a model of cortical processing in a latency-code framework.

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