



# Learning direction selectivity through spike-timing dependent modification of neurotransmitter release probability

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## Abstract

It has recently been proposed that the direction selectivity of simple cells emerges from an interplay of depressing and non-depressing synapses projecting in an asymmetric arrangement onto these cells. We show that such an asymmetric arrangement may develop from a temporally asymmetric spike-based learning rule. The rule redistributes the probability of vesicle discharge, producing synapses with high discharge probability and strong depression in one-half of the receptive field and low discharge probability and weak depression in the other. This spatial shift together with the temporal phase advance of the depressing synapses adds up with the response of the surrounding non-depressing synapses only when the stimulus moves in the preferred direction. © 2001 Elsevier Science B.V. All rights reserved.

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## 1. Introduction

Different models have been proposed to explain the direction selectivity (DS) of simple cells in V1 by specific receptive field properties, see [6,7], but it is still an open question how these receptive fields may develop, see [11]. As has recently been proposed, the DS of simple cells in V1 could be explained by the different dynamic behavior of depressing and non-depressing synapses [1]. The basic idea is that the response of a depressing synapse onto a sinusoidally modulated stimulus is phase

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advanced because during the peak of the stimulus the synaptic response is already depressed. If this phase advance matches the spatial shift of depressing against non-depressing synapses the synaptic response integrates for a stimulus in one direction but not in the other. Here we suggest how such an asymmetric synaptic arrangement may evolve activity-dependently by means of a temporally asymmetric synaptic modification rule [2,4].

## 2. Methods

We modeled our V1 cell by a single compartment integrate-and-fire neuron. The input onto this neuron was simulated by Poisson spike trains projecting from a large number of LGN afferents (4800). The instantaneous firing rates of these Poisson spike trains were modulated by a spatial linear filter and a subsequent half-rectification [3]. This mimics the processing of the LGN in response to a retinal stimulation with a drifting sinusoidal grating. The spatial arrangement of the synaptic projections onto the model V1 cell consists of a group of depressing synapses (1600) in the center of the receptive field (RF), flanked by two groups of non-depressing synapses (each of 1600 synapses, see Fig. 1).

To implement synaptic depression we used a stochastic version of the vesicle depletion model presented in [9,10]. In response to a presynaptic action potential a vesicle which at that time is recovered may discharge its neurotransmitter with probability  $P_{\text{dis}}$ . Immediately after discharge, the releasable pool is empty and the vesicle stochastically recovers with a slow time constant in the range of half a second.

To account for the temporally asymmetric synaptic modification we changed  $P_{\text{dis}}$  of the depressing synapses using a cross-gating of NMDA receptors [8,9]. Each vesicle

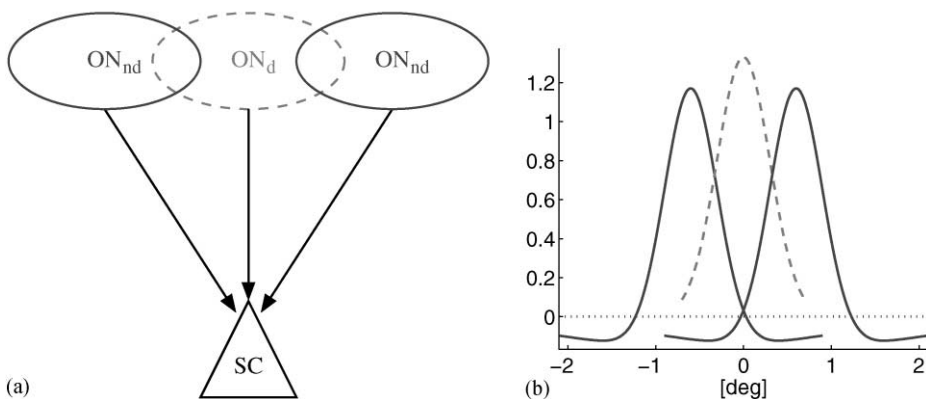


Fig. 1. (a) RF arrangement of non-depressing (full line) and depressing synapses (dashed line) projecting onto a simple cell in V1. (b) The synaptic weights of the depressing and non-depressing afferents which are kept fixed during the whole simulation. Depressing synapses receive input from the center of the RF (dashed line) while non-depressing synapses receive the input from the surround (full line, abscissa: angle within the RF on the retina).

discharge moves the NMDA receptors from a recovered state ( $N_{\text{rec}}$ ) into a state bound by glutamate ( $N_{\text{up}}$ ) while through a back-propagated postsynaptic action potential the recovered receptors are moved into a state  $N_{\text{down}}$  altered by postsynaptic calcium influx. From both of these states the NMDA receptors recover with a time constant in the range of hundred milliseconds. At each postsynaptic spike,  $P_{\text{dis}}$  is up-regulated proportionally to  $N_{\text{up}}$ , while at each presynaptic release,  $P_{\text{dis}}$  is down-regulated proportionally to  $N_{\text{down}}$ . For non-depressing synapses the vesicle immediately recovers after a release.

The training protocol consisted of a repeated retinal stimulation of 1 s per run. In every run, a sinusoidal grating moved over the receptive field with a spatial frequency of 1 cycle/deg and a temporal frequency of 4 cycles/s. The direction of motion was either kept fixed for all 104 runs, or chosen randomly and maintained for two consecutive runs. In the last four runs the direction was fixed to two runs in one direction and two runs in the opposite direction to test the resulting DS of the cell.

### 3. Results

During the repetitive stimulations with gratings moving in one direction the distribution of  $P_{\text{dis}}$  for the depressing synapses slowly shifts towards the stimulus (see Fig. 2). This is because the temporal relations between the synaptic releases and the postsynaptic spikes are different for the left and right half of the RF center: at the time when the peak stimulation is in the center of the receptive field and the postsynaptic activity is highest, the left half of the synapses have already been largely activated while the right part of the synapses is just going to be activated. According to the synaptic modification mechanism  $P_{\text{dis}}$  is up-regulated in the left half and down-regulated in the right half.

When testing the DS with a grating moving in the preferred direction the spatial shift in the  $P_{\text{dis}}$  distribution together with the temporal phase advance of the depressing synapses adds up such that they temporally integrate with the response of the non-depressing synapses in the left half of the surround. When stimulating in the non-preferred direction, however, the response of the depressing synapses falls into the trough of the non-depressing response at the RF center and no integration takes place.

The selectivity of the model simple cell for the learned direction is confined to a bandwidth of modulation frequencies between 1 and 16 Hz (see Fig. 4B) and depends on the number of runs the stimulus is presented. When presented only with a few drifting gratings, the simple cell cannot acquire full DS and responses to different temporal frequencies are high (see Fig. 3B). After a long learning session the distribution of  $P_{\text{dis}}$  can fully adapt to the stimulus presented and strong DS emerges. The response profiles of the model simple cell for the preferred direction and the non-preferred direction before and after learning closely resemble those experimentally measured in V1 cells of the cat (see Figs. 3A and 4A, reproduced from [7]). The overall drop in the response frequency during the experiment helps to stabilize the acquisition of DS.

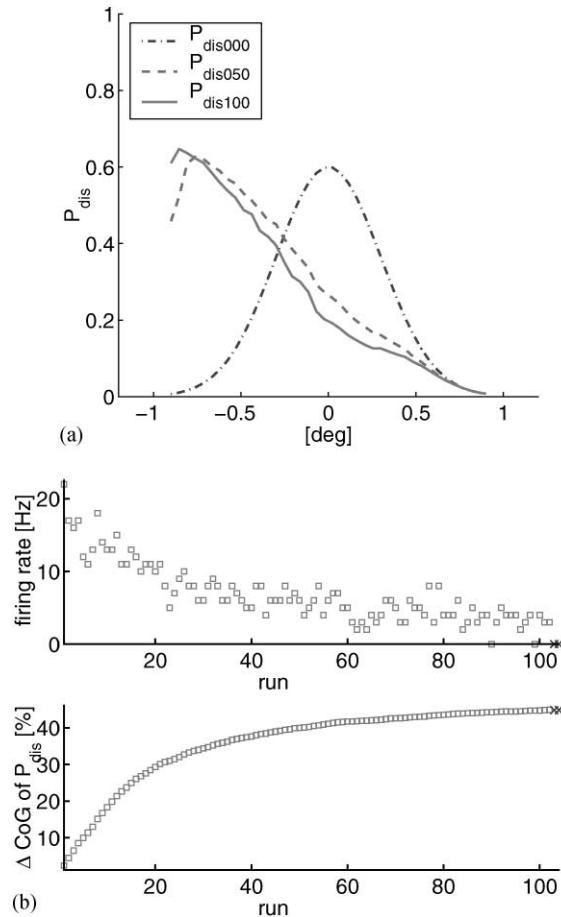


Fig. 2. (a) Spatial shift of the  $P_{dis}$  distribution during stimulation with a drifting grating moving in a fixed direction at the beginning, after 50 and after 100 presentations of the stimulus. (b) Firing rate of the model simple cell (top) and center of gravity (CoG) of the  $P_{dis}$  distribution (bottom) during the 104 runs (run 1–102 □: stimulus from left to right, run 103,104 ×: stimulus from right to left).

In trying to use a more realistic simulation protocol, we ran the same experiment as in Fig. 2, but now randomly chose the stimulus direction. The model simple cell again becomes direction selective, but the preferred direction is not fixed and can easily be reversed if enough stimuli moving in the other direction are chosen by chance (see Fig. 5B). If during the experiment the learning threshold (which is also observed in the experimental data, see [4,9]) is increased, the acquired DS would be stabilized.

#### 4. Conclusions

It is unclear whether a synaptic learning rule relying on the precise timing of individual spikes can meaningfully extract information hidden in Poisson spike trains

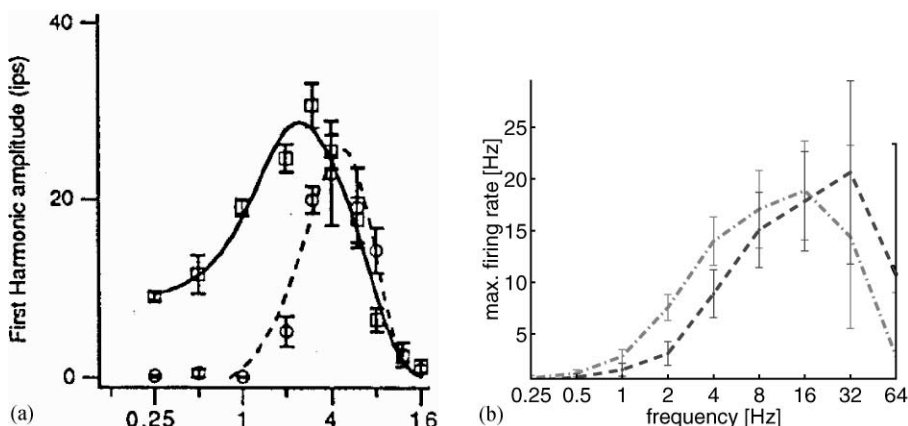


Fig. 3. Weakly directional simple cells after few learning cycles. (a) Temporal frequency tuning curves of DS, reproduced from [7] for stimuli moving in the preferred (full line) and non-preferred direction (dashed line). (b) Snapshot of the temporal frequency tuning curve of the model simple cell during the stimulation protocol, taken after 20 learning cycles, near the beginning of the stimulation protocol (full line: training direction, dashed line: opposite direction). Only weak DS emerges in the model simple cell.

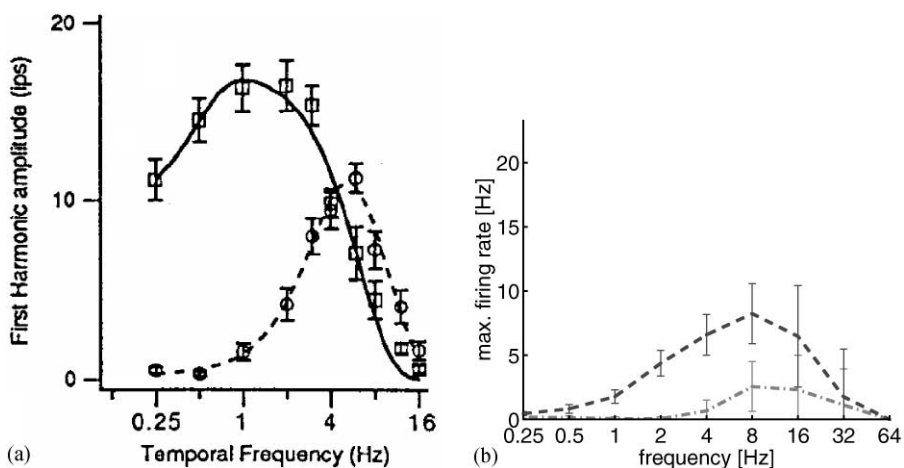


Fig. 4. Strong directional simple cell after learning. (a) The temporal frequency tuning curve is from the same cell as in Fig. 3A, but obtained 3 h later. Before the repetitive application of the stimulation protocol the cell was less direction selective. (b) Temporal frequency tuning curve of the model simple cell taken at the end of the stimulation protocol, after 100 learning cycles (see Fig. 2). Now the cell is strongly direction selective but has an overall smaller response (cf. Fig. 3B).

with a spike time variability exceeding the precision of the synaptic rule. The present example of learning DS for slowly drifting gratings shows that this is in fact possible. Although the width of the synaptic learning window is itself in the range of 50 ms it is possible to extract information about the modulation frequency of the grating and

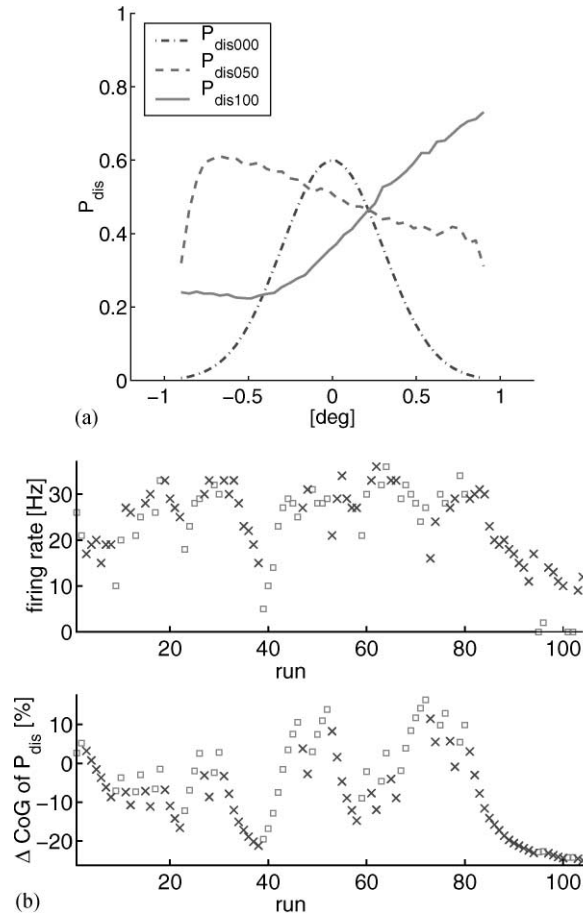


Fig. 5. Stimulation with randomly chosen and equally distributed stimulus direction. (a) Distribution of  $P_{dis}$  in the initial state (dashed–dotted), after 50 runs (dashed) and after 100 runs (full line). Without learning threshold, the skewness of the  $P_{dis}$  distribution may switch the polarity depending on the stimulus sequence. (b) During the course of the experiment the selectivity for one or the other direction is acquired (bottom trace). The CoG of the  $P_{dis}$  distribution slowly changes the side if multiple stimuli from the transiently un-preferred direction are presented ( $\square$ : stimulus from left to right,  $\times$ : stimulus from right to left).

thus to extract correlations in the stimulus which are of orders of magnitudes slower. The model faithfully reproduces the temporal frequency tuning curves of directional simple cells (we neglected the temporal LGN filtering and therefore obtained responses at frequencies above 16 Hz). The reversibility of the acquired DS indicates that either synaptic plasticity is lost, or that the experimentally observed threshold [4,9] is functionally relevant. The suggested mechanism for the activity dependent emergence of DS in V1 cells may play a role in an early stage of the neonatal development when the retina is invaded by spontaneously emerging waves of activity [5].

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