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# Simulating place field dynamics using spike timing-dependent plasticity

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#### Abstract

Spatial firing fields (place fields) of rat hippocampal cells undergo changes when the rat runs stereotyped routes. Previously, Mehta et al. [Experience-dependent asymmetric shape of hippocampal receptive fields, Neuron 25 (2000) 700–715] indicated that spike timingdependent plasticity (STDP) might explain the observed shift of the place field center of mass and the development of skewness. In this study, by using simulations of spiking neurons with STDP, we demonstrate that STDP may cause a shift and negative skewness in the synaptic weights vector; however, we explain why these changes do not necessarily result in negative skewness of place fields. We further explore the parameters and additional mechanisms that favor the development of skewness.  $\odot$  2006 Elsevier B.V. All rights reserved.

Keywords: Place cell; Hippocampus model; Backward shift; Skewness; STDP

# 1. Introduction

Firing rates of cells in the rat hippocampus correlate with the location of the animal [\[14\];](#page--1-0) such cells are called place cells, and their response regions are called place fields ([Fig. 1A\)](#page-1-0). Place fields are not static. They can become asymmetric (skewed) and their center of mass (COM) shifts backwards with experience when the rat runs stereotyped routes [\[4,6,11,12\].](#page--1-0) These experience-dependent changes could be involved in encoding sequences of locations in learned routes and might be important for navigation and sequence prediction [\[2,7,9\]](#page--1-0).

Mehta et al. [\[12\]](#page--1-0) presented a feed-forward, rate-based model that simulated the backward COM shift and the development of negative skewness observed in CA1 place fields. The learning rule used by Mehta et al. [\[12\]](#page--1-0) was a rate-based rule motivated by STDP [\[1,8,10\].](#page--1-0) Although Lee et al. [\[6\]](#page--1-0) replicated the backward shift of the place field COM in both CA1 and CA3, the development of robust negative skewness was seen only in CA3, not in CA1. To understand this discrepancy, the present study explored conditions under which place fields become negatively skewed. Additionally, we wished to determine whether the STDP mechanisms employed by Mehta et al. [\[12\]](#page--1-0) in a rate-based model would produce stable place fields in stochastic simulations with a spiking neuron model and whether such a stochastic model could explain the heterogeneous COM shifts exhibited by different individual place cells.

### 2. Methods

### 2.1. Model scheme

A feed-forward model was constructed with 1000 input cells (the input layer) and one output cell receiving weighted inputs from the input layer [\(Fig. 1B\)](#page-1-0). All of the input cells had identical, non-plastic, Gaussian place fields and the centers of these place fields were evenly distributed along a circular track with a circumference of 2 m. Unless otherwise indicated, the width (full-width at half-maximum) of the input place fields was set at 0.3 m, which was derived from empirical data [\[6,11,12\]](#page--1-0) and had been used in the previous model by Mehta et al. [\[12\].](#page--1-0) The place field's magnitude at a given location determined the probability that the respective input cell would generate a spike. For the stochastic model, every input cell had a probability of generating a spike at every time step. We also simulated a deterministic analog of the model in which input cells did not actually fire spikes, but instead the probability was used as a 'fractional spike'. This 'fractional spike'

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Fig. 1. Place field dynamics and the STDP model. (A) The firing pattern of a place cell recorded from a rat running clockwise on a circular track. The dots on the circular track are the positions where the place cell generated a spike. Left: firing on the first lap is almost symmetric. Right: on the third lap, lowfrequency firing starts to appear earlier on the track, causing the place field to become negatively skewed and the COM to shift earlier (backwards). (B) A feed-forward model consists of 1000 presynaptic cells (only 9 cells illustrated here) and a single postsynaptic output cell. The output cell receives weighted inputs from every input cell. The centers of the place fields of the input neurons are evenly distributed along a circular track (2 m circumference). The lines between the input layer and output cell represent synaptic connections, and the thickness of the lines indicates synaptic strength or synaptic weights. (C) The STDP modification function. F is the change of peak conductance or maximal synaptic strength due to a single pre- and postsynaptic event.  $\Delta t$  is the time of the presynaptic spike minus the time of the postsynaptic spike. When  $\Delta t < 0$ , the presynaptic spike leads the postsynaptic spike and the synapse is potentiated. When  $\Delta t \ge 0$ , the presynaptic spike lags or equals the postsynaptic spike and the synapse is depressed.  $A_+$  and  $A_-$  determine the maximal amounts of modification, which occur when  $\Delta t$  is close to 0.

contributed input to the postsynaptic cell and was used as a weighting number for plasticity events.

# 2.2. Stochastic input

The probability that an input cell will fire a spike is

$$
P_{\rm sp}(x_i|x_0) = \alpha e^{-(x_i - x_0)^2/2\sigma^2},
$$

where  $\alpha$  is a scaling factor that controls the firing rate of input cells,  $x_0$  is the center of the place field,  $x_i$  is the current position of the rat, and  $\sigma$  determines the width of the place field (full-width at half-height =  $2.355\sigma$ ). Total synaptic input to the postsynaptic cell is generated

randomly by  $I_{\rm s} = \sum$ i  $w_i\theta(P_{\text{sp}}(x_i|x_0) - \text{random}(i)),$ 

where  $w_i$  is the synaptic weight from input cell *i*, *random*(*i*) is a random number between 0 and 1 generated independently for each input,  $\theta$  is the heaviside function which has the value 0 if its argument is less than 0 and 1 if its argument is larger than 0.

#### 2.3. Deterministic input

An input cell fires a fractional spike at every time step. The size of the spike is

,

$$
S(x_i|x_0) = \alpha e^{-(x_i-x_0)^2/2\sigma^2}
$$

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