

Introduction

We investigated the development of topologically organized representations of a restricted region of skin in the primary somatosensory cortex (SI), more precisely, area 3b of SI. We devised a computational model based on the dynamic neural field theory and on an Oja-like learning rule at the level of feed-forward thalamocortical connections [1]. These connections reach area 3b through subthalamic and thalamic relays that convey information from the Merkel Ending Complexes (MECs), which are mechanoreceptors of the skin responsible for information related to touch and pressure. Both the critical and the post-critical periods of the SI development have been taken into consideration. In both periods SI is capable of reorganization in the presence of a cortical lesion [2] (e.g. stroke) or a sensory deprivation condition [3] (e.g. limb amputation). In order to examine if the model is capable of recovery from lesions, both cortical and sensory, we studied three different types of lesions on SI and on skin. As expected, the model is able to cope with such degenerative conditions and is able to recover a lot of the lost functionalities. Attention is another aspect that has been investigated because of its prominent role in reshaping receptive fields during execution of demanding touch perception tasks [4]. In this context we simulated some attentional mechanisms in order to investigate how attention affects the receptive fields of the model.

Materials & Methods

The model

The self-organized map is driven by an Oja-like learning rule, which in turn is driven by a dynamic neural field. The spatial convolution of excitatory part of the lateral connections, w_e , and the activity of the cortical sheet (neural field), u drive the self-organization process of feed-forward thalamocortical connections, w_f . The input to the model is conveyed from the skin receptors (Merkel's endings), which have been modeled as a discrete quasi-uniform distributed grid of two-dimensional points. The skin patch samples the applied stimuli (two-dimensional Gaussian functions) and transmit the information to the cortical model. The following equation describes the dynamics of neural field and the self-organization process.

$$\left. \begin{aligned} \tau \frac{\partial u(\mathbf{x}, t)}{\partial t} &= -u(\mathbf{x}, t) + \int_{\Omega} w_l(\mathbf{x}, \mathbf{y}) f(u(\mathbf{y}, t)) d\mathbf{y} + \alpha \frac{1}{k} |s(\mathbf{z}, t) - w_f(\mathbf{x}, t)| \\ \frac{\partial w_f(\mathbf{x}, t)}{\partial t} &= \gamma (s(\mathbf{z}, t) - w_f(\mathbf{x}, t)) \int_{\Omega} w_e(\mathbf{x}, \mathbf{y}) f(u(\mathbf{y}, t)) d\mathbf{y} \end{aligned} \right\} \quad (1)$$

Where, $u(\mathbf{x}, t)$ is the local activity of a population of neurons, located at position \mathbf{x} at time t , τ is the temporal decay constant of the synapse, α is a scaling constant, $s(\mathbf{z}, t)$ is the stimulus to the skin patch, n is the size of the field, and $w_f(\mathbf{x})$ is the feed-forward weights which modulate the input for each position \mathbf{x} , $w_l(\mathbf{x})$ is the strength of connections between neurons, according to $w_l(x) = w_e(x) - w_i(x)$ where, $w_e(x)$ and $w_i(x)$ are the excitatory and inhibitory kernels, respectively,

$$w_e(x) = K_e \exp\left(-\frac{x^2}{2\sigma_e^2}\right) \text{ and } w_i(x) = K_i \exp\left(-\frac{x^2}{2\sigma_i^2}\right) \quad (2)$$

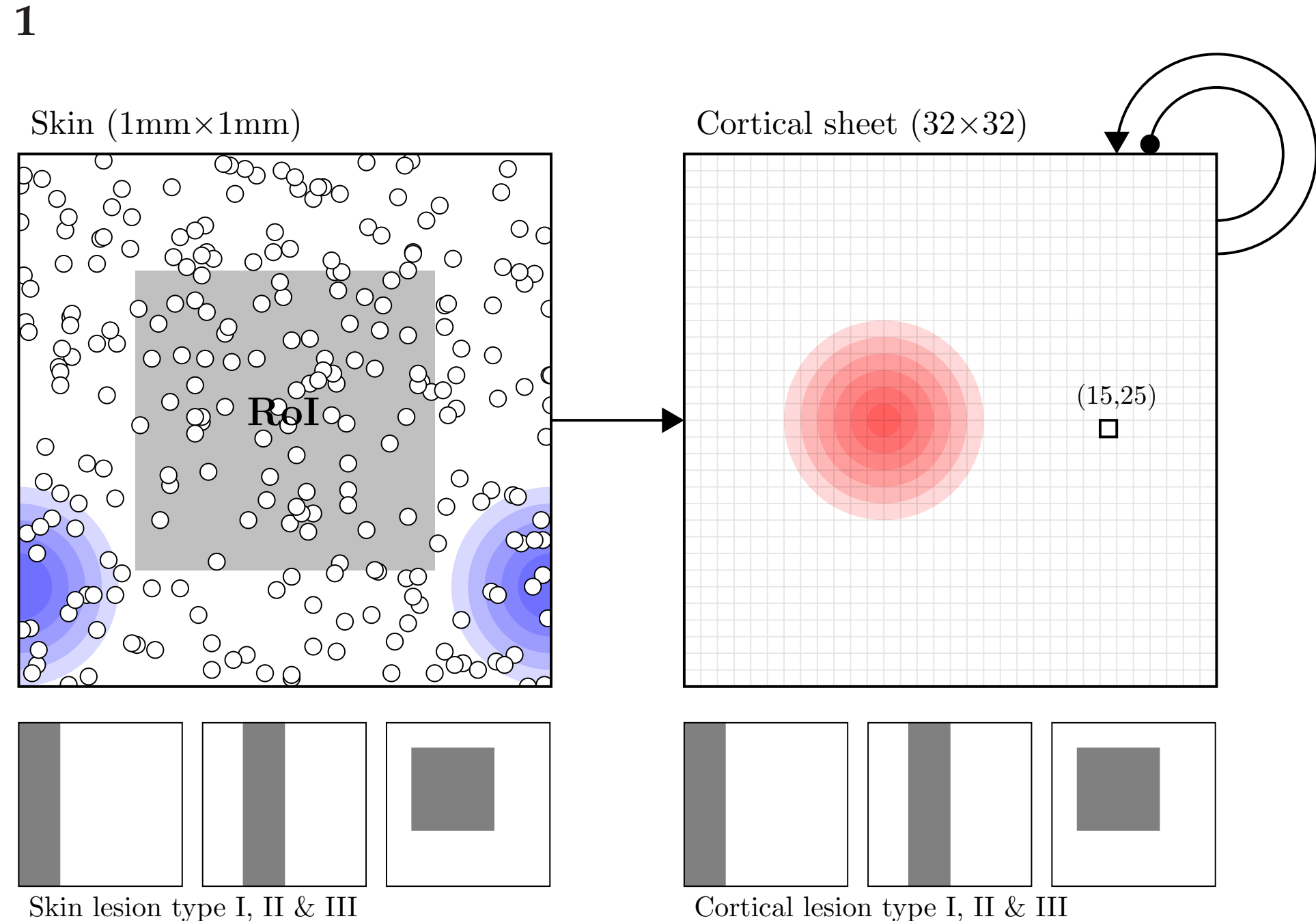
and $f(x)$ is the firing rate function of a single neuron,

$$f(x) = \begin{cases} \alpha x, & \text{if } x > 0 \text{ and } 0 < \alpha < 1 \\ 0, & \text{if } x \leq 0 \end{cases} \quad (3)$$

$\Omega \in \mathbb{R}^q$ where $q = 1, 2$. Additionally, the field is generally considered to be homogeneous using an isotropic kernel of the form $w_l(|\mathbf{x} - \mathbf{y}|)$.

Simulation details

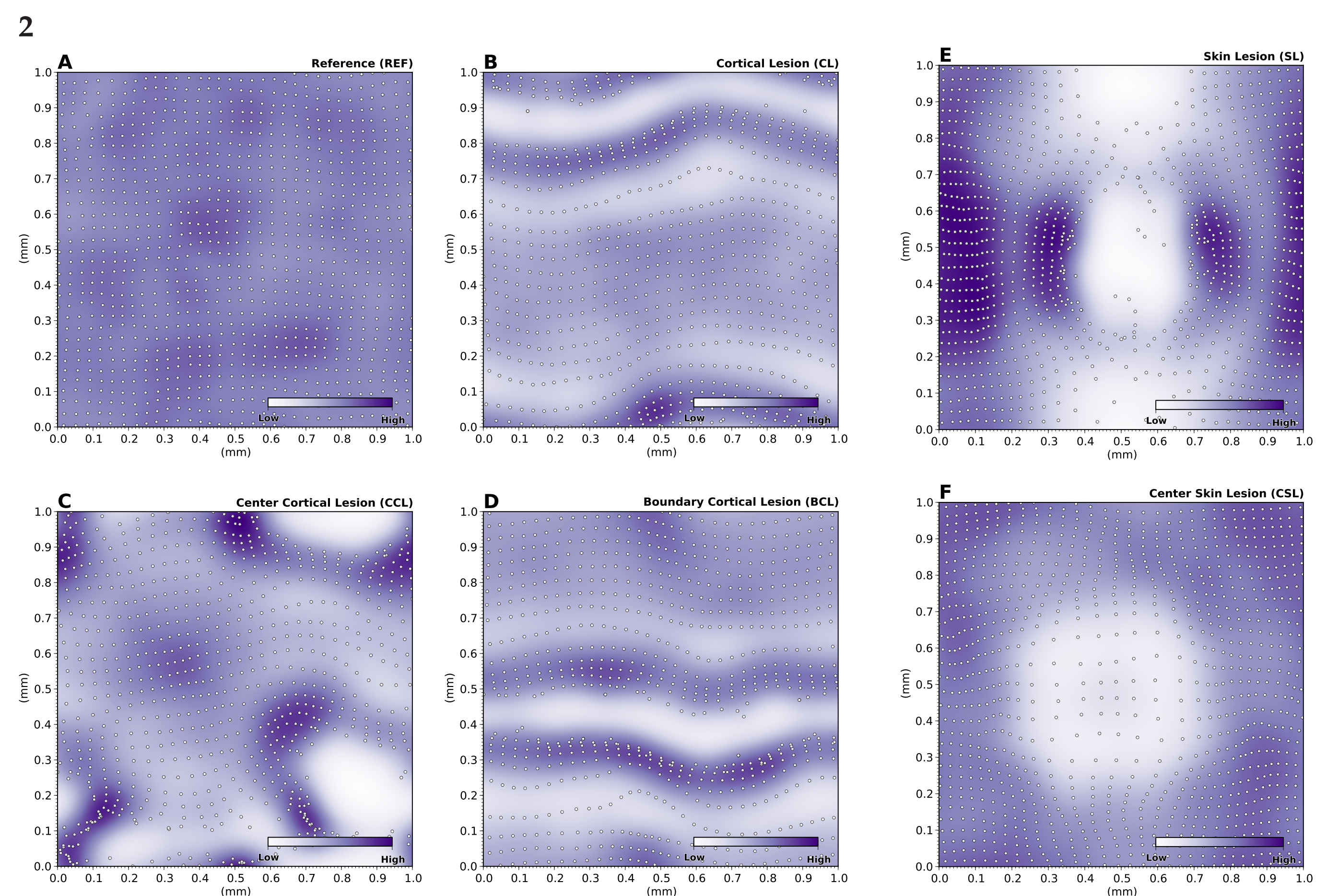
The system described by equation (1) has been discretized in a 32×32 grid and the Euler's forward method has been used in order to solve it numerically. The integral has been computed using the FFT. The skin model has been discretized using 256 receptors and the feed-forward connections are a matrix of dimensions $32 \times 32 \times 256$. The model is implemented on a torus in order to avoid some well-known problems of self-organization process. The cortical lesions and the sensory deprivations have been implemented as masks, which set to zero the corresponding values. In the cortical lesion case, this means that the affected neurons cannot transmit and process any kind of information. Furthermore, in case of skin lesion the mask applied on the skin receptors and therefore, they cannot transmit any kind of information to the cortical model. In figure 1 is illustrated a schematic of the model and the lesions.



Results I

The equation (1) has been used in order to investigate the formation of a topographic map of a 1mm^2 skin patch. The model has been trained over 35000 epochs starting from random initial feed-forward connections. At each epoch a stimulus is presented to the model and the system (1) is solved numerically. After the convergence of the self-organization a topographic map has emerged as it is depicted in figure 2A. Then cortical lesion and sensory deprivation masks have been applied as it is illustrated in figure 1. The model has been trained again over 35000 epochs and a new topographic maps has emerged indicating a reorganization of the initial topographic map. The results after a cortical lesion of type I, III and II can be found in figures 2B, 2C and 2D, respectively. The sensory deprivations of types III and II are depicted in figures 2E and 3F, respectively.

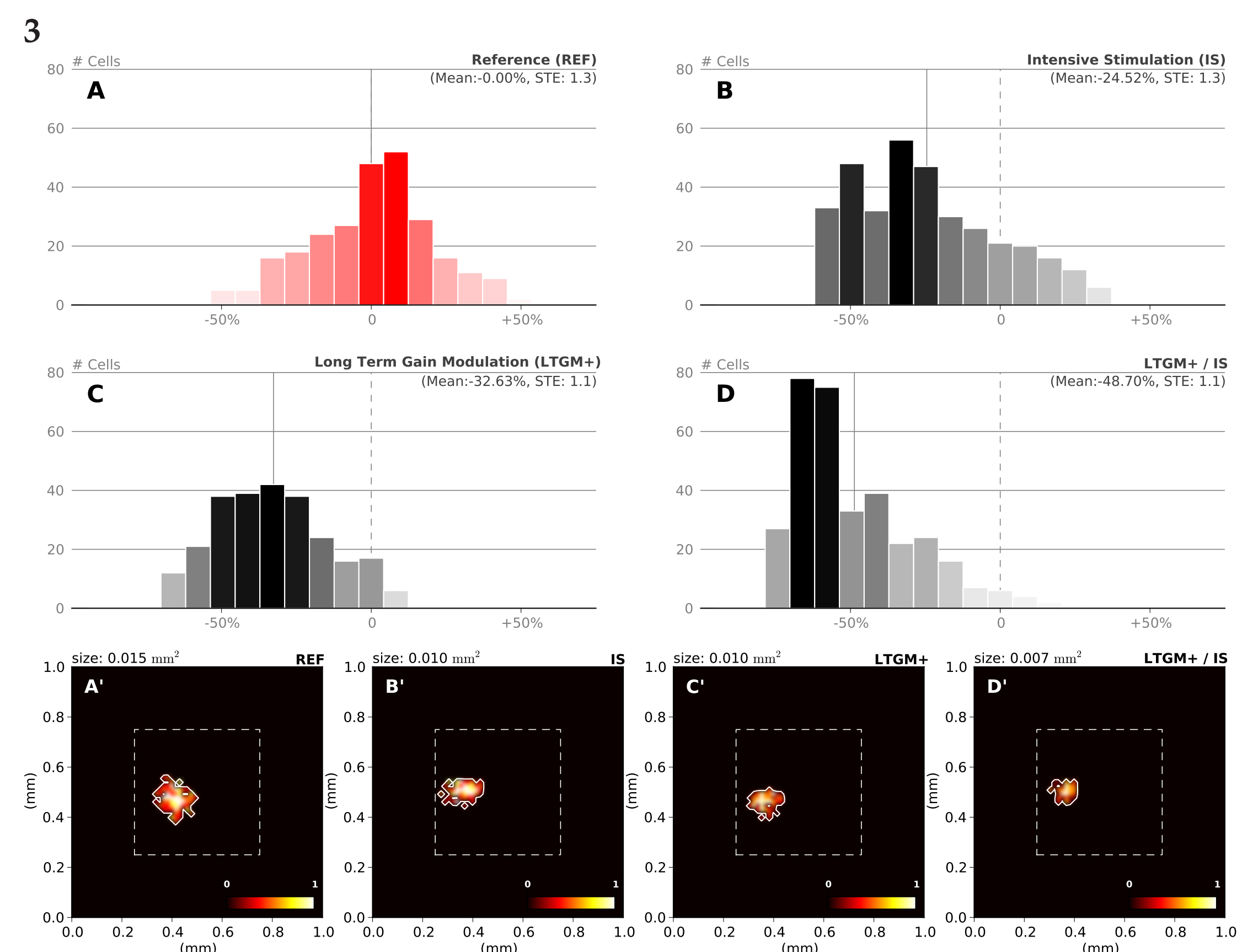
Results II



In order to study the effects of attention on area 3b a region of interest (RoI) has been defined on the skin patch. Every stimulus in the RoI is considered as attended and for each such stimulus the gains of the excitatory and inhibitory synaptic strengths have been modulated. Therefore, K_e and K_i have been increased when a stimulus lies within RoI. This leads to the modulation of response of neural field and therefore to alterations of receptive fields of neurons. Furthermore, four different cases have been studied.

- LTGM - long-term gain modulation, where the lateral gains have been changed before retraining of the model.
- IS - intensive stimulation, where there is no gain modulation, but an intensive stimulation of the RoI of skin patch.
- LTGM+IS, which is a combination of the LTGM case and the IS case.

The results for each of the aforementioned cases are illustrated in figures 3B, 3C and 3D, respectively. In addition, a third case has been studied. This case is called STGM (short term gain modulation), where gains have been altered dynamically without any further learning (results are not illustrated here).



Moreover, in figures from 3A' to 3D' are illustrated the alterations of a specific receptive field for each of the three aforementioned conditions (LTGM, IS, LTGM+IS).

Conclusions

The present model is able to form and maintain topographic maps. Furthermore, the model is able to cope with cortical lesion cases and sensory deprivations by reorganizing the receptive fields of neurons. The self-organization process is driven by the activity of a neural field, which models a part of the area 3b of SI. The reorganization relies on the balance between excitation and inhibition and because of the non-learning lateral connections the reorganization is not perfect after a cortical lesion or a sensory deprivation. This indicates that the thalamocortical connections are enough to promote self-organization and reorganization, however the lateral connections play an important role in the refinement of the receptive fields. In the case of attention, the model is capable of showing that the receptive fields of neurons within the attended area undergo a shrinkage and these outside the attended area undergo an expansion and a migration towards the attended signal representation.

References

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