

# Establishing retinotopy by lateral-inhibition type homogeneous neural fields

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**Abstract.** We study the topographic development of receptive fields by simulating the continuum field equations with learning on a two-dimensional lattice. The observed plasticity reveals a columnar organisation with spatial clustering of receptive field centres, and the development of oriented receptive fields, if certain conditions are met.

## 1. Introduction

The development of ordered receptive fields (RFs) is a biological phenomenon, which depends on a sequence of ontogenetic mechanisms to establish topographic connections between layers of neurons. It has been shown that the established map is able to reorganise its RFs, if the corresponding sensory area receives considerable more stimulation during a longer period, or is removed due to ablation. The connectivity pattern from the retina to the LGN/tectum and from there to the visual cortex has been subject both to physiological studies [3, 4, 6, 7, 9, 10, 12, 13, 16] and theoretical analysis [1, 2, 5, 8, 11, 14, 15, 17]. Although the development of orientation preference, ocular specificity and higher order visual feature selectivity may additionally constrain the development of the precise retinotopic layout, we limit our study, due to complexity constraints, to the development of a two-dimensional topographic RF structure. Mapping studies have revealed a random-walk like distribution of RF centres of adjacent cortical neurons. Whether this stochastic gradient is accompanied by a postulated systematic gradient with a specific mode has not been fully clarified. To further investigate the self-organisation of columnar structure we will use numerical analysis of nonlinear dynamical systems.

Here we will follow the theoretical analysis of continuum neural field theory using simulations to assess the self-organisation properties of the dynamical system. Next, the system equations will be presented, followed by a discussion of the evolved retinotopic and orientation maps. The paper concludes with a discussion of the observed plasticity phenomenon.

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## 2. Algorithm

The learning algorithm for the development of a topographic map can be divided into two stages: an initial recurrent phase, governed by a short time scale for the fast cortical adaptation to a new stimulus, and a second phase with a slower time scale for changing the weights to the retinal stimulus. The continuum neural field can be interpreted as a model for the average behaviour of large ensembles of cortical neurons allowing a macroscopic description of the system in terms of an activation variable  $u$ . The learning mechanism adapts to the environment represented by the stimulus set, thereby revealing an emergent order parameter of the nonlinear system. Since both mechanisms act on different time scales, they can be effectively decoupled, allowing the results of the fast dynamic field process to be regarded as a stationary state for the slow learning process.

### 2.1. The neural field

The dynamics of the activation variable  $u(z,t)$  is given by the nonlinear integro-differential equation:

$$\tau \dot{u}(z, t) = -u(z, t) - h + \int_{\Omega} w(z, z') \Phi(u(z, t)) dz' + \int s(z, t) a(z - z') dz \quad (1)$$

$u(z, t)$  is the membrane potential at cortical point  $z$  given a stimulus on the retinal plane relayed by the smoothing function  $a(z - z')$  and the cells RF weights  $s(z, t)$  to the cortical plane. The function  $h$  models recurrent feedback by tonic disinhibition, thereby allowing rich cortical RF properties to emerge. The function  $w$  defines an isotropic weight kernel which varies with weight and has been modelled in the simulations as a difference of two Gaussian kernels.  $\tau$  defines a time-constant and the function  $\Phi$  is set to a step-function. The RFs are assumed to be initialised to random values and the parameters should be appropriately chosen to ensure stability of the system in response to afferent stimulation.

### 2.2. The learning equation

The afferent weights  $s(z, t)$  were changed according to a Hebbian learning equation with a slower time constant than the field dynamics to ensure the proper development of a topographically organised structure:

$$\tau \dot{s}(z, t) = -s(z, t) + \epsilon a(z - z') \Phi[u(z, t)] \quad (2)$$

The weights are changed according to the correlation between the membrane potential  $u(z, t)$ , which evolved during the lateral-inhibition type process, and the sensoric input smoothed by the spread function  $a$ . To allow the developing of orientation selective RFs, the weight decay term has been replaced by a weight normalisation term.

### 3. Simulations

Figure 1 shows a sequence of activation patterns following the stimulation of the sensory plane using randomly distributed binary point stimuli of size  $4 \times 4$ . The time constant was set to 0.1 to achieve fast convergence of the system to the present stimulus. Shortly after onset of the new stimulus, the old stable focus vanishes and is replaced by a new stable equilibrium. A notable effect can be observed whenever the new stimulus lies in the RF of the previous activity bubble of the cortical layer: the bubble moves along the cortical surface and relaxes near the new input position.

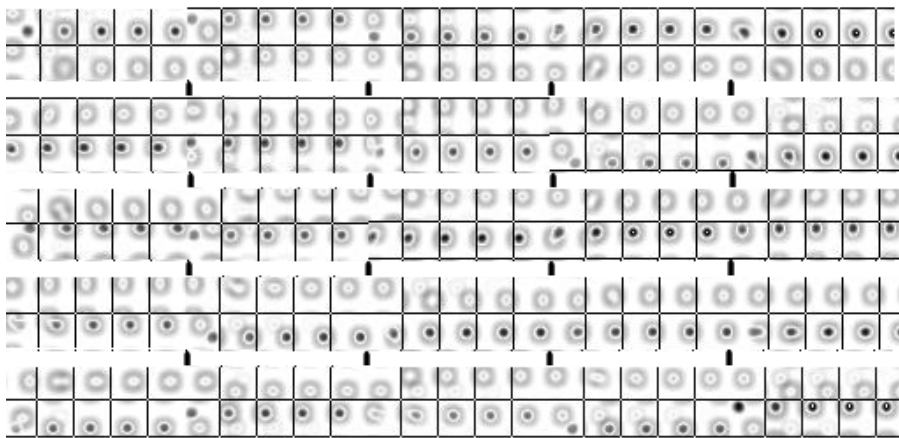


Figure 1: *Sequence of bubble activations on the cortical surface of size  $20 \times 20$  after stimulation with randomly distributed point stimuli from the retina (size  $64 \times 64$ ). For each stimulus presentation five time-steps of the relaxation into a stable equilibrium are shown. The next cycle, indicated by black marks, starts with a randomly positioned new stimulus. Note the apparent movement of the bubble if the new stimulus falls in the RF of the preceding activation.*

Figure 2 shows the distribution of the topographically ordered RFs after 100 simulation steps of the complete learning procedure. The dark spots, which mark the centres of the RFs, show the spatial clustering pattern, revealing a discontinuous advancement of the centres between clusters and some rare cases of neurons with multiple RF centres.

To explore the properties of the dynamical system on a more complex feature set, additional simulations were performed using small oriented bars as sensory input patterns. To allow the development of orientation selectivity, the learning equations had to be modified slightly by inclusion of a Gaussian weight normalisation term. Figure 3 shows the oriented RFs of 1600 cortical neurons, which developed following the presentation of 10,000 randomly placed and oriented stimuli from a retina of size  $32 \times 32$ .

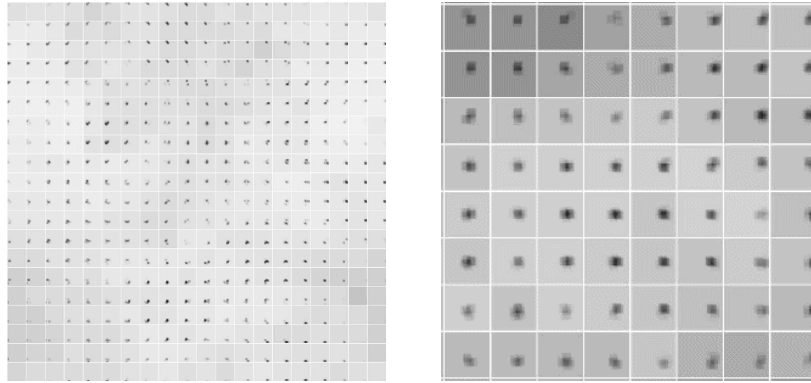


Figure 2: *left: Topographically ordered RFs, note the clustering of RF centres into discrete groups and the sudden jumps across the simulated cortical surface. Each of the 400 squares shows the weights of one cortical neuron to the retinal plane of size 64x64; right: enlarged RFs for a 8x8 region.*

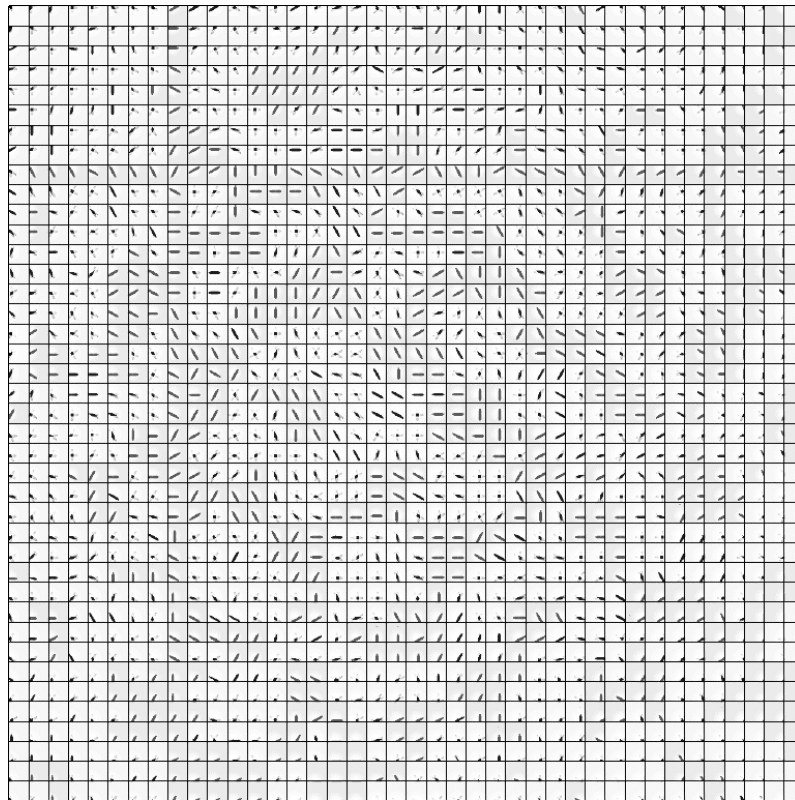


Figure 3: *Orientation selective RFs on a model cortex of size 40x40, the size of the retina is 32x32*

## 4. Conclusion

We have studied the topographic development of RFs by simulating the continuum field equations with learning on a two-dimensional lattice. It was shown that the emergent clustering phenomenon, which was observed previously for the one dimensional case [14], also holds for the two-dimensional case, and produces a patch-like, discontinuous structure of receptive field variation. Furthermore, we have shown that by replacing the weight-decay term of Equation (2) by a Gaussian weight normalisation term, the network can develop oriented RFs. The modification of the learning equation was necessary to produce oriented RFs, resembling biological visual RFs, since the original formulation of the learning equation with weight decay did not account for normalisation or weight redistribution effects. Biological neurones often show spatial shapes similar to Gabor functions, with an elongated excitatory centre surrounded by inhibitory surrounds. Closer inspection of the oriented RFs of the mapping revealed a similar RF organisation with inhibitory side-lobes next to the central excitatory region.

The results obtained from the simulation and presented in the previous section agree with the asymptotic solution which can be obtained for the dynamic and learning equations (1) and (2), using the analysis of [15], in the unstable case. The solution for a map of a one dimensional retina into a one dimensional cortex was already been simulated in [14], with a 'double staircase' solution obtained, in which the RFs of cortical neurons are successive intervals of the retinal line, jumping from one interval to the next one at a succession of discrete points. This can be extended to the case of a map of a two dimensional retina into a two dimensional cortex, with a similar 'double staircase' structure. It is this structure which is apparent in figure 2. The two-dimensional simulations indicate that the analytic solutions obtainable for (1) and (2) are attainable by simulation in the simpler cases.

In order to obtain orientation selectivity it is necessary to consider the case of an unstable map from three dimensional inputs (on a two dimensional retina) into a two dimensional cortex. The extra dimension of the input space is provided by considering orientations of bars of light instead of the random spots used in the simulation of section 3; the resulting solution of the learning equations (1) and (2) for bar inputs is a double staircase form, now with the third input dimension squashed into a linear map inside each square of the cortical double staircase.

Analytical and numerical considerations lead to two constraints, to allow the formation of orientation selectivity from randomly placed and randomly oriented retinal stimuli. First, the sum of the weights of each cortical unit must be kept approximately equal to the other neurones, to allow the uniform development of oriented RFs. Furthermore, since the RFs develop a topographic ordering, the weight normalisation term should have Gaussian form, centered on the centre of the RFs. This Gaussian weight normalisation term allows the development of inhibitory side-lobes similar to the RF-structure of visual cortical neurones.

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