7. MODELING THE SOMATOTOPIC MAP

7.1 The Somatotopic Map of the Body Surface

In this chapter we demonstrate the formation of a "somatotopic map" by means of a computer simulation of Kohonen's algorithm (Ritter and Schulten 1986). The *somatotopic map* is the projection of the body surface onto a brain area that is responsible for our sense of touch and that is called the *somatosensory cortex*. This projection connects neurons of the cortex with touch receptors in the skin surface such that neighborhood relations are preserved. Adjacent touch receptors in the skin surface are thus connected to adjacent neurons (Kaas et al. 1979). However, the projection is strongly distorted, since the density of touch receptors is very different in various skin regions. For example, hand and face regions are considerably more densely innervated with touch receptors than the skin on the arms and on the trunk. Correspondingly, the former have a much larger image area in the somatosensory cortex. Interestingly, the neural projections giving rise to these images are not rigid. Instead, they can change under the influence of sensory experience or as the result of a loss of sensory input, *e.g.*, after nerve damage. The necessary modifications of the connections between receptors and sensory neurons are thought to be, at least in part, activity driven. For example, experiments have revealed that frequent stimulation of confined skin regions leads to an expansion of their representation in the somatotopic map (Jenkins et al. 1984). Conversely, neurons whose receptors no longer receive any stimuli become sensitive to other receptors which are still active (Kaas et al. 1983). Such findings imply that a significant part of cortical organization may be shaped by a principle of competition between neurons, most likely operating at the synaptic level.

In the following we show that from a completely disordered initial connectivity, the structure of an ordered, neighborhood-preserving connection pattern between touch receptors and neurons of a "model somatosensory cortex" as well as a series of experimentally observed adaptation phenomena, can come about as a result of Kohonen's strongly idealized algorithm alone. According to current thought, this represents an idealization of the actual phenomena in which chemical control processes are also significantly involved (Campenot 1977). However, the value of such a demonstration is not primarily the description of biological detail, but the isolation of significant and simple functional principles and their capacity for contributing to important organizational processes in the nervous system.

A considerably more ambitious simulation model for the formation of somatotopic connectivity, as far as reproduction of biological details is concerned, was investigated by Pearson et al. (1987). Pearson's model assumes an initial connectivity which is diffuse, but already topographically ordered. The simulation investigates how, by aggregation into competing groups, individual neurons can focus their initially diffuse receptive fields into smaller regions while maintaining the initial topographic ordering. The main intention is a test of the group selection theory of Edelman (1978). According to this theory, aggregation of adjacent neurons into localized "functional groups" occurs. The "formal neurons" in Kohonen's model may possibly be viewed as an abstraction of such larger, functional units.

7.2 Simplification of the Dynamics

For the simulation, we consider a "model hand surface" with touch receptors distributed at locations $\mathbf{v}_\alpha \in \mathbb{R}^2,\ \alpha = 1, 2, \ldots K$. Figure 7.1 shows the hand surface used, together with $K = 1200$ randomly distributed touch receptor points. The touch receptors are connected through synapses to the 30×30 neurons of a square "model cortex" A. Let $w_{\mathbf{r}\alpha}$ denote the strength of the synapse through which receptor α excites the neuron at the position $\mathbf{r}$. Every localized touch stimulus on the hand surface leads to excitations ν_α of the receptors α. Receptors close to the stimulus location are strongly excited, and excitation decreases to zero with increasing distance. The excitations of the receptors are assumed to lead to an adaptation step

$$\Delta w_{\mathbf{r}\alpha} = \epsilon h_{\mathbf{rs}}(\nu_\alpha - w_{\mathbf{r}\alpha}), \tag{7.1}$$

for the synaptic strengths. Here, $\mathbf{s}$ again identifies the most strongly excited neuron and $h_{\mathbf{rs}}$ is the assumed excitation profile about $\mathbf{s}$. We now show how (7.1) can give rise to the formation of an ordered connectivity between neurons and touch receptors such that each neuron has synaptic connections only to receptors from a localized region of the hand surface, and adjacent neurons are connected to adjacent regions. For a useful simulation, however, several hundred touch receptors would be required, and an equal number of synaptic strengths would have to be stored and updated at each learning step and for each of the 900 model neurons.

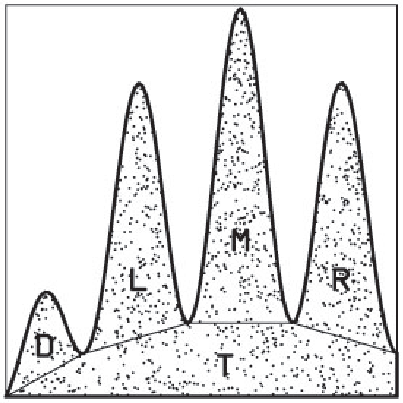

Abb. 7.1: Model hand surface with touch receptors. Letters **D, L, M, R,** and **T** denote five subregions: thumb, left, middle, and right fingers as well as the palm. The dots mark the locations of 1,200 touch receptors distributed at random over the hand surface.

However, one can approximate the system behavior by mapping the original dynamic variables, the synaptic strengths $w_{\mathbf{r}\alpha}$, onto a much smaller set of new variables, whose evolution then is governed by a correspondingly simpler, "effective dynamics." In this way, the resulting simulation effort is reduced considerably. For this simplification, we must make the following two additional assumptions:

1. The sum $S = \sum_\alpha \nu_\alpha$ of the excitatory strengths of the touch receptors should be the same for each touch stimulus.

2. The synaptic strength of each neuron should satisfy initially

$$\sum_\alpha w_{\mathbf{r}\alpha} = S. \tag{7.2}$$

The first assumption corresponds to a preliminary normalization of the activity of the input signal. By (7.1), one has for a learning step

$$\Delta \sum_\alpha w_{\mathbf{r}\alpha} = \epsilon h_{\mathbf{rs}} \left(S - \sum_\alpha w_{\mathbf{r}\alpha} \right). \tag{7.3}$$

Thus, the second assumption implies that the sum of the synaptic strengths of each neuron takes its stationary value from the beginning, which by (7.3) would otherwise only hold after some relaxation time.

With these assumptions, we can describe the development of the correspondence between the hand surface and the neurons directly using two-dimensional surface coordinates. We describe the touch stimulus by the location $\mathbf{v}$ of the center of gravity of the excitatory pattern of the touch receptors, *i.e.*,

$$\mathbf{v} := \frac{1}{S} \sum_\alpha \nu_\alpha \mathbf{v}_\alpha, \tag{7.4}$$

and replace the K synaptic strengths $w_{\mathbf{r}\alpha}$ per neuron by the two "formal synaptic strengths"

$$\tilde{w}_{\mathbf{r}i} := \frac{1}{S} \sum_\alpha v_{\alpha i} w_{\mathbf{r}\alpha}, \quad (i = 1,\ 2). \tag{7.5}$$

Here, $v_{\alpha 1},\ v_{\alpha 2}$ denote the cartesian coordinates at receptor location $\mathbf{v}_\alpha$, and we use arabic numerals as indices in order to distinguish the two formal synaptic locations $\tilde{w}_{\mathbf{r}i}$ from the K synaptic strengths $w_{\mathbf{r}\alpha}$. One can interpret $\tilde{\mathbf{w}}_\mathbf{r} := (\tilde{w}_{\mathbf{r}1}, \tilde{w}_{\mathbf{r}2})^T$ as the center-of-mass of the group of touch receptors attached to neuron $\mathbf{r}$. Here, each touch receptor is weighted in proportion to the strength of its connection with neuron $\mathbf{r}$. Thus, from (7.1) we obtain

$$\Delta \tilde{w}_{\mathbf{r}i} = \epsilon h_{\mathbf{rs}} (v_i - \tilde{w}_{\mathbf{r}i}), \qquad (i = 1,\ 2). \tag{7.6}$$

This equation establishes the desired "effective dynamics" for the new variables $\tilde{\mathbf{w}}_{\mathbf{r}i}$. Interestingly, it is of the same form as (7.1); however, now a simulation only requires taking into account the two-dimensional vectors $\mathbf{v}$ and $\tilde{\mathbf{w}}_\mathbf{r}$.

7.3 Results of the Simulation

The initial state of the simulation consisted of a random assignment of neurons to touch receptors. This assignment was arranged by setting the formal synaptic strengths $\tilde{\mathbf{w}}_{\mathbf{r}}$ to random values taken from a uniform distribution on the unit square circumscribing the hand surface in Fig. 7.1. [1] Precisely speaking, the initial distribution of formal synaptic strengths could be obtained from the receptor distribution together with an assignment of the $w_{\mathbf{r}\alpha}$ to random values (preserving the sum condition 2.). The values thus obtained would all lie within the convex hull of the hand surface. However, this difference is not important for the qualitative course of the organization process from a disordered initial state. The resulting map is shown in Fig. 7.2. For each neuron $\mathbf{r}$, a letter indicates which of the five regions **D, L, M, R,** and **T** contains the center of mass $\tilde{\mathbf{w}}_{\mathbf{r}}$ of the subset of receptors exciting that neuron. Neurons for which $\tilde{\mathbf{w}}_{\mathbf{r}}$ happens to lie outside of the hand surface are marked by a dot. This case occurs, for example, if a neuron has equally strong connections to the receptors of two adjacent fingers.

The initial connection pattern evidently leads to a map that does not reproduce the topological arrangement of the touch receptors in any way. For the subsequent learning steps, stimulus locations $\mathbf{v}$ were randomly selected from the hand region according to the the probability density $P(\mathbf{v}) = 1.5/\sqrt{4 - 3v_2}$. In this way, the increasing receptor density towards the finger tips, the locations of which correspond to $v_2 \approx 1$, was simulated (the touch receptor points illustrated in Fig. 7.1 are also distributed according to this density). During the first 5,000 learning steps, the Gaussian (68) with $\sigma(t) = 5 \cdot 0.4^{t/5000}$ and $\epsilon(t) = 0.5 \cdot 0.2^{t/5000}$ was assumed for $h_{\mathbf{rs}}$, while during the subsequent learning steps a Gaussian with $\sigma(t) = 2$ and $\epsilon(t) = 0.1$ was chosen. After 500 touch stimuli, a map has formed in which one can already recognize connected regions of neurons assigned to the same hand region (Fig. 7.3). Even the neighborhood relations between individual hand regions are already beginning to be reproduced correctly. Eventually, after 20,000 iterations, a map has been created (Fig. 7.4) which represents a topologically correct image of the individual hand regions, resembling maps obtained with electrode penetration experiments in animals. Figure 7.5 again shows this assignment of neurons to hand locations, using the familiar imbedding of the neuron lattice in the space V. Following an experiment of Kaas et al. (1983), at this stage of development of the map we "remove" the middle finger by not selecting any further stimuli from the region **M** for the remainder of the simulation (Fig. 7.6). Because of the remaining plasticity in the map-

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M L . . L . . T T T L L . . L . . L R . L M T . . . . . . M
. T . L R R . . R . R . M M D . T . M . R . . R . R M L . .
. . . . R T T . . M . M . . T R R . . L . . . M M T . . R .
. . . . R L L . . . . . R . . L M . T . L D . T . T . R T M
. R T . T M . . . . . T . R D L . L . . M . L . R . . . D L
T . L L R . . T . M . . . L . . . . . T . T R . . . L T . M
. . . . . T . . R M . . . T . T . T . . M M . T . R R . . .
. . . . . . . . . . M . R M . T T . . . R . . . . L R . R .
. M . . T R . . . L T . R L . R R . . T R . T . M . . M R .
. M T T R . . T M . T . . . . T . . . T T . . D D M . R L R
R T R T T D . . . . . . R . D T L . T . . T . . . . . T . M
L T T M . . . . . . . . . . . T . . . M . . . L . M . M . R
M T . T . . . T . . . L . . . M . . . . . . . R T T . . . .
. T . . . M . . M . . . . T . . . . T . . . . M T T . . . T
. R . D . . L R M M . . R . . . . . . . M . T . T M L . . .
M L . . R . R . R . . . . . M . . M . . . . . M . M . T . R
M T . L . . L R L . R T . . . . L . T L . T T T R . T . L .
. . . . . T . T . T . . . M R . . T . . . . T L D . . T . T
. . L . . L . . D T . . . L M . . . L . T L . . . T M . R D
M M T M L . . L . . . . M L T M M . . . . . . . . . . T . .
. . . M . . L T . M . . . T . . . T M T T . . L . . . T L T
M M L L . . T . R R R . M . M . R . L . . R . T . . M R T .
. . . T . . R . . . T M . M R R R . L . . R . L L . . . L M
. . . . . . . . R . T . . . . L L . . M L M . . . . T . . .
. L M T . L . . . L . . . R . . T T . . . . . M M T . T T .
. . M . . . T . R . . T R . R L . . . . L . T . R . . L . .
. . . . . M R T . . . R M T R L T . M L . . . M T L M L L .
M . . M M D R . . M T M . . R . . L . T . . . . L . . T . .
. . . . R T M M M . . . . T M R T M M . . . . . . M T . . .
. . M . R M . . . . . . . . . R . . M . R M . . . . M . R T
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Abb. 7.2: Initial assignment of the 900 neurons of a model cortex of 30×30 lattice sites to the hand surface of Fig. 7.1. Each lattice site $\mathbf{r}$ corresponds to one neuron, which is connected through synapses to touch receptors on the hand surface. The location $\tilde{\mathbf{w}}_{\mathbf{r}}$ of the center of gravity of these receptors is indicated by labeling the lattice site with one of the letters D, L, M, R and T, according to the region in Fig. 7.1 containing $\tilde{\mathbf{w}}_{\mathbf{r}}$. A dot indicates that $\tilde{\mathbf{w}}_{\mathbf{r}}$ happens to lie in the space between the fingers. As can be seen, the initial correspondence between neurons and locations in the hand surface is completely random and in particular not neighborhood preserving.

ping, the net readapts during the subsequent 50,000 learning steps, leading to the map in Fig. 7.7. The cortical region deprived of its former sensory inputs has established connections to receptors formerly driving neurons in the adjacent regions (labelled **L** and **R**). In the map, these regions "invade" the former territory of the amputated hand region **M**. Additionally, as a result of the readaptation, the local magnification factor of the mapping from the hand surface to the cortex has increased. This corresponds to an enhanced capacity for spatial discrimination in these regions. Qualitatively similar behavior has been observed experimentally (Kaas et al. 1983). To this end, the somatosensory map of the hand region of an adult monkey was

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M M M M M . . L L L L L T T T T T T T T T T T T T T T T T M
M M M M M M . L L L L L L T T T T T T T T T T T T T T T T T
M M M M M . . L L L L L L T T T T T T T T T T T T T T T T T
M M M M . . L L L L L L L T T T T T T T T T T T T T T T T T
M M M M . . L L L L L L L . T T T T T T T T T T T T T T T T
M M M . . L L L L L L L . . T T T T T T T T T T T T T T T T
M M . . . L L L L L L . . . D T T T T T T T T T T T T T T T
M M . . L L L L L L L . . . . . T T T T T T T T T T T T T T
M . . . L L L L L L L L . . . . . T T T T T T T T T T T T T
M . . . L L L L L L L L . . . . L L L L T T T T T T T T T T
M . . L L L L L L L L L L L L L L L L L L T T T T T T T T T
M . . L L L L L L L L L L L L L L L L L L T T T T T T T T T
M . . . L L L L L L L L L L L L L L L L . M T T T T T T T T
M . . . L L L L L L L L L L L L L L . M M M T T T T T T T T
M M . . L L L L L L L L L L L L L . . M M M M T T T T T T T
M M . . . L L L L L L L L L L L L . M M M M M T T T T T T T
M M M . . . L L L L L L L L L L . . M M M M M T T T T T T T
M M M . . . . L L L L L L L L . . . M M M M M T T T T T T T
M M M M . . . . . L L L L . . . . M M M M M M T T T T T T T
M M M M M . . . . . . . . . . M M M M M M M M T T T T T T T
M M M M M M M . . . M M M M M M M M M M M M M T T T T T T T
M M M M M M M M M M M M M M M M . . . . . . . T T T T T T T
M M M M M M M M M M M M . . . . . . R R R R R R T T T T T T
M M M . . . M M M M M M . . . R R R R R R R R R R T T T T T
. . . . . . . . M M M . . . R R R R R R R R R R R T T T T T
. . . . . . . . . M M . . . R R R R R R R R R R R T T T T T
. . . . . . . . . M M . . R R R R R R R R R R R R R T T T T
. . L L L L . . . . M M . . R R R R R R R R R R R R T T T T
L L L L L L L . . . M M . . R R R R R R R R R R R R T T T T
L L L L L L L L . . . M . . R R R R R R R R R R R R R T T T
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Abb. 7.3: After only 500 “touch stimuli,” a coarsely ordered assignment has replaced the completely disordered initial state of Fig. 7.2. Adjacent neurons have begun to specialize to adjacent regions of the hand surface.

determined using microelectrodes (Fig. 7.8a). The observed map resembles that in Fig. 7.4. To each finger corresponds one of the regions 1–5. Several weeks after amputation of the middle finger, the corresponding region 3 has “disappeared,” and the adjacent regions have become correspondingly larger (Fig. 7.8b).

We have thus demonstrated that under Kohonen’s algorithm a connection pattern forms between neurons and touch receptors; it arranges the centers of gravity $\tilde{\mathbf{w}}_{\mathbf{r}}$ of the neurons $\mathbf{r}$ connected to the touch receptors in the hand surface topologically, just as the corresponding neurons $\mathbf{r}$ are arranged in the somatosensory cortex. However, because of the use of the centers of gravity $\mathbf{w}_{\mathbf{r}}$ as simulation variables, the simulation makes no statement about the spatial scatter of the touch receptors in the hand surface to which a single neuron has finally formed synaptic contact. Therefore, we must still show that, under the algorithm, each neuron $\mathbf{r}$ concentrates its synaptic contacts to receptors from a small region about the center of gravity $\tilde{\mathbf{w}}_{\mathbf{r}}$.

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D D D D D D D D D T T T T T T T T T T T T T T T T T T T T T
D D D D D D D D D T T T T T T T T T T T T T T T T T T T T T
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. . . D D D D D D D D D T T T T T T T T T T T T T T T T T T
L L . . . . . . . . . . L L L T T T T T T T T T T T T T T T
L L L L L L L L L L L L L L L L L T T T T T T T T T T T T T
L L L L L L L L L L L L L L L L L L T T T T T T T T T T T T
L L L L L L L L L L L L L L L L L L L T T T T T T T T T T T
L L L L L L L L L L L L L L L L L L L T T T T T T T T T T T
L L L L L L L L L L L L L L L L L L L T T T T T T T T T T T
L L L L L L L L L L L L L L L L L . M M T T T T T T T T T T
L L L L L L L L L L L L L L L . M M M M M T T T T T T T T T
L L L L L L L L L L L L . . . M M M M M M T T T T T T T T T
L L L L L L L L L . . . M M M M M M M M M M T T T T T T T T
L L L L L L L L . . M M M M M M M M M M M M T T T T T T T T
L L L L L L . . M M M M M M M M M M M M M M T T T T T T T T
L L L L L . . M M M M M M M M M M M M M M M M T T T T T T T
L L L L . . M M M M M M M M M M M M M M M M M T T T T T T T
L L L . . M M M M M M M M M M M M M M M M M M T T T T T T T
L L . . M M M M M M M M M M M M M M M M M M M T T T T T T T
L . . M M M M M M M M M M M M M M M M M . . R T T T T T T T
. . M M M M M M M M M M M M M M M . . . R R R R T T T T T T
M M M M M M M M M M M M M M . . . R R R R R R R T T T T T T
M M M M M M M M M M . . . . R R R R R R R R R R R T T T T T
M M M M M M M M . . . R R R R R R R R R R R R R R T T T T T
M M M M M M . . . R R R R R R R R R R R R R R R R T T T T T
M M M M M . . R R R R R R R R R R R R R R R R R R R T T T T
M M M M . . R R R R R R R R R R R R R R R R R R R R T T T T
M M M . . R R R R R R R R R R R R R R R R R R R R R T T T T
M M M . R R R R R R R R R R R R R R R R R R R R R R R T T T
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Abb. 7.4: After a total of 20,000 touch stimuli, the connections between the neurons and the hand regions have become completely ordered. This assignment is now neighborhood preserving, and it reproduces the correct topological arrangement of the regions D, L, M, R and T. The map created here is also in good qualitative agreement with maps experimentally found in the cortex.

7.4 Development of Receptive Fields

The skin region within which touch stimuli lead to excitation of a neuron $\mathbf{r}$ forms the *"receptive field"* of this neuron. A measure of the size of this field is the average surface area $G_{\mathbf{r}} = \pi\langle \mathbf{r}^2 \rangle$ of the "scattering circle" of the touch receptors connected to the neuron. Here, $\langle \mathbf{r}^2 \rangle$ is the average value of the squared distance of the receptors from the center of the circle (their center of gravity $\tilde{\mathbf{w}}_{\mathbf{r}}$), weighted by the synaptic strengths $w_{\mathbf{r}\alpha}$ of their connections with neuron $\mathbf{r}$. Thus

$$G_{\mathbf{r}} = \frac{\pi}{S} \sum_{\alpha} (\mathbf{v}_{\alpha} - \tilde{\mathbf{w}}_{\mathbf{r}})^2 w_{\mathbf{r}\alpha}. \tag{7.7}$$

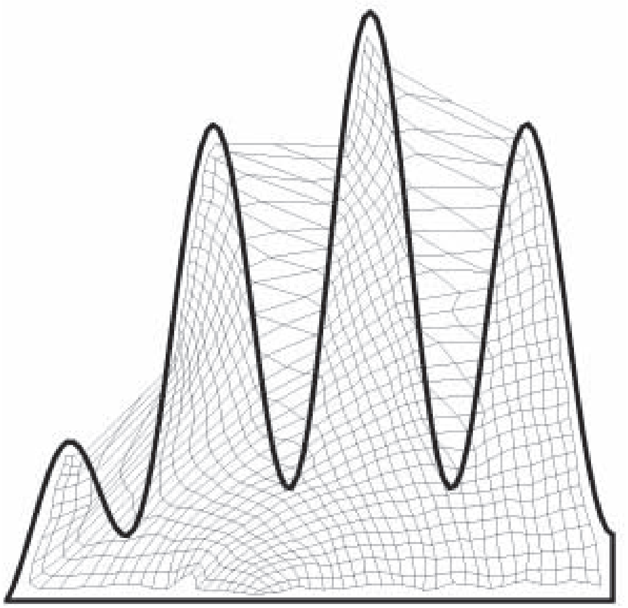


Abb. 7.5: Here, the assignment of Fig. 7.4 is represented as the familiar "imbedding" of the neuron lattice in the space V, i.e., on the hand surface. To this end, each neuron is marked at the position of the center of gravity $\tilde{\mathbf{w}}_{\mathbf{r}}$ of the touch receptors from which it receives input, and the resulting locations are connected by lines if the neurons are adjacent in the lattice.

A touch stimulus at location $\mathbf{v}$ leads to the following change of $G_{\mathbf{r}}$ (we neglect contributions of quadratic order in ϵ)

$$\begin{aligned}\Delta G_{\mathbf{r}} &= \frac{2\pi\epsilon}{S} h_{\mathbf{rs}} \sum_{\alpha} (\tilde{\mathbf{w}}_{\mathbf{r}} - \mathbf{v}_{\alpha}) \cdot (\mathbf{v} - \tilde{\mathbf{w}}_{\mathbf{r}}) w_{\mathbf{r}\alpha} \\ &\quad + \frac{\pi\epsilon}{S} h_{\mathbf{rs}} \sum_{\alpha} (\tilde{\mathbf{w}}_{\mathbf{r}} - \mathbf{v}_{\alpha})^2 (\nu_{\alpha} - w_{\mathbf{r}\alpha}) \\ &= -\epsilon h_{\mathbf{rs}} \left[G_{\mathbf{r}} - \Gamma(\mathbf{v}) - \pi(\tilde{\mathbf{w}}_{\mathbf{r}} - \mathbf{v})^2 \right]. \end{aligned} \tag{7.8}$$

In this equation, we have made the definition

$$\Gamma(\mathbf{v}) := \frac{\pi}{S} \sum_{\alpha} (\mathbf{v} - \mathbf{v}_{\alpha})^2 \nu_{\alpha}. \tag{7.9}$$

One can interpret $\Gamma(\mathbf{v})$ as the surface area of the distribution of touch receptor excitations triggered by the touch stimulus. The expectation value

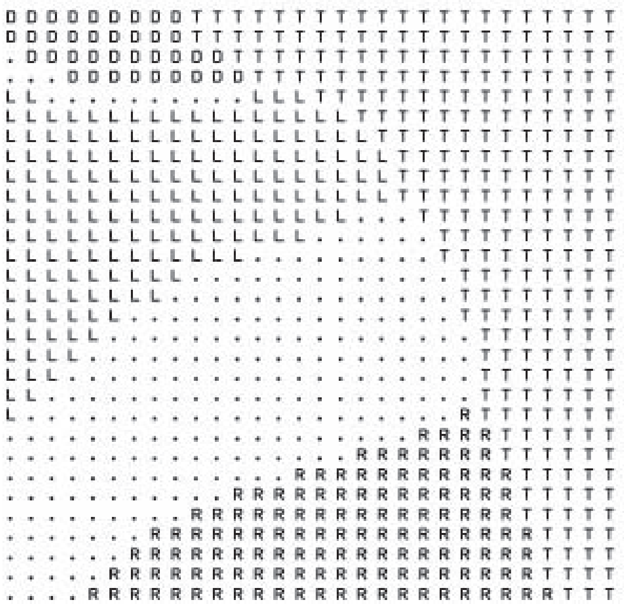


Abb. 7.6: After the map of Fig. 7.4 has been obtained, the middle finger M is “amputated”, i.e., for the rest of the simulation touch stimuli are no longer selected from this region; consequently the neurons designated by dots, which were previously connected to M, are now deprived of their former sensory inputs.

$E(\Delta G_{\mathbf{r}}|G_{\mathbf{r}})$ for the change of $G_{\mathbf{r}}$ is therefore

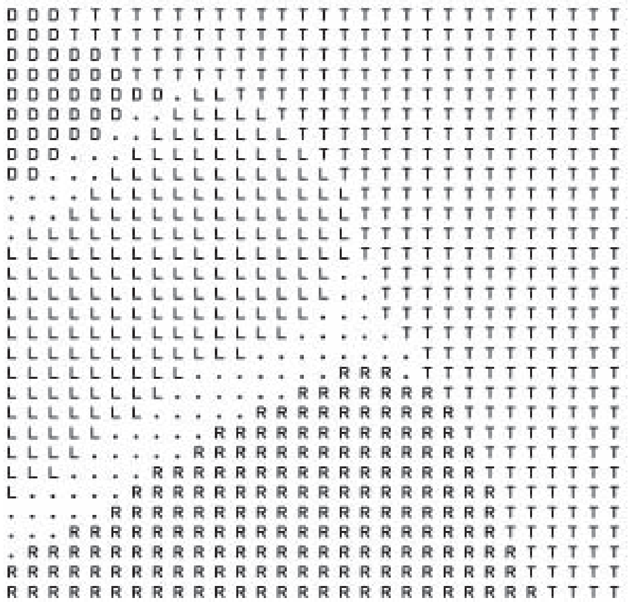
$$E(\Delta G_{\mathbf{r}}|G_{\mathbf{r}}) = -\epsilon \int h_{\mathbf{r}\phi(\mathbf{v})} \Big[G_{\mathbf{r}} - \langle \Gamma(\mathbf{v}) \rangle - \pi(\tilde{\mathbf{w}}_{\mathbf{r}} - \mathbf{v})^2 \Big] P(\mathbf{v}) \, d\mathbf{v}. \tag{7.10}$$

Here, ϕ is the mapping from the hand surface to the neuron lattice, and $\langle \Gamma(\mathbf{v}) \rangle$ is the average excited surface area of the receptor layer due to the touch stimulus at position $\mathbf{v}$. For sufficiently small learning step size ϵ, the resulting asymptotic value $G_{\mathbf{r}}^{\infty}$ of $G_{\mathbf{r}}$ becomes

$$G_{\mathbf{r}}^{\infty} \approx \frac{\int h_{\mathbf{r}\phi(\mathbf{v})} \Big[\langle \Gamma(\mathbf{v}) \rangle + \pi(\tilde{\mathbf{w}}_{\mathbf{r}} - \mathbf{v})^2 \Big] P(\mathbf{v}) \, d\mathbf{v}}{\int h_{\mathbf{r}\phi(\mathbf{v})} P(\mathbf{v}) \, d\mathbf{v}}. \tag{7.11}$$

This permits us to rewrite (7.10) in the more suggestive form

$$E(\Delta G_{\mathbf{r}}|G_{\mathbf{r}}) = -\epsilon \bigg[\int h_{\mathbf{r}\phi(\mathbf{v})} P(\mathbf{v}) \, d\mathbf{v} \bigg] \cdot (G_{\mathbf{r}} - G_{\mathbf{r}}^{\infty}). \tag{7.12}$$



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D D D T T T T T T T T T T T T T T T T T T T T T T T T T T T
D D D T T T T T T T T T T T T T T T T T T T T T T T T T T T
D D D D D T T T T T T T T T T T T T T T T T T T T T T T T T
D D D D D D T T T T T T T T T T T T T T T T T T T T T T T T
D D D D D D D D . L L T T T T T T T T T T T T T T T T T T T
D D D D D D . . L L L L L T T T T T T T T T T T T T T T T T
D D D D D . . L L L L L L L T T T T T T T T T T T T T T T T
D D D . . . L L L L L L L L L T T T T T T T T T T T T T T T
D D . . . L L L L L L L L L L L T T T T T T T T T T T T T T
. . . . L L L L L L L L L L L L L T T T T T T T T T T T T T
. . . L L L L L L L L L L L L L L T T T T T T T T T T T T T
. L L L L L L L L L L L L L L L L T T T T T T T T T T T T T
L L L L L L L L L L L L L L L L L T T T T T T T T T T T T T
L L L L L L L L L L L L L L L L . . T T T T T T T T T T T T
L L L L L L L L L L L L L L L L . . T T T T T T T T T T T T
L L L L L L L L L L L L L L L . . . T T T T T T T T T T T T
L L L L L L L L L L L L L L . . . . . T T T T T T T T T T T
L L L L L L L L L L L L . . . . . . . . T T T T T T T T T T
L L L L L L L L L . . . . . . . R R R . T T T T T T T T T T
L L L L L L L L . . . . . . R R R R R R R T T T T T T T T T
L L L L L L L . . . . . R R R R R R R R R R T T T T T T T T
L L L L L . . . . . R R R R R R R R R R R R T T T T T T T T
L L L L . . . . . R R R R R R R R R R R R R R T T T T T T T
L L L . . . . R R R R R R R R R R R R R R R R T T T T T T T
L . . . . . R R R R R R R R R R R R R R R R R R T T T T T T
. . . . . R R R R R R R R R R R R R R R R R R R T T T T T T
. . . R R R R R R R R R R R R R R R R R R R R R T T T T T T
. R R R R R R R R R R R R R R R R R R R R R R R R T T T T T
R R R R R R R R R R R R R R R R R R R R R R R R R T T T T T
R R R R R R R R R R R R R R R R R R R R R R R R R R T T T T
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Abb. 7.7: After another 50,000 touch stimuli, the map has reorganized itself in such a way that only a few neurons are still silent. The representation of the remaining hand regions D, L, R and T is now distributed over a larger number of neurons and, therefore, possesses a higher spatial resolution than before the "amputation."

We see from (7.12) that on the average the surface area of a receptive field tends exponentially to its asymptotic equilibrium value $G_{\mathbf{r}}^{\infty}$. If any variation of $P(\mathbf{v})$ and $\langle\Gamma(\mathbf{v})\rangle$ occurs only on a much longer spatial scale than $h_{\mathbf{r}\phi(\mathbf{v})}$ and the mapping ϕ conserves angles (*i.e.*, is conformal) at the position $\mathbf{w}_{\mathbf{r}}$, then (7.11) can be simplified further to yield

$$G_{\mathbf{r}}^{\infty} \approx \langle\Gamma(\mathbf{v})\rangle + M^{-1}\pi\sigma^2, \tag{7.13}$$

where the quantity M is the local magnification factor of the mapping ϕ, and $\sigma^2 = \int h_{\mathbf{rs}}(\mathbf{r}-\mathbf{s})^2\, d^2\mathbf{s} / \int h_{\mathbf{rs}}\, d^2\mathbf{s}$. This equation shows that in the present model each neuron restricts its inputs to receptors within an area given by the the sum of two contributions. The first contribution is the average surface area $\langle\Gamma(\mathbf{v})\rangle$ of the excitation distribution in the receptor layer caused by each touch stimulus. The second contribution is the surface area $\pi\sigma^2/M$ of that region in the receptor layer which corresponds, under the mapping ϕ, to a

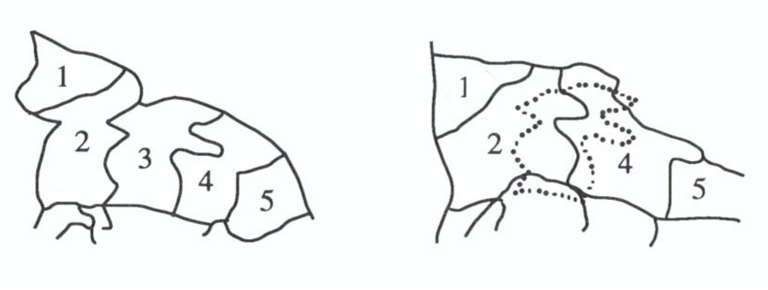

Abb. 7.8: Readaptation of the somatosensory map of the hand region of an adult nocturnal ape due to the amputation of one finger. (a) (left) Before the operation, each finger in the map is represented as one of the regions 1-5. (b) (right) Several weeks after amputation of the middle finger, the assigned region 3 has disappeared, and the adjacent regions have correspondingly spread out (after Fox, 1984).

cortical region of radius σ, *i.e.*, a cortical area the size of which is determined by the spread of the excitation profile $h_{\mathbf{rs}}$. Assuming localized touch stimuli, *i.e.*, small $\langle\Gamma(\mathbf{v})\rangle$, and a short-range excitation response $h_{\mathbf{rs}}$ towards the end of the simulation, the resulting synaptic connections for each neuron become concentrated to receptors of a narrowly focused region.

In this chapter we have shown that the rather abstract organizational principles in Kohonen's algorithm are sufficient to construct a neighborhood preserving connectivity between a receptor layer and a neuron layer from disordered initial connections. The only information driving this process is the stochastic stimulation of the receptors. At the end of the process, every neuron possesses synaptic connections to receptors of a narrowly limited region in the receptor layer. The assignment of neurons to regions preserves mutual neighborhood relations and represents a two-dimensional map of the hand surface. For the formation of this map, it turned out to be immaterial whether the algorithm obtains the information about touch stimuli explicitly in the form of two-dimensional coordinates or instead is directly supplied with high-dimensional receptor activity patterns. This illustrates the ability of the algorithm to automatically extract hidden lower-dimensional information, in this case the stimulus location, from a sequence of high-dimensional signals (the excitation at all the receptors on the hand), and to represent it in a two-dimensional map. In the present case, the dimensions of the implicit information and of the map agree and a continuous mapping results.

7.5 Simulating the High-Dimensional Model on a Parallel Computer

While the main purpose of the preceding sections was the investigation of a model for the self-organized formation of a topographically ordered somatosensory map, they also illustrate a typical methodological difficulty in the investigation of neural models: even if highly abstract approaches are used, such as Kohonen's model of self-organizing maps, the simulation of biological neural nets still requires in many cases an enormous computational effort. The previous sections demonstrate by means of an example how in such a situation a partial mathematical analysis can reduce the simulation effort to a more manageable level. However, such a simplification usually involves additional approximations and thus can no longer describe some properties of the original model. In the case of the somatosensory map, the introduction of the low-dimensional "effective dynamics" by means of ((7.4) does offer the possibility of describing the average size of the receptive fields, but detailed questions concerning the form of receptive fields, such as the possibility of the formation of multiple centers (defined as a cortical neuron receiving input from two or more distinct areas of the hand surface), are excluded through this simplification, although these questions could have been addressed in the framework of the original model.

Therefore, even if there is some possibility of mathematical simplification, the capacity to carry out detailed simulations of the model in its original formulation is desirable. This capacity is offered by a new generation of high-performance computers, whose architecture, interestingly enough, is strongly influenced by the structure of neural systems. One of the most well-known computers of this kind, the "Connection Machine," can use 65,768 one-bit processors in parallel (Hillis 1985).

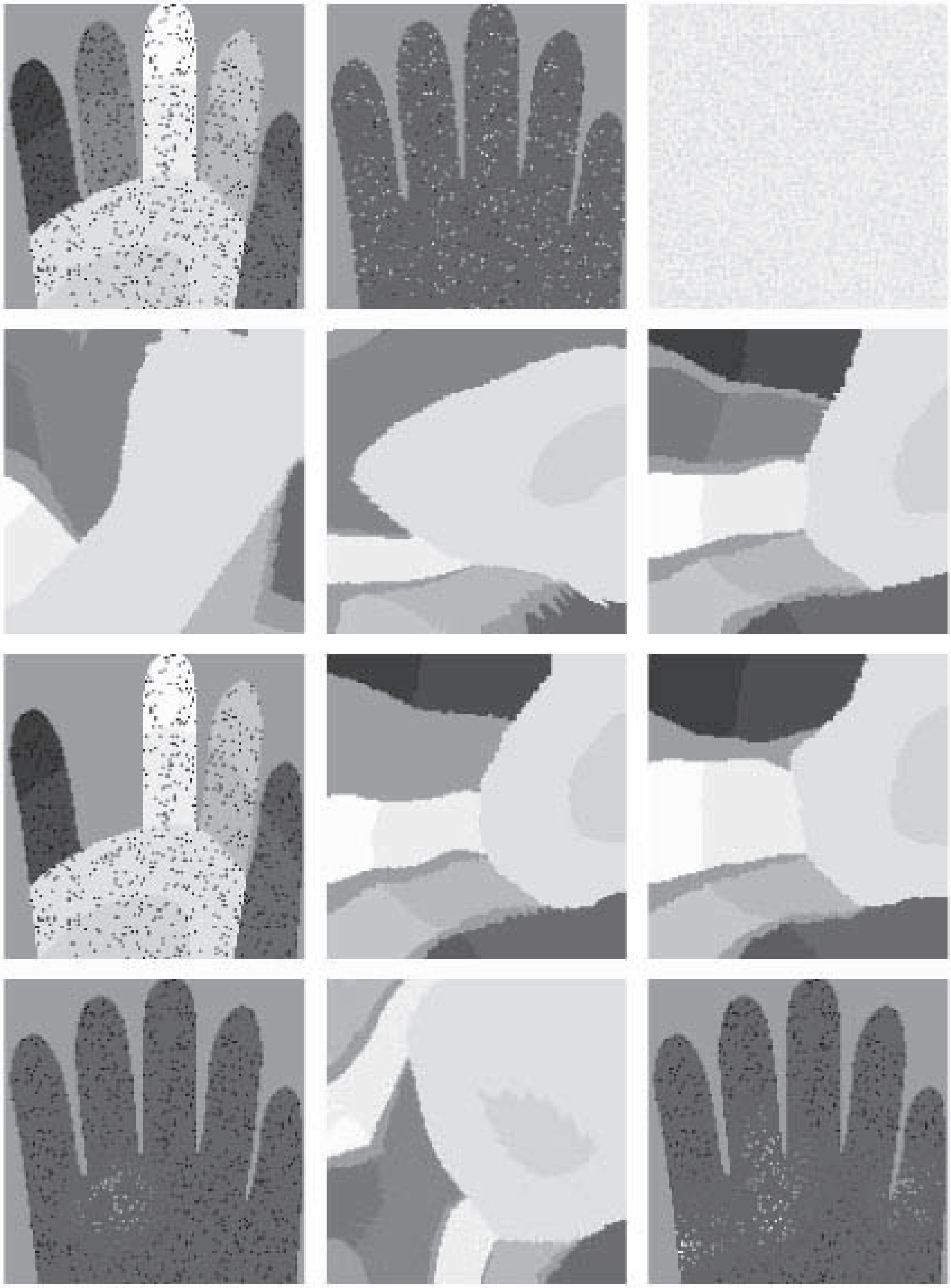

Abb. 7.9: Formation of a somatosensory map. From upper left to lower right: Fig. 7.9a–l. For explanation see Section 7.5.

Each of these processors is equipped with its own memory, and the data communication paths between the processors can be configured by software in such a way as to realize various lattice topologies. This offers the possibility of a very natural and direct "mapping" of neural algorithms and models onto the processors of this computer. In the following section, we report on some results of a simulation of Kohonen's model that were carried out on such a machine (Obermayer, Ritter, and Schulten 1989, 1990a,b).

The simulation again concerns the formation of a somatosensory map. This time, our point of departure is a "model cortex" consisting of 16,384 neurons arranged in a 128×128 square-lattice. Each neuron possesses synaptic connections to 800 touch receptors which are distributed stochastically over the hand surface (see Fig. 7.9a). Each neuron is assigned, along with the 800 values of its synaptic connections, to one processor of the Connection Machine. For each neuron, its 800 connection strengths to the receptors are initialized to independently chosen random values. Figure 7.9b illustrates this for a randomly selected neuron $\mathbf{r}$: each receptor location is marked by a small spot, the brightness of which is proportional to the strength of the connection from the receptor to the selected neuron. The receptor excitation pattern caused by a touch stimulus is assumed to follow in its intensity a Gaussian centered at some location $\mathbf{v}_{stim}$, *i.e.*,

$$\nu_\alpha \quad \propto \quad \exp\Big(-(\mathbf{v}_\alpha - \mathbf{v}_{stim})^2/2a^2\Big).$$

The centers $\mathbf{v}_{stim}$ of the successive touch stimuli are scattered randomly over the complete hand surface. However, in contrast to the model using the "effective dynamics" simplification, every touch stimulus is now described by a 800-dimensional vector $(\nu_1, \nu_2, \ldots, \nu_{800})^T$, and the adaptation process takes place in the space of the 16,384 weight vectors $w_{\mathbf{r}} = (w_{\mathbf{r}1}, w_{\mathbf{r}2}, \ldots, w_{\mathbf{r}800})^T$, each of dimension 800 (for additional details of the simulation, see Obermayer, Ritter, and Schulten 1990a,b).

The figures 7.9c–f show the development of the somatotopic map. Each picture shows a view of the 128×128 model cortex, where each pixel corresponds to one neuron. To identify for each neuron the source of its receptor input, the same gray values as in Fig. 7.9a are used, *i.e.*, the gray value at a location $\mathbf{r}$ indicates which hand region of Fig. 7.9a contains the center of gravity $\tilde{\mathbf{w}}_{\mathbf{r}}$ of the receptors exciting neuron $\mathbf{r}$. The nearly uniform gray in Fig. 7.9c is a consequence of the initially random connectivity: each cell is "diffusely" connected to nearly the complete hand surface and all centers of gravity lie approximately in the central part of the hand surface. After about 200 touch stimuli, a specialization of the neurons begins to emerge (7.9d). After 1200 touch stimuli, this specialization has progressed further, and the correct topographic arrangement is already evident for four of the finger regions. After 10,000 touch stimuli, a complete and well-resolved topographic map of the hand surface has emerged (7.9f). Figs. 7.9g and 7.9h show a repeat of the "amputation experiment" depicted in Figs. 7.6 and 7.7. Figure 7.9g shows the region of the map which is deprived of its former input signals after the "amputation" of a finger. After a further 10,000 adaptive steps, the map has readjusted itself (7.9h) so that the representation of the fingers adjacent to the amputated digit has expanded to partially fill the "silent" region.

Figure 7.9j shows a typical "receptive field" of a cell from the map of Fig. 7.5f. A good spatial localization is discernible, and the extension of the field corresponds approximately to the diameter of the receptor excitation pattern caused by a touch stimulus. Figure 7.9k shows an only partially ordered map from another simulation run. Here, a "doubling" map of the sensory surface has formed. Such maps frequently contain cells the receptive fields of which have multiple centers as shown in Fig. 7.9l. Such cells are also encountered in the somatosensory cortex, but they are apparently rare. The investigation of the formation and the role of such receptive fields is an important motivation for carrying out simulations of this kind.

This aspect is even more evident in more complex maps such as those which occur in the visual cortex. There, signals from two sensory surfaces, the two retinas, are combined into one map. Aside from the information on the spatial location of a light stimulus, "ocularity information," *i.e.*, information about the origin of stimuli from the right or the left eye, as well as information about the orientation of, for example, brightness edges, is represented topographically in the map. This high-dimensional simulation model offers an extremely valuable tool for a theoretical understanding of the formation of such maps. The simulations, again performed on a Connection Machine, yield very close agreement to the visual maps observed in the striate cortex of monkeys, reproducing well the retinotopic characteristics as well as the organization of orientation columns and occularity stripes (see Obermayer, Ritter, and Schulten 1990c; Obermayer, Blasdel, and Schulten 1991).

In the brain such topographically ordered maps serve as the initial processing stages of sensory information. Subsequent cortical areas have the task of re-coding the received information step by step and transforming it into an appropriate form for the eventual control of muscles, which constitute the main output targets of the nervous system. However, in practically all cases, we are still far from understanding most of the phenomena that participate in that process. This is partly due to the fact that we often cannot precisely characterize the processing stages that are involved in the behavior of even simple organisms. For certain stages, however, the situation is a bit less unfavorable, particularly for such aspects of motor coordination that can be described mathematically as control problems or coordinate transformations. In Part III we therefore extend Kohonen's model in a suitable way to enable the solution of such problems. However, it would be improper to seek close biological correspondences. Instead, our intention will be to investigate biologically motivated model assumptions with respect to their performance in solving more complex problems, in particular those that biological nervous systems have to face.