Self-Organized Development of Retinotopic Projections

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Abstract. We use a general model for the development of retinotopic projections between manifolds of different geometries to investigate one- and two-dimensional Euclidean manifolds. The generation of retinotopic projections between two strings turns out to be very similar to the case of discrete linear chains analyzed previously by Häussler and v. d. Malsburg. We show that both for strings and for planes the retinotopic states correspond to stationary solutions of the Häussler equations.

Introduction

Neural connections in the visual system of vertebrates exhibit the essential feature that they conserve neighbourhood relations between different sheets of nerve cells. Neighbouring cells of the retina, e.g., project onto neighbouring cells of the tectum, a part of the brain which plays an important role in processing optical information. Such *retinotopic projections* arise during ontogenesis from rather undifferentiated connections via self-organization.

Other examples of retinotopic projections are the connections between the retina and the corpus geniculatum laterale, and between the retina and the visual cortex. Futhermore there are analogous neural maps in other parts of the nervous system. For example, somatotopy means that neighbouring mechanoreceptors of the skin are connected with neighbouring cells of the somatosensorial cortex. In the case of tonotopy similar frequencies excite neighbouring cells of the auditorial cortex, i.e. a topographic representation of tone frequencies is realized.

Some time ago the development between one-dimensional discrete cell arrays was modelled analytically in detail in Ref. [1]. The case of continuously distributed cells on a spherical shell was partially discussed in Ref. [2].

Our Model

In Ref. [3] we generalized the approach of Häussler and v. d. Malsburg by developing a model which is independent of the special geometry of the problem. Let us start with reviewing the essential ideas and results. The two cell sheets retina and tectum are represented by general manifolds $\mathcal{M}_T$ and $\mathcal{M}_R$, respectively. We define measures for the magnitudes of the manifolds by

$$M_T = \int_t dt, \qquad M_R = \int_r dr.$$

Every ordered pair $(t,r) \in \mathcal{M}_T \times \mathcal{M}_R$ is connected by a *connection weight* $w(t,r)$. The equations of evolution of these connections are assumed to be given by a generalization of the *Häussler equations* [1]:

$$\dot{w}(t,r) = f(t,r,w) - \frac{w(t,r)}{M_T + M_R} \int_{t'} dt' f(t',r,w) - \frac{w(t,r)}{M_T + M_R} \int_{r'} dr' f(t,r',w),$$

where the growth rate of the connection between retina cell r and tectal cell t is given by

$$f(t,r,w) = \alpha + w(t,r) \int_{t'} dt' \int_{r'} dr' c_T(t,t') c_R(r,r') w(t',r').$$

Here α denotes the homogeneous growth-rate of new synapses onto the tectum, and the positive coefficients $c_T(t,t')$, $c_R(r,r')$ represent measures for cooperativity within each manifold. These cooperativity coefficients are normalized and are larger when the points t,t' and r,r' lie closer to each other.

In a next step we define the Laplace-Beltrami operators on the manifolds and solve the eigenvalue problems

$$\Delta_j \psi_{\lambda_j}(x_j) = \chi_{\lambda_j} \psi_{\lambda_j}(x_j),$$

with $j = T,R$ and $x_T = t$, $x_R = r$. By construction the eigenfunctions form a complete orthonormal system, i.e. they fulfill the conditions

$$\int_x dx \psi^*_\lambda(x) \psi_{\lambda'}(x) = \delta_{\lambda\lambda'}, \qquad \sum_\lambda \psi^*_\lambda(x) \psi_\lambda(x') = \delta(x - x').$$

Therefore we can expand the cooperativity coefficients according to

$$c_j(x,x') = \sum_\lambda f^j_\lambda \psi_\lambda(x) \psi^*_\lambda(x').$$

Synergetic Analysis

Using the methods of synergetics [4,5] the system is investigated in the vicinity of the stationary solution $w_0(t,r)$. A linearization of the generalized Häussler equations with respect to the deviation $v(t,r) = w(t,r) - w_0(t,r)$ leads to the eigenvalue problem

$$\hat{L}(t, r, v(t, r)) = \Lambda v(t, r),$$

with a linear operator $\hat{L}$. By changing the control parameter α in a suitable way, some eigenvalues become positive and the system can be driven to the neighbourhood of an instability. In this region the relations hold

$$\Lambda_{\lambda_T^u \lambda_R^u} \approx 0, \qquad \Lambda_{\lambda_T \lambda_R} << 0, \qquad (\lambda_T, \lambda_R) \neq (\lambda_T^u, \lambda_R^u)$$

and consequently

$$\left|\Lambda_{\lambda_T^u \lambda_R^u}\right| << \left|\Lambda_{\lambda_T \lambda_R}\right|, \quad (\lambda_T, \lambda_R) \neq (\lambda_T^u, \lambda_R^u).$$

Therefore we can decompose the deviation $v(t,r)$ close to the instability according to

$$v(t, r) = U(t, r) + S(t, r).$$

Here

$$U(t, r) = \sum_{\lambda_T^u \lambda_R^u} U_{\lambda_T^u \lambda_R^u} \psi_{\lambda_T^u}(t) \psi_{\lambda_R^u}(r)$$

denotes the contribution of the unstable modes and

$$S(t, r) = \sum_{\lambda_T \lambda_R} S_{\lambda_T \lambda_R} \psi_{\lambda_T}(t) \psi_{\lambda_R}(r), \quad (\lambda_T, \lambda_R) \neq (\lambda_T^u, \lambda_R^u)$$

the contribution of the stable modes. The system generates a *time-scale hierarchy,* i.e. the stable modes evolve on a faster time scale than the unstable modes:

$$\tau_u = \frac{1}{|\Lambda_{\lambda_T^u \lambda_R^u}|} >> \tau_s = \frac{1}{|\Lambda_{\lambda_T \lambda_R}|}, \qquad (\lambda_T, \lambda_R) \neq (\lambda_T^u, \lambda_R^u).$$

This leads to the *slaving principle* of synergetics: the stable modes are enslaved by the unstable modes. Thus we can write

$$S_{\lambda_T \lambda_R} = H_{\lambda_T \lambda_R}(U_{\lambda_T^u \lambda_R^u}).$$

By determining the center manifold H the original high-dimensional problem can be reduced to a low-dimensional one for the order parameters U. Applying these methods to the Häussler equations, we obtain (with Einstein's summation convention)

$$\dot{U}_{\lambda_T^u \lambda_R^u} = \Lambda_{\lambda_T^u \lambda_R^u} U_{\lambda_T^u \lambda_R^u} + A^{\lambda_R^u, \lambda_R^{u\prime}, \lambda_R^{u\prime\prime}}_{\lambda_T^u, \lambda_T^{u\prime}, \lambda_T^{u\prime\prime}} U_{\lambda_T^{u\prime} \lambda_R^{u\prime}} U_{\lambda_T^{u\prime\prime} \lambda_R^{u\prime\prime}}$$

$$+ B^{\lambda_R^u, \lambda_R^{u\prime}, \lambda_R^{u\prime\prime}, \lambda_R^{u\prime\prime\prime}}_{\lambda_T^u, \lambda_T^{u\prime}, \lambda_T^{u\prime\prime}, \lambda_T^{u\prime\prime\prime}} U_{\lambda_T^{u\prime} \lambda_R^{u\prime}} U_{\lambda_T^{u\prime\prime} \lambda_R^{u\prime\prime}} U_{\lambda_T^{u\prime\prime\prime} \lambda_R^{u\prime\prime\prime}}.$$

The coefficients *A* and *B* can be expressed in terms of the eigenfunctions and the expansion coefficients $f^{T,R}_{\lambda_{T,R}}$. The coefficients *B* consist of two parts, one stemming from the order parameters themselves and the other representing the influence of the center manifold *H*.

Examples

Specifying the geometry means inserting the corresponding eigenfunctions of the Laplace-Beltrami operators in the order parameter equations.

Strings

The simplest example is given by two one-dimensional manifolds. Instead of discrete cell arrays with the same number of cells, which was treated in [1], here we consider continuously distributed cells on strings of different lengths. Linearizing the Häussler equations around the homogeneous stationary solution $w_0(t,r) = 1$ the eigenfunctions are given by

$$\psi_{\lambda_T}(t) = \frac{1}{\sqrt{L_T}} \exp\left(i \frac{2\pi}{L_T} \lambda_T t \right), \qquad \psi_{\lambda_R}(r) = \frac{1}{\sqrt{L_R}} \exp\left(i \frac{2\pi}{L_R} \lambda_R r \right),$$

with $t \in [0, L_T)$, $r \in [0, L_R)$. The order parameters turn out to follow from a potential dynamics, which reads

$$\dot{U}_{\lambda_T^u \lambda_R^u} = \Lambda_{\lambda_T^u \lambda_R^u} U_{\lambda_T^u \lambda_R^u} + B_1 U^2_{\lambda_T^u \lambda_R^u} U_{-\lambda_T^u - \lambda_R^u} + B_2 U_{\lambda_T^u \lambda_R^u} U_{-\lambda_T^u \lambda_R^u} U_{\lambda_T^u - \lambda_R^u},$$

with real coefficients B_1, B_2. Transformation to real variables leads to constant phase-shift angles. Thus the system can be reduced to two variables, which correspond to the amplitudes of the two diagonal modes. Competition between these two modes leads to the extinction of one of them.

Now we set, for the sake of simplicity, $f^{T,R}_{\lambda_{T,R}} = 0$ if $\lambda_{T,R} \neq 0, \pm 1$. Then the ansatz

$$w_0(t,r) = \sum_{\lambda} \varepsilon^{|\lambda|} \exp\left[i 2\pi \lambda \left(\frac{t}{L_T} \pm \frac{r}{L_R} \right) \right]$$

corresponds to a stationary solution of the Häussler equations. Here ε is given by

$$\varepsilon^2 = \frac{\gamma - \alpha}{\gamma},$$

with $\gamma = f_1^T f_1^R$. For $\alpha = \gamma$ we have the homogeneous state $w_0(t,r) = 1$. By decreasing the control parameter α to zero, the system settles in the long-time limit into a 1-1-retinotopic state, i.e. the connection weights become

$$w_0(t,r) = \delta\left(\frac{t}{L_T} \pm \frac{r}{L_R}\right).$$

Planes

Retina and tectum are represented by planes of lengths L_1^T, L_2^T and L_1^R, L_2^R, respectively, and the measures are given by $M_T = L_1^T L_2^T$, $M_R = L_1^R L_2^R$. Linearizing again around the stationary homogeneous solution $w_0(t,r) = 1$ the eigenfunctions read

$$\psi_{\lambda_T}(t) = \frac{1}{\sqrt{M_T}} \exp\left(i \frac{2\pi}{L_1^T} \lambda_{T1} t_1\right) \exp\left(i \frac{2\pi}{L_2^T} \lambda_{T2} t_2\right),$$

$$\psi_{\lambda_R}(r) = \frac{1}{\sqrt{M_R}} \exp\left(i \frac{2\pi}{L_1^R} \lambda_{R1} r_1\right) \exp\left(i \frac{2\pi}{L_2^R} \lambda_{R2} r_2\right).$$

The unstable modes are given by $\lambda_{T,R}^u = (0, \pm 1), (\pm 1, 0)$. Calculating the order parameter equations shows that the quadratic term vanishes, as in case of strings. Thus we obtain sixteen order parameter equations

$$\dot{U}_{\lambda_T^u \lambda_R^u} = \Lambda_{\lambda_T^u \lambda_R^u} U_{\lambda_T^u \lambda_R^u} + B^{\lambda_R^u, \lambda_R^{u\prime}, \lambda_R^{u\prime\prime}, \lambda_R^{u\prime\prime\prime}}_{\lambda_T^u, \lambda_T^{u\prime}, \lambda_T^{u\prime\prime}, \lambda_T^{u\prime\prime\prime}} U_{\lambda_T^{u\prime}, \lambda_R^{u\prime}} U_{\lambda_T^{u\prime\prime}, \lambda_R^{u\prime\prime}} U_{\lambda_T^{u\prime\prime\prime}, \lambda_R^{u\prime\prime\prime}}.$$

The cubic terms contain only those which fulfill the conditions

$$\lambda_{T,R}^{u'} + \lambda_{T,R}^{u''} + \lambda_{T,R}^{u'''} = \lambda_{T,R}^{u}.$$

This reduces the number of cubic terms in the order parameter equations to fourteen. By analogy with the string we assume for simplicity

$$f_{\lambda_{T,R}}^{T,R} = 0, \qquad \lambda_{T,R} \neq (0,0), (\pm 1,0), (0,\pm 1),$$

and set $L_1^{T,R} = L_2^{T,R} = L$. Then the retinotopic states turn out to be stationary solutions of the Häussler equations for the plane. For example, the ansatz

$$w_0(t,r) = \sum_{\lambda,\lambda'} \varepsilon^{|\lambda|+|\lambda'|} \exp\left[i \frac{2\pi}{L} \lambda (t_1 - r_1) \right] \exp\left[i \frac{2\pi}{L} \lambda' (t_2 - r_2) \right]$$

leads to

$$\varepsilon^2 = \frac{\gamma^{10,10} + \gamma^{01,01} - \alpha}{\gamma^{10,10} + \gamma^{01,01}},$$

with $\gamma^{10,10} = f_{10}^T \; f_{10}^R$. In particular $\varepsilon = 0$ for $\alpha = \gamma^{10,10} + \gamma^{01,01}$, which corresponds to the homogeneous state $w_0(t,r) = 1$. Reducing α to zero leads to the retinotopic state

$$w_0(t,r) = L^2 \delta(t_1 - r_1) \delta(t_2 - r_2).$$

There are in total eight retinotopic states, which correspond to all possible combinations between the retina- and tectum coordinates, e.g.

$$w_0(t,r) = L^2 \delta(t_1 - r_2) \delta(t_2 + r_1).$$

The state which is finally realized is a result of the competition between the sixteen unstable modes and depends on the initial conditions. The retinotopic states of the plane turn out to be products of the corresponding retinotopic states of the strings. But with regard to the order parameter equations it should be emphasized that there is no trivial decoupling into two strings. In particular we have no constant phase-shift angles, and therefore the number of variables cannot be reduced.

The extension of this approach to spherical and pseudospherical geometries is in progress.

References

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