Self-Organized Formation of Retinotopic Projections Between Manifolds of Different Geometries – Part 3: Spherical Geometries

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We follow our general model in Ref. [3] and analyze the formation of retinotopic projections for the biologically relevant situation of spherical geometries. To this end we elaborate both a linear and a nonlinear synergetic analysis which results in order parameter equations for the dynamics of connection weights between two spherical cell sheets. We show that these equations of evolution provide stable stationary solutions which correspond to retinotopic modes. A further analysis of higher modes furnishes proof that our model describes the emergence of a perfect one-to-one retinotopy between two spheres.

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I. INTRODUCTION

An essential precondition for a correct operation of the nervous system consists in well-ordered neural connections between different cell sheets. An example, which has been explored both experimentally and theoretically in detail, is the formation of ordered projections between retina and tectum, a part of the brain which plays an important role in processing optical information [1]. At an initial stage of ontogenesis, retinal ganglion cells have random synaptic contacts with the tectum. In the adult animal, however, a so-called retinotopic projection is realized: Neighboring cells of the retina project onto neighboring cells of the tectum. A detailed analytical treatment of Häussler and von der Malsburg described these ontogenetic processes in terms of self-organization [2]. In that work retina and tectum were treated as one-dimensional discrete cell arrays. The dynamics of the connection weights between retina and tectum were assumed to be governed by the so-called Häussler equations. In Ref. [3] we generalized these equations of evolution to continuous manifolds of arbitrary geometry and dimension. Furthermore, we performed an extensive synergetic analysis [4, 5] near the instability of stationary uniform connection weights between retina and tectum. The resulting generic order parameter equations served as a starting point for analyzing retinotopic projections between Euclidean manifolds in Ref. [6]. Our results for strings turned out to be analogous to those for discrete linear chains, i.e. our model included the special case of Häussler and von der Malsburg [2]. Additionally, we could show in the case of planar geometries that superimposing two modes under suitable conditions provides a state with a pronounced retinotopic character.

In this paper we apply our general model [3] again to projections between two-dimensional manifolds. Now, however, we consider manifolds with constant positive curvature. Typically, the retina represents approximately a hemisphere, whereas the tectum has an oval form [1]. Thus, it is biologically reasonable to model both cell sheets by spherical manifolds. Without loss of generality we assume that the two cell sheets for retina and tectum are represented by the surfaces of two unit spheres, respectively. Thus, in our model, the corresponding continuously distributed cells are represented by unit vectors \( \hat{r} \) and \( \hat{t} \). Every ordered pair \((\hat{t}, \hat{r})\) is connected by a positive connection weight \( w(\hat{t}, \hat{r}) \) as is illustrated in Figure 1. The generalized Häussler equations of Ref. [3] for these connection weights are specified as follows

\[
\dot{w}(\hat{t}, \hat{r}) = f(\hat{t}, \hat{r}, w) - \frac{w(\hat{t}, \hat{r})}{8\pi} \int d\Omega' f(\hat{t}', \hat{r}, w) - \frac{w(\hat{t}, \hat{r}')}{8\pi} \int d\Omega' f(\hat{t}, \hat{r}', w). \tag{1}
\]
FIG. 1: The cells of retina and tectum, which are assumed to be continuously distributed on unit spheres, are represented by their unit vectors \( \hat{r} \) and \( \hat{t} \), respectively. The two cell sheets are connected by positive connection weights \( w(\hat{t}, \hat{r}) \).

The first term on the right-hand side describes cooperative synaptic growth processes, and the other terms stand for corresponding competitive growth processes. The total growth rate is defined by

\[
f(\hat{t}, \hat{r}, w) = \alpha + w(\hat{t}, \hat{r}) \int d\Omega_t \int d\Omega_r c_T(\hat{t} \cdot \hat{t}^\prime) c_R(\hat{r} \cdot \hat{r}^\prime) w(\hat{t}^\prime, \hat{r}^\prime),
\]

where \( \alpha \) denotes the global growth rate of new synapses onto the tectum, and is the control parameter of our system. The cooperativity functions \( c_T(\hat{t} \cdot \hat{t}^\prime) \), \( c_R(\hat{r} \cdot \hat{r}^\prime) \) represent the neural connectivity within each manifold. They are assumed to be positive, symmetric with respect to their arguments, and normalized. The integrations in (1) and (2) are performed over all points \( \hat{t}, \hat{r} \) on the manifolds, where \( d\Omega_t, d\Omega_r \) represent the differential solid angles of the corresponding unit spheres. Note that the factors \( 8\pi \) in Eq. (1) are twice the measure \( M \) of the unit sphere, which is given by

\[
M = \int d\Omega_t = \int d\Omega_r = 2\pi \int_0^\pi \int_0^{2\pi} \sin \vartheta d\vartheta d\varphi = 4\pi.
\]

If the global growth rate of new synapses onto the tectum \( \alpha \) is large enough, the long-time dynamics is determined by a uniform connection weight. However, we shall see within a linear analysis in Section [II] that this stationary solution becomes unstable at a critical value of the global growth rate. Therefore, we have to perform a nonlinear synergetic analysis, in Section [III] which yields the underlying order parameter equations in the vicinity of this bifurcation. As in the case of Euclidean manifolds, we show that they have no quadratic terms, represent a potential dynamics, and allow for retinotopic modes. In Section [IV] we include the influence of higher modes upon the connection weights, which leads to recursion relations for the corresponding amplitudes. If we restrict ourselves to special cooperativity functions, the resulting recursion relations can be solved analytically by using the method of generating functions. As a result of our analysis we obtain a perfect one-to-one retinotopy if the global growth rate \( \alpha \) is decreased to zero.

II. LINEAR ANALYSIS

According to the general reasoning in Ref. [3] we start with fixing the metric on the manifolds and determine the eigenfunctions of the corresponding Laplace-Beltrami operator. Afterwards, we expand the cooperativity functions with respect to these eigenfunctions and perform a linear analysis of the stationary uniform state.

A. Laplace-Beltrami Operator

For the time being we neglect the distinction between retina and tectum, because the following considerations are valid for both manifolds. Using spherical coordinates, we write the unit vector on the sphere as
\( x = (\sin \vartheta \cos \varphi, \sin \vartheta \sin \varphi, \cos \vartheta) \). The Laplace-Beltrami operator on a manifold reads quite generally 

\[
\Delta = \frac{1}{\sqrt{g}} \partial_\lambda \left( g^{\lambda \mu} \sqrt{g} \partial_\mu \right). 
\]  

(4)

For the sphere the components of the covariant tensor \( g_{\mu\nu} \) are

\[
g_{11} = \left( \frac{\partial \hat{x}}{\partial \vartheta} \right)^2 = 1, \quad g_{12} = g_{21} = \frac{\partial \hat{x}}{\partial \vartheta} \frac{\partial \hat{x}}{\partial \varphi} = 0, \quad g_{22} = \left( \frac{\partial \hat{x}}{\partial \varphi} \right)^2 = \sin^2 \vartheta. 
\]

(5)

With this the determinant of the covariant metric tensor reads \( g = \sin^2 \vartheta \) and the components of the contravariant metric are given by

\[
g^{11} = 1, \quad g^{12} = g^{21} = 0, \quad g^{22} = \frac{1}{\sin^2 \vartheta}, 
\]

whence the Laplace-Beltrami operator for the sphere takes the well-known form

\[
\Delta_{\vartheta,\varphi} = \frac{1}{\sin \vartheta} \frac{\partial}{\partial \vartheta} \left( \sin \vartheta \frac{\partial}{\partial \vartheta} \right) + \frac{1}{\sin^2 \vartheta} \frac{\partial^2}{\partial \varphi^2}. 
\]

(7)

Its eigenfunctions are known to be given by spherical harmonics \( Y_{lm}(\hat{x}) \):

\[
\Delta_{\vartheta,\varphi} Y_{lm}(\hat{x}) = -l(l+1)Y_{lm}(\hat{x}). 
\]

(8)

With \( l = 0, 1, 2, \ldots \) and \( m = -l, -l+1, \ldots, l-1, l \) they are \((2l+1)\)-fold degenerate and form a complete orthonormal system on the unit sphere:

\[
\int d\Omega_x Y_{lm}(\hat{x}) Y_{l'm'}(\hat{x}) = \delta_{ll'} \delta_{mm'}, \quad \sum_{l=0}^{\infty} \sum_{m=-l}^{l} Y_{lm}(\hat{x}) Y_{lm}(\hat{x'}) = \delta(\hat{x} - \hat{x'}). 
\]

(9) \hspace{1cm} (10)

**B. Cooperativity Functions**

The argument of the cooperativity functions \( c(\hat{x} \cdot \hat{x'}) \) is the scalar product \( \hat{x} \cdot \hat{x'} \) which takes values between \(-1\) and \(+1\). Therefore the cooperativity functions can be expanded in terms of Legendre functions \( P_l(\hat{x} \cdot \hat{x'}) \), which form a complete orthogonal system on this interval [2.721.1]:

\[
\int_{-1}^{1} P_l(\sigma) P_{l'}(\sigma') d\sigma = \frac{2}{2l+1} \delta_{ll'}, 
\]

(11)

\[
\frac{1}{2} \sum_{l=0}^{\infty} (2l+1) P_l(\sigma') P_l(\sigma) = \delta(\sigma - \sigma'). 
\]

(12)

Then the expansion of the cooperativity functions read

\[
c(\hat{x} \cdot \hat{x'}) = \sum_{l=0}^{\infty} \frac{2l+1}{4\pi} f_l P_l(\hat{x} \cdot \hat{x'}), 
\]

(13)

where \( f_l \) denote the respective expansion coefficients. Using the Legendre addition theorem [13]

\[
P_l(\hat{x} \cdot \hat{x'}) = \frac{4\pi}{2l+1} \sum_{m=-l}^{l} Y_{lm}(\hat{x}) Y_{lm}(\hat{x'}), 
\]

(14)

we arrive, for each manifold, at the expansion

\[
c_T(\hat{t} \cdot \hat{t'}) = \sum_{L=0}^{\infty} \sum_{M=-L}^{L} f_{LM}^{T}(\hat{t}) Y_{LM}(\hat{t'}) Y_{LM}^{*}(\hat{t'}), \quad c_R(\hat{r} \cdot \hat{r'}) = \sum_{L=0}^{\infty} \sum_{M=-L}^{L} f_{LM}^{R}(\hat{r}) Y_{LM}(\hat{r'}) Y_{LM}^{*}(\hat{r'}). 
\]

(15)

Note that the normalization of the cooperativity functions and the orthonormality relations [9] lead to the constraints \( f_{00}^{T} = f_{00}^{R} = 1 \).
C. Eigenvalues

The initial state of ontogenesis with randomly distributed synaptic contacts is described by the stationary uniform solution of the generalized Häussler equations, \( u_0(\hat{t}, \hat{r}) = 1 \). Its stability is analyzed by linearizing the Häussler equations with respect to the deviation \( v(\hat{t}, \hat{r}) = w(\hat{t}, \hat{r}) - u_0(\hat{t}, \hat{r}) \). The resulting linearized equations read

\[
\dot{v}(\hat{t}, \hat{r}) = \hat{L}(\hat{t}, \hat{r}, v)
\]

with the linear operator

\[
\hat{L}(\hat{t}, \hat{r}, v) = -\alpha v(\hat{t}, \hat{r}) - \frac{1}{8\pi} \int d\Omega \nu \left[ v(\hat{t}', \hat{r}) + \int d\Omega' \int d\Omega'' c_T(\hat{t} \cdot \hat{v}'') c_R(\hat{r} \cdot \hat{r}'') v(\hat{t}'', \hat{r}'') \right]
\]

\[
- \frac{1}{8\pi} \int d\Omega \nu \left[ v(\hat{t}, \hat{r}') + \int d\Omega' \int d\Omega'' c_T(\hat{t} \cdot \hat{v}'') c_R(\hat{r} \cdot \hat{r}'') v(\hat{t}'', \hat{r}'') \right] + \int d\Omega \nu \int d\Omega' c_T(\hat{t} \cdot \hat{v}') c_R(\hat{r} \cdot \hat{r}') v(\hat{t}', \hat{r}').
\]

To solve Eq. (16), we have to consider the eigenvalue problem of the linear operator (17). It has the eigenfunctions

\[
v_{LM}^{Mm}(\hat{t}, \hat{r}) = Y_L^T(\hat{t}) Y_M^R(\hat{r})
\]

and the spectrum of eigenvalues reads (3):

\[
\Lambda_{LM}^{m} = \left\{ \begin{array}{ll}
-\alpha - 1 & L = M = l = m = 0 \\
-\alpha + (f_L^T f_R^T - 1)/2 & L = M = 0, (l, m) \neq (0, 0) \\
-\alpha + f_L^T f_R^T & l = m = 0, (L, M) \neq (0, 0) \\
& \text{otherwise}
\end{array} \right.
\]

By changing the uniform growth rate \( \alpha \) in a suitable way, the real parts of some eigenvalues become positive and the system can be driven to the neighborhood of an instability. Which eigenvalues become unstable in general depends on the respective values of the given expansion coefficients \( f_L^T, f_R^R \). If we assume monotonically decreasing expansion coefficients \( f_L^T, f_R^R \),

\[
1 = f_1^T \geq f_2^T \geq \cdots \geq 0, \quad 1 = f_0^R \geq f_1^R \geq f_2^R \geq \cdots \geq 0
\]

the maximum eigenvalue in (19) is given by \( \lambda_{\text{max}} = \Lambda_{11} = -\alpha + f_1^T f_1^R \). Thus, the instability occurs when the global growth rate reaches its critical value \( \alpha_c = f_1^T f_1^R \). At this instability point all nine modes with \( (L^u, l^u) = (1, 1) \) and \( M^u = 0, \pm 1, m^u = 0, \pm 1 \) become unstable, where we have introduced the index \( u \) for the unstable modes.

III. NONLINEAR ANALYSIS

In this section we specialize the generic order parameter equations of Ref. [3] to unit spheres. We observe that the quadratic term vanishes and derive selection rules for the appearance of cubic terms. Furthermore, we essentially simplify the calculation of the order parameter equations by taking into account the symmetry properties of the cubic terms. We show that the order parameter equations represent a potential dynamics, and determine the underlying potential.

A. General Structure of Order Parameter Equations

The linear stability analysis motivates treating the nonlinear Häussler equations near the instability by decomposing the deviation \( v(\hat{t}, \hat{r}) = w(\hat{t}, \hat{r}) - u_0(\hat{t}, \hat{r}) \) in unstable and stable contributions,

\[
v(\hat{t}, \hat{r}) = U(\hat{t}, \hat{r}) + S(\hat{t}, \hat{r}).
\]

Using Einstein’s sum convention the expansion of the unstable modes reads

\[
U(\hat{t}, \hat{r}) = U_{11}^{M^u m^u} Y_{LM}^T(\hat{t}) Y_{im}^R(\hat{r}),
\]

and, correspondingly, the contribution of the stable modes is given by

\[
S(\hat{t}, \hat{r}) = S_{11}^{M^u m^u} Y_{LM}^T(\hat{t}) Y_{im}^R(\hat{r}).
\]
Note that the summation in Eq. 28 is performed over all parameters \((L, l)\) except for \((L^u, l^u) = (1, 1)\), i.e. from now on the parameters \((L, l)\) stand for the stable modes alone. With the help of the slide principle of synergetics the original high-dimensional system can be reduced to a low-dimensional one which only contains the unstable amplitudes. The resulting order parameter equations read

\[
U^{M^u m^u} = \Lambda U^{M^u m^u} + A^{m^u m^u m^u} U^{m^u m^u m^u} U^{M^u m^u m^u} B^{m^u m^u m^u m^u m^u} U^{m^u m^u m^u} U^{M^u m^u m^u} U^{M^u m^u m^u} \ . \tag{24}
\]

They contain, as usual, a linear, a quadratic, and a cubic term of the order parameters. The corresponding coefficients can be expressed in terms of the expansion coefficients \(f_L^T, J_R^T\) of the cooperativity functions \(J^M\) and integrals over products of the eigenfunctions \(Y_{lm}(\hat{x})\):

\[
I_{l(l(1)) \ldots (l(n))}^{m(m(1)) \ldots (m(n))} = \int d\Omega x Y_{lm}^*(\hat{x}) Y_{l(1)(m(1))}(\hat{x}) Y_{l(2)(m(2))}(\hat{x}) \ldots Y_{l(n)(m(n))}(\hat{x}) , \tag{25}
\]

\[
J_{l(l(1)) \ldots (l(n))}^{m(m(1)) \ldots (m(n))} = \int d\Omega x Y_{l(1)(m(1))}(\hat{x}) Y_{l(2)(m(2))}(\hat{x}) \ldots Y_{l(n)(m(n))}(\hat{x}) . \tag{26}
\]

The quadratic coefficients read

\[
A^{m^u m^u m^u m^u m^u} = f_T^T J_R^T I_{1,1,1}^{M^u, M^u, M^u, m^u, m^u} I_{1,1,1}^{m^u, m^u, m^u, m^u, m^u} , \tag{27}
\]

whereas the cubic coefficients are

\[
B^{m^u m^u m^u m^u m^u m^u m^u m^u m^u m^u} = -\frac{1}{8\pi} f_T^T f_R^T \left( I_{1,1,1}^{M^u, M^u, M^u, M^u, M^u, m^u, m^u} \delta_{m^u, m^u} J_{1,1}^{m^u, m^u} + I_{1,1,1}^{m^u, m^u, m^u, m^u, m^u, m^u, m^u, m^u} \delta_{m^u, M^u, M^u} J_{1,1}^{m^u, m^u, m^u, m^u} \right) + \left( f_T^T f_R^T + f_R^T f_T^T \right) I_{1,1,1}^{M^u, M^u, M^u, m^u, m^u} \frac{1}{4\sqrt{\pi}} \left[ \delta_{L0} \delta_{M0} \delta_{M^u, M^u} \delta_{M^u, M^u, M^u} \delta_{M^u, M^u, M^u, M^u} + \delta_{L0} \delta_{m^u, m^u} \frac{1}{1 + f_T^T} I_{1,1,1}^{m^u, m^u, m^u, m^u, m^u, m^u, m^u, m^u, m^u, m^u, m^u} \right] \ . \tag{28}
\]

Note that Eq. 28 involves a summation over all stable modes \((L, M; l, m)\). As is common in synergetics, the cubic coefficients 28 consist in general of two parts, one stemming from the order parameters themselves and the other representing the influence of the center manifold \(H\) on the order parameter dynamics according to

\[
S_{L1}^{M^u m^u} = H_{L1}^{M^u m^u m^u m^u} U^{M^u m^u} U^{M^u m^u} . \tag{29}
\]

Here the center manifold coefficients \(H_{L1}^{M^u m^u m^u m^u m^u}\) are defined by

\[
H_{L1}^{M^u m^u m^u m^u m^u} = \frac{f_T^T f_R^T}{2\Lambda - \Lambda_{L1}} I_{1,1,1}^{M^u, M^u, M^u, m^u, m^u} I_{1,1,1}^{m^u, m^u, m^u, m^u, m^u} - \frac{1}{4\sqrt{\pi}} \left( J_{1,1,1}^{M^u, m^u, m^u, m^u, m^u} I_{1,1,1}^{m^u, m^u, m^u, m^u, m^u} \delta_{L0} + J_{1,1,1}^{m^u, m^u, m^u, m^u, m^u} I_{1,1,1}^{M^u, m^u, m^u, m^u, m^u} \delta_{L0} \right) . \tag{30}
\]

\[
B^{m^u m^u m^u m^u m^u m^u m^u m^u m^u m^u} = \left( -1 \right)^m \delta_{m^u, m^u} \ . \tag{31}
\]

\[
Y_{l-m}(\hat{x}) = \left( -1 \right)^m Y^{*}_{lm}(\hat{x}) , \tag{32}
\]

\[
Y_{l_1, m_1}(\hat{x}) Y_{l_2, m_2}(\hat{x}) = \sum_{l_3 = |l_1 - l_2|}^{l_1 + l_2} \sum_{m_3 = |m_1 - m_2|}^{l_3} \sqrt{\frac{2(l_1 + 1)(2l_2 + 1)}{4\pi(2l_3 + 1)}} C(l_1, 0, l_2, 0 | l_3, 0) C(l_1, m_1, l_2, m_2 | l_3, m_3) Y_{l_3, m_3}(\hat{x}) , \tag{33}
\]

B. Integrals

The order parameter equations contain the following integrals: \(J^{m^u m^u}_{1,1,1}, J^{m^u m^u m^u}_{1,1,1}, J^{m^u m^u m^u}_{1,1,1}, I^{m^u m^u m^u}_{1,1,1}, I^{m^u m^u m^u m^u}_{1,1,1}, I^{m^u m^u m^u m^u m^u m^u m^u m^u m^u m^u}_{1,1,1}\). The first integral is obtained by the orthonormality relation 12 and

\[
Y_{l-m}(\hat{x}) = \left( -1 \right)^m \delta_{m^u, m^u} \ . \tag{31}
\]
where $C(l_1, m_1, l_2, m_2|l_3, m_3)$ represent the Clebsch-Gordan coefficients [10]. Applying [32] to integrals over three spherical harmonics leads to

$$I_{l',l''}^{m,m''} = \sqrt{\frac{(2l'+1)(2l''+1)}{4\pi(2l+1)}} C(l',0,l'',0|l,0) C(l',m',l'',m''|l,m).$$  \tag{33}$$

For $l' = l'' = 1$ it follows

$$I_{1,1}^{m,m''} = \frac{3}{\sqrt{4\pi(2l+1)}} C(1,0,1,0|l,0) C(1, m', 1, m''|l,m).$$ \tag{34}$$

As the Clebsch-Gordan coefficients $C(l_1,0,l_2,0|l_3,0)$ vanish if the sum $l_1 + l_2 + l_3$ is odd [10], we obtain $I_{1,1}^{m,m''} = 0$. Thus, the quadratic contribution [27] to the order parameter equations [24] vanishes, by analogy with Euclidean manifolds [8]. Furthermore, non-vanishing integrals [34] can only occur for $l = 0$ and $l = 2$. For $l = 0$ we obtain from the Clebsch-Gordan coefficients [10] the result

$$I_{0,11}^{m,m''} = \frac{(-1)^m}{\sqrt{4\pi}} \delta_{m',m''}. \tag{35}$$

For $l = 2$ we find, correspondingly, the nonvanishing integrals

$$I_{2,11}^{0,00} = \frac{1}{\sqrt{4\pi}}, \quad I_{2,11}^{0,01} = \frac{1}{\sqrt{5\pi}}, \quad I_{2,11}^{0,10} = \frac{1}{\sqrt{4\pi}}, \quad I_{2,11}^{0,11} = \frac{1}{\sqrt{20\pi}},$$

$$I_{2,11}^{2,10} = I_{2,11}^{1,01} = I_{2,11}^{2,10} = \frac{3}{2\sqrt{15\pi}}, \quad I_{2,11}^{2,11} = \frac{3}{\sqrt{30\pi}}, \quad I_{2,11}^{2,21} = -\frac{3}{\sqrt{30\pi}}. \tag{36}$$

Furthermore, the integrals $I_{1,1l}^{m,m''}$ follow from

$$I_{1,1l}^{m,m''} = (-1)^{m'} \delta_{m''} I_{l,11}^{m',-m} \tag{37}$$

Integrals over four spherical harmonics can also be calculated with the help of [32], and the result is

$$I_{l'l''l'''l''''}^{m,m''m''m''} = \sum_{l_3=|l'-l''|}^{l_3} \sum_{m_3=-l_3}^{l_3} \sqrt{\frac{(2l'+1)(2l''+1)(2l'''+1)(2l''''+1)}{4\pi(2l_3+1)}} C(l',0,l'',0|l_3,0) C(l'',m'',l''',m''''|l_3,m_3) I_{l,l'l''l'''}^{m,m''m''m''}. \tag{38}$$

Specializing [38] to $l = l' = l'' = l''' = 1$ and taking into account [38] leads to $I_{1,111}^{m,m''m''m''} \propto \delta_{m'+m''+m'''}m$. Thus, we obtain the selection rule that the nonvanishing integrals $I_{1,111}^{m,m''m''m''}$ fulfill the condition $m' + m'' + m''' = m$. The detailed evaluation yields for those the respective values

$$I_{1,111}^{0,000} = \frac{9}{20\pi}, \quad I_{1,111}^{0,110} = I_{1,111}^{0,110} = I_{1,111}^{0,110} = I_{1,111}^{0,101} = I_{1,111}^{0,011} = I_{1,111}^{0,011} = \frac{3}{20\pi},$$

$$I_{1,111}^{1,010} = I_{1,111}^{0,100} = I_{1,111}^{1,010} = I_{1,111}^{1,010} = I_{1,111}^{1,010} = I_{1,111}^{1,010} = \frac{3}{20\pi},$$

$$I_{1,111}^{1,111} = I_{1,111}^{1,111} = I_{1,111}^{1,111} = I_{1,111}^{1,111} = I_{1,111}^{1,111} = I_{1,111}^{1,111} = \frac{3}{10\pi}. \tag{39}$$

### C. Order Parameter Equations

To simplify the calculation of the cubic coefficients [28] in the order parameter equations [24], we perform some basic considerations which lead to helpful symmetry properties. To this end we start with replacing $m''$ by $-m''$. Using Eq. (31) we obtain $I_{1,111}^{m,m''m''m''} = I_{1,111}^{m,-m''-m'''}$. Corresponding symmetry relations can also be derived for the other terms in [28]. Therefore, we conclude that the order parameter equation for $U_{-M''-m''}$ is obtained from
that of $U^M m^n$ by negating all indices $M^n$ and $m^n$ with unchanged factors. Thus, instead of explicitly calculating nine order parameter equations, it is sufficient to restrict oneself determining the order parameter equations for $U^{00}$, $U^{10}$, $U^{01}$, and $U^{11}$. The remaining five order parameter equations follow instantaneously from those by applying the symmetry relations. With this the order parameter equations result in

\[
\begin{aligned}
\dot{U}^{00} &= \Lambda U^{00} + \beta_1 (U^{00})^3 - 2\beta_2 U^{00}U^{10} - 2\gamma U^{00}U^{01} + 2\beta_3 U^{00}U^{11} - 2\gamma U^{00}U^{11}, \\
\dot{U}^{11} &= \Lambda U^{11} + \beta_4 U^{01}U^{00} + \beta_5 (U^{01})^2 U^{11} + \beta_6 U^{01}U^{11} + \beta_7 U^{01}U^{11} + \beta_8 (U^{11})^2 U^{11}, \\
\dot{U}^{01} &= \Lambda U^{01} + \beta_4 U^{01}U^{00} + \beta_5 (U^{01})^2 U^{11} + \beta_6 U^{01}U^{11} + \beta_7 U^{01}U^{11} + \beta_8 (U^{11})^2 U^{11}, \\
\dot{U}^{10} &= \Lambda U^{10} + \beta_4 U^{10}U^{00} + \beta_5 (U^{10})^2 U^{11} - 2\beta_3 U^{10}U^{11} + \beta_4 U^{10}U^{11} + \beta_7 U^{10}U^{11} - 2\beta_3 U^{10}U^{11}, \\
\dot{U}^{01} &= \Lambda U^{01} + \beta_4 U^{01}U^{00} + \beta_5 (U^{01})^2 U^{11} + \beta_6 U^{01}U^{11} + \beta_7 U^{01}U^{11} + \beta_8 (U^{11})^2 U^{11}.
\end{aligned}
\]

With the abbreviations $\tilde{\gamma} = \gamma/\pi^2$, $\gamma = f^T J f$ and $\gamma^L = f^T J^L f$, the respective coefficients in (40) read

\[
\begin{aligned}
\beta_1 &= -\frac{9}{80} \tilde{\gamma} + \frac{2\gamma + \gamma^2}{2} + \frac{\gamma}{2} + \frac{\gamma^2}{2} - 1 + \frac{\gamma}{25} + \frac{\gamma + \gamma^2}{2}, \\
\beta_2 &= -\frac{9}{80} \tilde{\gamma} + \frac{2\gamma + \gamma^2}{2} + \frac{\gamma}{2} + \frac{\gamma^2}{2} - 1 + \frac{\gamma}{25} + \frac{\gamma + \gamma^2}{2}, \\
\beta_3 &= -\frac{3}{40} \tilde{\gamma} + \frac{2\gamma + \gamma^2}{2} + \frac{\gamma}{2} + \frac{\gamma^2}{2} - 1 + \frac{\gamma}{25} + \frac{\gamma + \gamma^2}{2}, \\
\beta_4 &= \frac{3}{40} \tilde{\gamma} + \frac{2\gamma + \gamma^2}{2} + \frac{\gamma}{2} + \frac{\gamma^2}{2} - 1 + \frac{\gamma}{25} + \frac{\gamma + \gamma^2}{2}, \\
\beta_5 &= \frac{3}{40} \tilde{\gamma} + \frac{2\gamma + \gamma^2}{2} + \frac{\gamma}{2} + \frac{\gamma^2}{2} - 1 + \frac{\gamma}{25} + \frac{\gamma + \gamma^2}{2}, \\
\beta_6 &= \frac{3}{20} \tilde{\gamma} + \frac{2\gamma + \gamma^2}{2} + \frac{\gamma}{2} + \frac{\gamma^2}{2} - 1 + \frac{\gamma}{25} + \frac{\gamma + \gamma^2}{2}, \\
\beta_7 &= -\frac{3}{10} \tilde{\gamma} + \frac{2\gamma + \gamma^2}{2} + \frac{\gamma}{2} + \frac{\gamma^2}{2} - 1 + \frac{\gamma}{25} + \frac{\gamma + \gamma^2}{2}, \\
\beta_8 &= -\frac{3}{10} \tilde{\gamma} + \frac{2\gamma + \gamma^2}{2} + \frac{\gamma}{2} + \frac{\gamma^2}{2} - 1 + \frac{\gamma}{25} + \frac{\gamma + \gamma^2}{2}, \\
\beta_9 &= -\frac{3}{10} \tilde{\gamma} + \frac{2\gamma + \gamma^2}{2} + \frac{\gamma}{2} + \frac{\gamma^2}{2} - 1 + \frac{\gamma}{25} + \frac{\gamma + \gamma^2}{2}, \\
\end{aligned}
\]

(41)
The first term proportional to $\dot{\gamma}$ describes the influence of the order parameters themselves, while the other terms stand for the contributions of the center manifold.

### D. Real Variables

To investigate how the complex order parameter equations contribute to the one-to-one retinopathy, we transform them to real variables according to

$$u_0 = \frac{U_{00}}{\sqrt{2}} , \quad u_1 = (U_{11} + U_{-11})/2 , \quad u_2 = i(U_{11} - U_{-11})/2$$

$$u_3 = (U_{11} + U_{-11})/2 , \quad u_4 = i(U_{11} - U_{-11})/2 , \quad u_5 = (U_{01} - U_{0-1})/2$$

$$u_6 = i(U_{01} + U_{0-1})/2 , \quad u_7 = (U_{10} - U_{-10})/2 , \quad u_8 = i(U_{10} + U_{-10})/2 .$$

Then the equations of evolution for the real variables $u_i$ read

$$\dot{u}_0 = \Lambda u_0 + 2\beta_1 u_1^3 + 2\beta_2 u_0 u_3^2 + u_0^4 + 2\beta_2 u_0 u_1^2 + u_0^2 + u_3^2 + u_4^2$$

$$+ \sqrt{2} \beta_4 (u_1 u_5 u_7 + u_2 u_5 u_8 + u_2 u_4 u_7 - u_1 u_4 u_7 - u_1 u_5 u_8 - u_3 u_4 u_8) ,$$

$$\dot{u}_1 = \Lambda u_1 + \sqrt{2} \beta_4 u_0 (u_5 u_7 - u_6 u_8) + \beta_5 (u_3 u_5 u_7 - u_3 u_4 u_8) - \beta_6 u_1 (u_7 + u_8)$$

$$+ 2\beta_1 u_3 u_1 + \beta_3 (u_3 u_5 u_7 - u_3 u_4 u_8) + 2\beta_7 u_1 (u_7^2 + u_8^2) + \beta_8 u_1 (u_7^2 + u_8^2) ,$$

$$\dot{u}_2 = \Lambda u_2 + \sqrt{2} \beta_4 u_0 (u_5 u_7 - u_6 u_8) + \beta_5 (u_3 u_5 u_7 - u_3 u_4 u_8) - \beta_6 u_2 (u_7^2 + u_8^2)$$

$$+ 2\beta_1 u_3 u_2 + \beta_3 (u_3 u_5 u_7 - u_3 u_4 u_8) + \beta_7 u_2 (u_7^2 + u_8^2) + \beta_8 u_2 (u_7^2 + u_8^2) ,$$

$$\dot{u}_3 = \Lambda u_3 - \sqrt{2} \beta_4 u_0 (u_5 u_7 - u_6 u_8) + \beta_5 (u_3 u_5 u_7 - u_3 u_4 u_8) - \beta_6 u_3 (u_7^2 + u_8^2)$$

$$+ 2\beta_1 u_3 u_3 + \beta_3 (u_3 u_5 u_7 - u_3 u_4 u_8) + \beta_7 u_3 (u_7^2 + u_8^2) + \beta_8 u_3 (u_7^2 + u_8^2) ,$$

$$\dot{u}_4 = \Lambda u_4 + \sqrt{2} \beta_4 u_0 (u_5 u_7 - u_6 u_8) + \beta_5 (u_3 u_5 u_7 - u_3 u_4 u_8) - \beta_6 u_4 (u_7^2 + u_8^2)$$

$$+ 2\beta_1 u_3 u_4 + \beta_3 (u_3 u_5 u_7 - u_3 u_4 u_8) + \beta_7 u_4 (u_7^2 + u_8^2) + \beta_8 u_4 (u_7^2 + u_8^2) ,$$

$$\dot{u}_5 = \Lambda u_5 + 2\beta_2 u_2 u_3 - \beta_3 u_5 (u_3^2 + u_5^2) + 2\beta_4 u_2 u_5^2 + \sqrt{2} \beta_4 u_0 (u_5 u_7 - u_6 u_8 + u_2 u_8 - u_4 u_8)$$

$$- \beta_6 u_5 (u_7^2 + u_8^2) + 2\beta_7 u_5 (u_7^2 + u_8^2) - 2\beta_8 u_5 (u_7^2 + u_8^2) ,$$

$$\dot{u}_6 = \Lambda u_6 + 2\beta_2 u_2 u_6 - \beta_3 u_6 (u_3^2 + u_5^2) + 2\beta_4 u_2 u_6^2 + \sqrt{2} \beta_4 u_0 (u_2 u_7 + u_2 u_8 + u_1 u_8 - u_3 u_8)$$

$$- \beta_6 u_6 (u_7^2 + u_8^2) + 2\beta_7 u_6 (u_7^2 + u_8^2) - 2\beta_8 u_6 (u_7^2 + u_8^2) ,$$

$$\dot{u}_7 = \Lambda u_7 + 2\beta_2 u_2 u_7 - \beta_3 u_7 (u_3^2 + u_5^2) + 2\beta_4 u_2 u_7^2 + \sqrt{2} \beta_4 u_0 (u_1 u_8 + u_3 u_8 + u_2 u_6 - u_4 u_6)$$

$$- \beta_6 u_7 (u_7^2 + u_8^2) + 2\beta_7 u_7 (u_7^2 + u_8^2) - 2\beta_8 u_7 (u_7^2 + u_8^2) ,$$

$$\dot{u}_8 = \Lambda u_8 + 2\beta_2 u_2 u_8 - \beta_3 u_8 (u_3^2 + u_5^2) + 2\beta_4 u_2 u_8^2 - \sqrt{2} \beta_4 u_0 (u_1 u_8 - u_3 u_8 - u_2 u_6 + u_4 u_6)$$

$$- \beta_6 u_8 (u_7^2 + u_8^2) + 2\beta_7 u_8 (u_7^2 + u_8^2) - 2\beta_8 u_8 (u_7^2 + u_8^2) .$$

Note that the real order parameter equations follow according to

$$\dot{u}_i = -\frac{\partial V(u_j)}{\partial u_i}$$

from the potential

$$V(u_j) = -\frac{\Lambda}{2} \sum_{i=0}^{8} u_j^2 - \frac{\beta_3}{2} u_0^4 - \beta_2 u_0^2 (u_3^2 + u_5^2) - \beta_2 u_0^2 (u_3^2 + u_5^2) - \beta_3 u_0^2 (u_3^2 + u_5^2) + 2\beta_4 u_0^2 (u_3^2 + u_5^2)$$

$$- \sqrt{2} \beta_4 u_0 (u_5 u_7 - u_6 u_8) + \sqrt{2} \beta_4 u_0 (u_5 u_7 - u_6 u_8) - \beta_5 (u_7^2 + u_8^2) - \beta_6 (u_7^2 + u_8^2) - \beta_7 (u_7^2 + u_8^2) - \beta_8 (u_7^2 + u_8^2) .$$

Naturally, a complete analytical determination of all stationary states of the real order parameter equations is impossible. However, we are able to demonstrate that certain stationary states admit for retinotopic modes.
E. Special Case

To this end we consider the special case $u_1, u_2, u_5, u_6, u_7, u_8 = 0$. Then the equations (53), (56), and (57) for the non-vanishing amplitudes $u_0, u_3, u_4$ reduce to

\[
\begin{align*}
\dot{u}_0 &= \Lambda u_0 + 2\beta_1 u_0^3 + 2\beta_3 (u_3^2 + u_4^2) u_3, \\
\dot{u}_3 &= \Lambda u_3 + 2\beta_3 u_0^2 u_3 + \beta_8 (u_3^2 + u_4^2) u_3, \\
\dot{u}_4 &= \Lambda u_4 + 2\beta_3 u_0^2 u_4 + \beta_8 (u_3^2 + u_4^2) u_4. \\
\end{align*}
\]

Due to the relation

\[
\frac{\dot{u}_3}{u_3} = \frac{\dot{u}_4}{u_4}
\]

one obtains constant phase-shift angles, i.e. it holds $u_3 \propto u_4$. Therefore, the system of three coupled differential equations can be reduced to two variables. To this end we introduce the new variable

\[
\xi = \sqrt{u_3^2 + u_4^2},
\]

which leads to

\[
\begin{align*}
\dot{u}_0 &= \Lambda u_0 + 2\beta_1 u_0^3 + 2\beta_3 \xi^2 u_0, \\
\dot{\xi} &= \Lambda \xi + 2\beta_3 u_0^2 \xi + \beta_8 \xi^3. \\
\end{align*}
\]

The stationary solution, which corresponds to a coexistence of the two modes, is given by

\[
u_0^0 = \frac{\Lambda}{2(\beta_3 + \beta_8)}, \quad \xi^2 = -\frac{\Lambda}{\beta_3 + \beta_8}, \quad (58)
\]

where we used the relation $\beta_8 = \beta_1 + \beta_3$ following from (51). Demanding real amplitudes $u_0, \xi$ leads to the coexistence condition

\[
\beta_3 + \beta_8 < 0.
\]

Furthermore, we require stability for this state. Therefore we consider the corresponding potential $V(u_0, \xi)$, which can be read off from (54) and (56):

\[
V(u_0, \xi) = -\frac{\Lambda}{2} (u_0^2 + \xi^2) - \frac{\beta_1}{2} u_0^2 - \beta_3 u_0^2 \xi^2 - \frac{\beta_4}{4} \xi^4.
\]

Stable states correspond to a minimum of $V$, which leads to the conditions

\[
2\beta_3 - \beta_8 > 0, \quad \beta_3 - \beta_8 > 0.
\]

The inequalities (59), (61) can be summarized according to

\[
\beta_8 < 0, \quad \beta_3 < -\beta_8, \quad 2\beta_3 > \beta_8.
\]

If they are valid, both the $u_0$- and the $\xi$-mode coexist. If we set $u_4 = 0$, without loss of generality, the solution reads in complex variables according to (56)

\[
U_{10} = \sqrt{-\frac{\Lambda}{\beta_3 + \beta_8}}, \quad U_{1-1} = U_{-11} = -\sqrt{-\frac{\Lambda}{\beta_3 + \beta_8}}.
\]

Thus, the unstable part is given by

\[
U(\hat{t}, \hat{r}) = \sqrt{-\frac{\Lambda}{\beta_3 + \beta_8}} \left[ Y_{10}(\hat{t}) Y_{10}^R(\hat{r}) - Y_{10}^T(\hat{t}) Y_{10}^R(\hat{r}) - Y_{1-1}^T(\hat{t}) Y_{11}^R(\hat{r}) \right].
\]

Using the Legendre addition theorem reduces (64) to

\[
U(\hat{t}, \hat{r}) = \sqrt{-\frac{\Lambda}{\beta_3 + \beta_8}} P_1(\hat{t}, \hat{r})
\]

with $P_1(\hat{t}, \hat{r}) = \hat{t} \cdot \hat{r}$. Thus, the unstable part is minimal, if $\hat{t}$ and $\hat{r}$ are antiparallel, i.e. the distance of the corresponding points on the unit sphere is maximum. Decreasing of the angle between $\hat{t}$ and $\hat{r}$ leads to increasing values of $U(\hat{t}, \hat{r})$, and the maximum occurs for parallel unit vectors. This justifies calling the mode retinotopic.
IV. ONE-TO-ONE RETINOTOPY

Now we investigate whether the generalized H"aussler equations \(1\) describe the emergence of a perfect one-to-one retinotopy between two spheres. To this end we follow the unpublished suggestions of Ref. \([11]\) and treat systematically the contribution of higher modes. Because the Legendre functions form a complete orthogonal system \([11], [12]\) for functions defined on the interval \([-1, +1]\), their products can always be written as linear combinations of Legendre functions. This motivates that the influence of higher modes upon the connection weights, which obey the generalized H"aussler equations \(1\), can be included by the ansatz

\[
w(\sigma) = \sum_{l=0}^{\infty} (2l + 1)Z_lP_l(\sigma),
\]

where the amplitudes \(Z_l\) are time dependent.

A. Recursion Relations

Inserting (66) into the generalized H"aussler equations \(1\) and performing the integrals over the respective unit spheres leads to

\[
\sum_{l=0}^{\infty} (2l + 1)\dot{Z}_lP_l(\sigma) = \alpha \left[ 1 - \sum_{l=0}^{\infty} (2l + 1)Z_lP_l(\sigma) \right] + \sum_{l=0}^{\infty} (2l + 1)Z_lP_l(\sigma) \sum_{l'=0}^{\infty} (2l' + 1)Z_{l'}f_{l'}^T f_{l'}^R [P_{l'}(\sigma) - Z_l].
\]

The products of Legendre functions occurring in (67) can be reduced to linear combinations of single Legendre functions according to the standard decomposition \([9, 8.915]\)

\[
P_l(\sigma)P_{l'}(\sigma) = \sum_{k=0}^{l} A_{l,l',k} P_{l+l'-2k}(\sigma), \quad l \leq l'
\]

with the coefficients

\[
A_{l,l',k} = \frac{(2l' + 2l - 4k + 1) a_{l'-k}a_{k-l}}{(2l' + 2l - 2k + 1) a_{l+l'-k}}, \quad a_k = \frac{(2k - 1)!!}{k!}.
\]

Thus, contributions to the polynomial \(P_l(\sigma)\) only occur iff the relation \(k = (l + l' - \tilde{l})/2\) is fulfilled. Furthermore, using the orthonormality relation \(1\) yields the following recursion relation for the amplitudes \(Z_l\):

\[
(2l + 1)\dot{Z}_l = \alpha [\delta_{l,0} - (2l + 1)Z_l] - (2l + 1)Z_l (Z_l^2 + 3f_l^T f_l^R Z_l^2) + \sum_{l'=0}^{\infty} (2l' + 1)Z_{l'} \left[ \sum_{l''=0}^{l} (2l'' + 1)Z_{l''} f_{l''}^T f_{l''}^R \sum_{k=0}^{l''} A_{l'',l',k} \delta_{k,(l''+l'-\tilde{l})/2} \right] \times \sum_{k=0}^{l''} A_{l'',l',k} \delta_{k,(l''+l'-\tilde{l})/2} + \sum_{l''=l'+1}^{\infty} (2l'' + 1)Z_{l''} f_{l''}^T f_{l''}^R \sum_{k=0}^{l''} A_{l'',l',k} \delta_{k,(l''+l'-\tilde{l})/2} \right].
\]

Note that Eq. (70) cannot be solved analytically for arbitrary expansion coefficients \(f_l^T, f_l^R\) of the cooperativity functions. Therefore, we restrict ourselves from now on to a special case.

B. Special Cooperativity Functions

For simplicity we assume that the expansion of the cooperativity functions \(1\) breaks down after the first order:

\[
c_T(\hat{t} \cdot \hat{t}') = \frac{1}{4\pi} [1 + 3f_1^T P_1(\hat{t} \cdot \hat{t}')], \quad c_R(\hat{t} \cdot \hat{t}') = \frac{1}{4\pi} [1 + 3f_1^R P_1(\hat{t} \cdot \hat{t}')].
\]

With this choice the recursion relation (70) for \(l = 0\) reduces to

\[
\dot{Z}_0 = -(\alpha + Z_0^2 + 3\gamma Z_1^2)(Z_0 - 1),
\]
where we have used again the abbreviation $\gamma = f_l^T f_l^R$. For $l \neq 0$, by taking into account (69), we obtain

$$\dot{Z}_l = -(\alpha + Z_0^2 + 3\gamma Z_1^2)Z_l + Z_0 Z_l + 3\gamma Z_l \frac{lZ_{l-1} + (l+1)Z_{l+1}}{2l + 1}.$$  (73)

The long-time behavior of the system corresponds to its stationary states. They are determined by $Z_0 = 1$ from (72), whereas (73) leads to a nonlinear recursion relation for the amplitudes $Z_l$ with $l \neq 0$. However, by introducing the variable

$$u = \frac{\alpha + 3\gamma Z_1(u)^2}{3\gamma Z_1(u)},$$  (74)

this nonlinear recursion relation can be formally transformed into the linear one

$$(l + 1)Z_{l+1}(u) = (2l + 1)uZ_l(u) + lZ_{l-1}(u), \quad l \geq 1.$$  (75)

Thus, solving the nonlinear recursion relation (73) amounts to solving the linear recursion relation (75) for $Z_l(u)$ in such a way that the self-consistency condition (74) is fulfilled.

C. Generating Function

To determine the amplitudes $Z_l(u)$ we calculate their generating function

$$E(x, u) = \sum_{l=0}^{\infty} Z_l(u) x^l,$$  (76)

where we have the normalization

$$E(0, u) = Z_0(u) = 1.$$  (77)

Multiplying both sides of (76) with $x^l$ and summing over $l \geq 1$ leads to an inhomogeneous nonlinear partial differential equation of first order for the generating function:

$$(x^2 - 2ux + 1) \frac{\partial E(x, u)}{\partial x} = (u - x)E(x, u) + Z_1(u) - u.$$  (78)

At first, we consider the homogeneous equation corresponding to (78):

$$(x^2 - 2ux + 1) \frac{\partial E_{\text{hom}}(x, u)}{\partial x} = (u - x)E_{\text{hom}}(x, u).$$  (79)

It is solved by the method of separating variables, yielding

$$E_{\text{hom}}(x, u) = \frac{K(u)}{\sqrt{x^2 - 2ux + 1}},$$  (80)

where $K(u)$ is an integration constant. Afterwards, we determine a particular solution of the inhomogeneous equation (78) by using the method of varying constants. Using the ansatz

$$E_{\text{part}}(x, u) = \frac{K(x, u)}{\sqrt{x^2 - 2ux + 1}},$$  (81)

leads to the differential equation

$$\frac{\partial K(x, u)}{\partial x} = \frac{Z_1(u) - u}{\sqrt{x^2 - 2ux + 1}},$$  (82)

which is solved by using [9, 2.261]:

$$K(x, u) = \frac{[Z_1(u) - u] \ln[2\sqrt{x^2 - 2ux + 1} + 2(x - u)]}{\sqrt{x^2 - 2ux + 1}}.$$  (83)
Thus, the complete solution \( E(x, u) = E_{\text{hom}}(x, u) + E_{\text{part}}(x, u) \) of Eq. (78) reads as follows:

\[
E(x, u) = \frac{K(u) + [Z_1(u) - u]\ln[2\sqrt{x^2 - 2ux + 1} + 1] + 2(x - u)]}{\sqrt{x^2 - 2ux + 1}}.
\] (84)

Furthermore, using the normalization condition (77) fixes the integration constant to \( K(u) = 1 - [Z_1(u) - u]\ln(2 - 2u). \)

Thus, the generating function is finally given by

\[
E(x, u) = \frac{1 + [Z_1(u) - u]\ln[\sqrt{x^2 - 2ux + 1} + x - u]}{\sqrt{x^2 - 2ux + 1}}.
\] (85)

### D. Decomposition

We now determine the unknown amplitudes \( Z_l(u) \). From the mathematical literature it is well-known that the recursion relation (75) holds both for the Legendre functions of first kind \( P_l(u) \) and second kind \( Q_l(u) \), respectively. Thus, we expect that the generating function (85) can be represented as a linear combination of the generating functions of the Legendre functions of both first and second kind, which are given by [9, 8.921] and [9, 8.791.2]:

\[
E_P(x, u) = \sum_{l=0}^{\infty} P_l(u)x^l = \frac{1}{\sqrt{x^2 - 2ux + 1}},
\] (86)

\[
E_Q(x, u) = \sum_{l=0}^{\infty} Q_l(u)x^l = \frac{\ln[\sqrt{x^2 - 2ux + 1} + u - x]}{\sqrt{u^2 - 1}}.
\] (87)

Indeed, taking into account the explicit form of the Legendre function of second kind for \( l = 0 \):

\[
Q_0(u) = \frac{1}{2}\ln\frac{u + 1}{u - 1},
\] (88)

the generating function (85) decomposes according to

\[
E(x, u) = \{1 + [Z_1(u) - u]Q_0(u)\}E_P(x, u) - [Z_1(u) - u]E_Q(x, u).
\] (89)

Inserting (86), (87) and performing a comparison with (76) then yields the result

\[
Z_l(u) = \{1 + [Z_1(u) - u]Q_0(u)\}P_l(u) - [Z_1(u) - u]Q_l(u).
\] (90)

Thus, the amplitudes \( Z_l(u) \) turn out to be linear combinations of \( P_l(u) \) and \( Q_l(u) \). To fix the yet undetermined amplitude \( Z_1(u) \) in the expansion coefficients of (88), we have to take into account the boundary condition that the sum in the ansatz (85) has to converge.

### E. Boundary Condition

Because the Legendre functions \( P_l(\sigma) \) do not vanish with increasing \( l \), we must require

\[
\lim_{l \to \infty} Z_l(u) = 0.
\] (91)

The series of Legendre functions of first kind \( P_l(u) \) with fixed \( u > 1 \) diverges for \( l \to \infty \) according to [9, 8.917]

\[
P_0(u) < P_1(u) < P_2(u) < \ldots < P_n(u) < \ldots, \quad u > 1.
\] (92)

The Legendre functions of second kind \( Q_l(u) \), however, converge to zero (see Figure 2). Thus, performing the limit \( l \to \infty \) in Eq. (90), we obtain

\[
1 + [Z_1(u) - u]Q_0(u) = 0.
\] (93)
FIG. 2: The Legendre functions of first and second kind $P_l(u)$ and $Q_l(u)$ for $u > 1$. We have $P_l(1) = 1$, whereas $Q_l(u)$ diverges for $u \downarrow 1$. Important for the boundary condition of $Z_l(u)$ is the different behavior for increasing values of $l$: $P_l(u)$ diverges according to (92), whereas $Q_l(u)$ converges to zero.

From the explicit form $Q_1(u) = uQ_0(u) - 1$ it follows that $Z_1(u)$ is fixed according to

$$Z_1(u) = \frac{Q_1(u)}{Q_0(u)}.$$  

(94)

With this we obtain that the result finally reads

$$Z_l(u) = \frac{Q_l(u)}{Q_0(u)},$$  

(95)

which is not valid only for $l \neq 0$ but also for $l = 0$ due to (77).

**F. Connection Weight**

Inserting (95) into (66) yields the following solution for the connection weight:

$$w(\sigma) = \frac{1}{Q_0(u)} \sum_{l=0}^{\infty} (2l + 1)Q_l(u)P_l(\sigma).$$  

(96)

Using the identity

$$\sum_{l=0}^{\infty} (2l + 1)Q_l(u)P_l(\sigma) = \frac{1}{u - \sigma},$$  

(97)

and (88), we obtain for the connection weight

$$w(\sigma) = \frac{2}{u - \sigma} \left( \ln \frac{u + 1}{u - 1} \right)^{-1}.$$  

(98)

Note that integrating (98) over the unit sphere leads to

$$\int_0^{2\pi} d\varphi \int_{-1}^{+1} d\sigma w(\sigma) = 4\pi,$$

(99)

i.e. the total connection weight coincides with the measure (3).
FIG. 3: a) Relation (100) between the control parameter $\alpha$ and the variable $u$. b) The connection weight for different values of the control parameter $\alpha$. For decreasing values of $\alpha$ the connection weight around $\sigma = +1$ is growing. In the limiting case $\alpha \to 0$ the connection weight $w(\sigma)$ becomes Dirac’s delta function (107).

On the other hand we have to take into account that the self-consistency condition (94) yields an explicit relation between the variable $u$ and the control parameter $\alpha$. Indeed, we infer from (94) and (95) the following transcendental relation between $\alpha$ and $u$

$$\frac{\alpha}{\gamma} = -\frac{2}{3} \left( \ln \frac{u + 1}{u - 1} \right)^{-1} \left[ 2 \left( \ln \frac{u + 1}{u - 1} \right)^{-1} - u \right],$$

which is depicted in Figure 3a.

G. Limiting Cases

The limiting value of (100) for $u \to \infty$ is determined with the help of the expansion [1, 1.513]

$$\ln \frac{1 + x}{1 - x} = 2 \sum_{k=1}^{\infty} \frac{1}{2k - 1} x^{2k-1}, \quad x^2 < 1,$$

and reads

$$\lim_{u \to \infty} \alpha = \gamma.$$  

Thus, we conclude that the case $u \to \infty$ corresponds to the instability point $\alpha_c = f_T^R f_1^L$, which was obtained from the linear stability analysis in Section II. Correspondingly, using again (100), we observe that the connection weight (98) coincides in the limit $u \to \infty$ with a uniform distribution:

$$\lim_{\alpha \uparrow \alpha_c} w(\sigma) = 1.$$  

Another biological important special case is $u \downarrow 1$, where we obtain from (100)

$$\lim_{u \downarrow 1} \alpha = 0.$$  

Furthermore, considering the limit $u \downarrow 1$ in (98) for $\sigma \neq u$, we obtain

$$\lim_{u \downarrow 1} \frac{2}{u - \sigma} \left( \ln \frac{u + 1}{u - 1} \right)^{-1} = 0.$$  

On the other hand, integrating (98) for $u \downarrow 1$ over $\sigma$ yields

$$\lim_{u \downarrow 1} \int_{-1}^{1} \frac{2}{u - \sigma} \left( \ln \frac{u + 1}{u - 1} \right)^{-1} d\sigma = 2.$$  

Therefore, we conclude that the connection weight \( w(\sigma) \) becomes in this limit Dirac’s delta function:

\[
\lim_{\alpha \to 0} w(\sigma) = 4\delta(\sigma - 1).
\] (107)

Thus, decreasing the control parameter \( \alpha \) means that the projection between two spheres becomes sharper and sharper (see Figure 5b). A perfect one-to-one retinotopy is achieved for \( \alpha = 0 \) when the uniform and undifferentiated formation of new synapses onto the tectum is completely terminated.

V. SUMMARY

In this series of three papers we have analyzed in detail the self-organized formation of retinotopic projections between manifolds of different geometries. Applying our generalized Häußler equations to Euclidean manifolds, and to spheres in the present paper, led to remarkably analogous results. Both for one-dimensional strings and for spheres we have furnished proof that our generalized Häußler equations describe, indeed, the emergence of a perfect one-to-one retinotopy. Furthermore, we have shown in both cases that the underlying order parameter equations follow from a potential dynamics and do not contain quadratic terms. However, in contrast to strings, spherical manifolds represent a more adequate description for retina and tectum. Therefore, the present paper represents an essential progress in the understanding of the ontogenetic development of neural connections between retina and tectum.

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