Steps toward numerical mode analysis of organizing systems

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Abstract A well established method to analyze dynamical systems described by coupled nonlinear differential equations is to determine their normal modes and reduce the dynamics, by adiabatic elimination of stable modes, to a much smaller system for the amplitudes of unstable modes and their nonlinear interactions. So far, this analysis is possible only for idealized symmetric model systems. We aim to build a framework in which realistic systems with less symmetry can be analyzed automatically. In this paper we present a first example of mode analysis with the assistance of numerical computation. Our method is illustrated using a model system for the ontogenesis of retinotopy, and the results reproduce those from theoretical analysis precisely. Aspects of organization generalized from this model system are discussed.

Keywords Organization · Symmetry · Amplitude equation · Mode · Adiabatic elimination · Ontogenesis of retinotopy

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1 Introduction

An important issue for coming years is to gain better understanding of organization such as is manifest in the living cell, the organism, the brain, ecosystems, human
society and information technology. Important for progress on this front is adequate mathematical formulation of the processes of organization. Organizing systems are both complex, due to their many interacting elements, and at the same time simple, given their tendency to coordinate subsystems and thus contract their state space. Coupled nonlinear differential equations form a natural basis for the description of organizing systems. To solve these explicitly is rarely a viable option. In most cases of interest, the coupling constants, or even form of terms, of these equations are not known in any detail, and even if they were, analytical solutions are in general not available and numerical solutions may be almost as incomprehensible as the system itself.

In order to understand organizing systems, it fortunately is not necessary, nor is it desirable, to know all system details and variables. Of interest is the study of transitions from less structured initial states to more structured later states, when control parameters pass critical values [7]. Near the onset of instability, system dynamics can be reduced to that on a low-dimensional manifold [3,21], described by the temporal evolution of a small number of variables, namely the amplitude of modes that become unstable (principal modes or order parameters). Other modes of the system (stable or ancillary modes) have negative linear growth and decay exponentially. They can be eliminated through adiabatic approximation (the slaving principle [12]). In systems without spectral gap one has to deal with spatially varying amplitudes of bands in terms of envelope equations [12,18]. Amplitude equations come in a few universal forms, signaling different types of bifurcations, which are selected by the symmetry of the system [6,7]. The details of the original microscopic equations get expressed only in the coefficients of the amplitude equations. They can be derived using the perturbation method by separating fast and slow scales [2,14], or the projection (or basis function) method [5,9,12,13,20], in which normal modes are eigenfunctions of the linearization of the system about a simple initial state.

Although some argue that the structure of amplitude equations contains all interesting information about a system, one may continue to solve and analyze the equations. Certain interesting properties of a system’s dynamics can be obtained already from the linear terms, see for instance Turing’s theory of ontogenetic pattern formation on the basis of reaction–diffusion systems [20]. The major role of nonlinearities is to saturate the exponential growth of unstable modes and to select (combinations of) modes [7]. Thus, the plane-wave modes in spatially homogeneous two-dimensional systems might cooperate to form square or hexagon patterns or might compete [8,16,19]. Note that amplitude equations are strictly valid only in weakly nonlinear conditions [14], and the center manifold is only an approximation that captures the qualitative behavior of the system near the instability, to any desired degree of accuracy. An exact solution of the system would need a complete analysis of the subsystem composed of winning principal modes and all ancillary modes excited by them [13].

So far, these methods have been applied only to ideal systems with simplifying conditions, such as high degrees of symmetry and simple boundary conditions, such that the normal modes belong to one of the analytically known function systems (plane-waves, spherical harmonics or Bessel functions and so on), a serious limitation of the approach. The organizing systems of interest, on the other hand, typically undergo cascades of differentiation, one organizational process setting the structure and boundary conditions for the next. This is well exemplified by ontogenesis, the
development of eggs to animals. Boundary conditions may have profound influence on the shape and robustness of pattern formation [1].

This paper describes first steps toward the development of a numerical methodology to overcome these limitations, so that the normal mode methods can be applied routinely and effortlessly. To this end we have worked out an example that closely follows the steps of an analytical treatment of a problem of neural network organization, the Häussler system for the ontogenesis of retinotopy [13], repeating its steps using numerical tools and generalizing it to conditions for which no analytical treatment is available. Our discussion is based on systems with polynomial dynamics, but the method can be applied to general systems with the help of polynomial expansion. The paper is organized as follows: Sect. 2 reviews the formulation and analysis of the model Häussler system [13], Sect. 3 presents a method to perform numerical analysis, Sect. 4 shows numerical results applied to the Häussler system, and Sect. 5 is summary and discussion.

2 The analytical normal mode analysis

In this section, we focus on the projection method for normal mode analysis, using the Häussler system for the ontogenesis of retinotopy [13] as an example. This model system is typical for brain organization, and at the same time is simple enough to admit an analytical treatment. It serves as a motivation for our search for methods to analyze more realistic self-organizing systems.

2.1 A self-organizing system for the ontogenesis of retinotopy

The Häussler system for the ontogenesis of retinotopy [13] addresses the establishment of ordered projections between two brain areas, retina and tectum. These are modeled as one-dimensional chains with \( N \) elements each. The domain has been generalized to general manifolds [10,11], but we will use one-dimensional chain for simplicity. The projection between the two brain areas is represented by a set of links \((\tau, \rho)\), where \( \tau \) and \( \rho \) are points in the tectum and retina, respectively. The weight \( w_{\tau \rho} \) of link \((\tau, \rho)\) indicates the strength with which \( \tau \) and \( \rho \) are connected, with a value zero representing the absence of a connection. The set of all links forms a mapping \( W = (w_{\tau \rho}) \). The Häussler system is described by the set of \( n = N \times N \) differential equations:

\[
\dot{w}_{\tau \rho} = f_{\tau \rho}(W) - \frac{1}{2N} w_{\tau \rho} \left( \sum_{\tau'} f_{\tau' \rho}(W) + \sum_{\rho'} f_{\tau \rho'}(W) \right) \\
\equiv H_{\tau \rho}(W),
\]

(1)

where the growth term \( f_{\tau \rho}(W) \) of link \( w_{\tau \rho} \) expresses the cooperation from all its neighbors, and \( \alpha \) is a non-negative link formation rate:

\[
f_{\tau \rho}(W) = \alpha + w_{\tau \rho} \sum_{\tau', \rho'} C(\tau, \tau', \rho, \rho') w_{\tau' \rho'}.
\]

(2)
The coupling function $C(\tau, \tau', \rho, \rho')$, which in [13] was assumed to be separable and isotropic, describes the mutual cooperative support that link $(\tau, \rho)$ receives from its neighbor $(\tau', \rho')$. This mutual help is thought to be mediated by electrical [17] or chemical [22] signals. The term $\sum_{\tau', \rho'} C(\tau, \tau', \rho, \rho') w_{\tau' \rho'}$ is the convolution of the weight matrix with the coupling function. As convolutions are properly defined only for infinite domains, $W$ has to be continued outside the $N \times N$ domain either by wrapping around (periodic boundary condition) or by assuming it to vanish (zero boundary condition).

2.2 Analytical treatment of the Häussler system

An analytical treatment of the Häussler system was given in [13], where it was shown that from an unstructured initial state, the final state of the system is a precise topological projection. We summarize that analysis in this subsection.

The following definitions were introduced to simplify notation. The element-wise multiplication of two matrices $X$ and $Y$, $(X \cdot Y)_{\tau \rho} = X_{\tau \rho} Y_{\tau \rho}$, is denoted as $X \cdot Y$. The convolution $C_{\tau \rho}(W) = \sum_{\tau', \rho'} C(\tau, \tau', \rho, \rho') w_{\tau' \rho'}$ is denoted as operator $C$. The expression $B_{\tau \rho}(X) = \frac{1}{2N} \left( \sum_{\tau'} X_{\tau' \rho} + \sum_{\rho'} X_{\tau \rho'} \right)$ is denoted as operator $B$, which acts on a matrix $X$ and is matrix-valued. With these abbreviations, the Häussler system can be written in matrix form as

$$\dot{W} = -\alpha (W - 1) + W \cdot (C(W) - B(W \cdot C(W)))$$

(3)

Under periodic boundary conditions, the homogeneous state $W_0 = 1$ (where 1 is the unit matrix in which all entries equal 1) is a fixed point of the system. Analysis is performed around $W_0$, by introducing the deviation $V = W - W_0$ as a new variable. The system is then

$$\dot{V} = L(V) + Q(V) + K(V),$$

(4)

with

$$L(V) = -\alpha V + C(V) - B(V) - B(C(V))$$

(5)

$$Q(V) = V \cdot (C(V) - B(V) - B(C(V))) - B(V \cdot C(V))$$

(6)

$$K(V) = -V \cdot B(V \cdot C(V)),$$

(7)

as linear, quadratic, and cubic terms, respectively.

Under periodic boundary conditions and certain symmetry properties of the coupling function $C$, the linear term $L(V)$ has explicit eigenfunctions in the form of the Fourier basis $e^{kl}, k, l \in \mathbb{Z}_n$:

$$e^{kl}(\tau, \rho) = \exp \left( i \frac{2\pi}{N} (k\tau + l\rho) \right).$$

(8)
These are also eigenvectors of the $C$ and $B$ operators. The eigenvalues of the linear term (5) are

$$\lambda^{kl} = \begin{cases} 
-\alpha - 1, & k = l = 0 \\
-\alpha + (\gamma^{kl} - 1)/2, & k = 0, l \neq 0, \text{ or } k \neq 0, l = 0 \\
-\alpha + \gamma^{kl}, & \text{otherwise}
\end{cases} \tag{9}$$

where $\gamma^{kl}$ is the eigenvalue of the $C$ operator for mode $e^{kl}$.

It was shown that the four diagonal modes $e^{\pm 1 \pm 1}$ have the same maximal eigenvalue $\lambda$. The multiplicity is due to the symmetry of $C$ and the periodic boundary conditions.

The control parameter $\alpha$ is set such that $\lambda$ is the only positive eigenvalue, leading to the growth of its corresponding modes (principal modes). All other modes will decay because they have negative eigenvalues (ancillary modes).

Amplitude equations for the four principal modes are obtained by using properties of these modes and straightforward computation, and by adiabatic elimination of the ancillary modes from the original system. Complex Fourier modes can also be combined to form real modes. Let the amplitude of the real modes $e^{11} + e^{-1 - 1}$, $e^{1 - 1} + e^{-11}$, and $i(e^{1 - 1} - e^{-11})$ be $\xi_c, \xi_s, \eta_c, \eta_s$, respectively. Their dynamics are then described by the amplitude equations:

$$\begin{align*}
\dot{\xi}_c &= \left( \gamma - \frac{\gamma}{4}(2'(\xi_c^2 + \xi_s^2) + 4'(\eta_c^2 + \eta_s^2)) \right) \xi_c \\
\dot{\xi}_s &= \left( \gamma - \frac{\gamma}{4}(2'(\xi_c^2 + \xi_s^2) + 4'(\eta_c^2 + \eta_s^2)) \right) \xi_s \\
\dot{\eta}_c &= \left( \gamma - \frac{\gamma}{4}(2'(\eta_c^2 + \eta_s^2) + 4'(\xi_c^2 + \xi_s^2)) \right) \eta_c \\
\dot{\eta}_s &= \left( \gamma - \frac{\gamma}{4}(2'(\eta_c^2 + \eta_s^2) + 4'(\xi_c^2 + \xi_s^2)) \right) \eta_s,
\end{align*} \tag{10}$$

where $\gamma = \gamma^{\pm 1 \pm 1}$, $2' = 2 - \frac{\gamma^0 + \gamma^{\pm 2 \pm 2}}{\alpha - \gamma^{\pm 2 \pm 2}}$, and $4' = 4 - \frac{\gamma^0 + (\gamma^{\pm 20 - 1})/2}{\alpha - (\gamma^{\pm 20 - 1})/2} - \frac{\gamma^0 + (\gamma^{0 \pm 2 - 1})/2}{\alpha - (\gamma^{0 \pm 2 - 1})/2}$.

From the amplitude equations (10), one can see that the two diagonal patterns ($\xi_c$ and $\xi_s$ being the amplitudes of modes of one orientation, versus $\eta_c$ and $\eta_s$ those of the other orientation) compete with each other, and the one which is favored in the initial configuration wins. As shown in [13], the winning diagonal then activates ancillary modes of the same orientation, to form a narrow diagonal, which corresponds to a precise retinotopic projection.

2.3 More general conditions and less symmetry

In order to obtain analytical results, systems have to be idealized. In the analysis of the Häussler system, for example, periodic boundary conditions and separable and isotropic coupling function $C$ have been assumed, to make it possible to derive eigenvectors and their eigenvalues analytically.

In the real world, unfortunately, less regularity is encountered. One asymmetry is on the boundary conditions. Biological tissues are, for example, neither periodic nor
infinite. At any stage of differentiation, boundary conditions set by the previous stage have to be considered. Another interesting asymmetry concerns the coupling function. Biological systems are plastic in that they develop, learn and adapt. The Häussler system, first proposed as a model for the ordered projection between two brain areas, has also been applied successfully as a mechanism for establishing correspondence between two images, an important task in vision [24]. The isotropic coupling function $C$ can be viewed as a naturally given mechanism [17] in a naive system to establish a correspondence in the form of a continuous map. With repeated establishment of correspondence the system may learn by Hebbian plasticity, for instance, a task-adapted coupling function. If all correspondences that are found agree as to their relative orientation (e.g., top mapping to top), then the coupling function $C$ will be transformed into a function $T$ that is specialized to that relative orientation. By computer simulation we have shown that the task-adapted function $T$ makes the system faster and more robust (more likely to develop continuous mappings) than the original $C$ system [24]. We are very interested in analyzing the differences in the behavior of the $T$ and $C$ systems. The above analytical treatment for $C$ is not applicable for the $T$ system as the $T$ function is no longer separable or isotropic, and new methods are required.

3 Numerical normal mode analysis

We present a method for numerical normal mode analysis, on the general nonlinear system of third degree polynomial:

$$\dot{V} = LV + Q(V) + K(V), \quad (11)$$

where $V = (v_1, \ldots, v_n)^T$ (with $^T$ for transpose) is the $n$-dimensional state vector, $L$ is the matrix representing the linear term, and $Q(V)$ and $K(V)$ are quadratic and cubic functions, respectively. The Häussler system is a special case of this system (with $n = N^2$), and will be used as an example to illustrate the application of this method.

3.1 Linear modes

The modes of system (11) are the eigenvectors of $L$, $u^i$, $i = 1, \ldots, n$:

$$L u^i = \lambda_i u^i.$$

Given $L$, these modes $u^i$ and their corresponding eigenvalues $\lambda_i$ can be conveniently obtained by numerical methods in the general case.

When obtaining $L$ from the original system equations, it is important to specify at which point the system is linearized. The $L$ in Eq. (11) corresponds to $V = 0$, and the $L(V)$ of Eq. (5) is the linear term for $W = 1$. If one wants to linearize the system at any state $W^*$, a more direct way is to compute its Jacobian matrix $J$ explicitly, and evaluate it at $W = W^*$. 

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In system (1), $J$ is an $N^2 \times N^2$ matrix whose entries are $\frac{\partial H_{\tau\rho}}{\partial w_{\tau'\rho'}}$, which is calculated as follows [23]. Define the following terms as functions of $\tau, \tau', \rho, \rho'$:

$$J_t = w_{\tau\rho} \left[ C(\tau, \tau', \rho, \rho') - \frac{1}{2N} \left( \sum_{\tau''} C(\tau'', \tau', \rho, \rho') w_{\tau''\rho} \right. \right.$$

$$\left. \left. + \sum_{\rho''} C(\tau, \tau', \rho'', \rho') w_{\tau\rho''} \right) \right]$$

$$J_{t1} = \frac{1}{2N} w_{\tau\rho} \sum_{\tau''\rho''} C(\tau', \tau'', \rho', \rho'') w_{\tau''\rho''}$$

$$J_{t2} = \sum_{\tau''\rho''} C(\tau, \tau'', \rho, \rho'') w_{\tau''\rho''} - \frac{1}{2N} \left( \sum_{\tau''} f_{\tau''}(W) + \sum_{\rho''} f_{\tau\rho''}(W) \right).$$

We then have

$$\frac{\partial H_{\tau\rho}}{\partial w_{\tau'\rho'}} = \begin{cases} 
J_t, & \tau \neq \tau', \rho \neq \rho' \\
J_t - J_{t1}, & \tau = \tau', \rho \neq \rho', \text{ or } \tau \neq \tau', \rho = \rho' \\
J_t - 2J_{t1} + J_{t2}, & \tau = \tau', \rho = \rho', 
\end{cases}$$

(12)

An analogous formulation is valid if the coupling function $C$ is replaced by $T$.

3.2 Full amplitude equations

With the field $V$ being represented as the superposition of modes:

$$V(t) = \sum_i \xi_i(t) u^i,$$

(13)

system (11) can be reformulated exactly in terms of differential equations for the amplitudes $\xi_i$. A derivation of these equations is given in [25], which we present briefly as follows. By inserting Eq. (13) into the dynamics (11) we get

$$\sum_j \dot{\xi}_ju^j = \mathbf{L} \sum_j \xi_j u^j + Q(V) + K(V)$$

$$= \sum_j \xi_j \lambda_j u^j + Q(V) + K(V).$$

(14)

$\mathbf{L}$ has a set of left eigenvectors $\bar{u}^i, i = 1, \ldots, n$: $\bar{u}^i \mathbf{L} = \lambda_i \bar{u}^i$. They are orthonormal to the normal modes ($\bar{u}^i u^j = \delta_{ij}$). Multiplying both sides of Eq. (14) by $\bar{u}^i$ from the left, we obtain

$$\dot{\xi}_i = \lambda_i \xi_i + \bar{u}^i Q(V) + \bar{u}^i K(V).$$

(15)
We now express the two nonlinear terms in explicit numerical form. The polynomial terms \( Q(V) \) and \( K(V) \) can be expressed in matrix form, through the matrix direct product (also called the Kronecker product) of two vectors \( V = (v_1, \ldots, v_n)^T \) and \( V' = (v'_1, \ldots, v'_m)^T \) which is defined as vector

\[
V \otimes V' \equiv \begin{pmatrix}
v_1 v'_1 \\
v_1 v'_2 \\
\vdots \\
v_n v'_m
\end{pmatrix}.
\]

\( V^{(2)} = V \otimes V = (v_1 v_1, v_1 v_2, \ldots, v_n v_n)^T \) is then a vector of all monomials of degree 2 in the \( n \) variables of \( V \). Therefore, because each element of \( Q(V) \) is a linear combination of monomials of degree 2, for any \( Q(V) \), there exists a matrix \( Q \) (of size \( n \times n(n+1)/2 \)) such that \( Q(V) = Q V^{(2)} \). Similarly there exists a matrix \( K \) such that \( K(V) = K V^{(3)} \).

Expanding the elements of \( V^{(2)} \), showing only a general term \( v_i v_j \):

\[
\begin{pmatrix}
v_i v_j
\end{pmatrix} = \left( \sum_l \xi_l u_l^i \right) \left( \sum_{l'} \xi_{l'} u_{l'}^j \right) = \sum_{ll'} \xi_l \xi_{l'} u_l^i u_{l'}^j,
\]

we get

\[
V^{(2)} = \sum_{ll'} \xi_l \xi_{l'} \left( u_l^i \otimes u_{l'}^j \right).
\]

Multiplying both sides by \( Q \) from the left we get

\[
Q V^{(2)} = Q \sum_{ll'} \xi_l \xi_{l'} \left( u_l^i \otimes u_{l'}^j \right) = \sum_{ll'} \xi_l \xi_{l'} Q \left( u_l^i \otimes u_{l'}^j \right),
\]

where \( Q(u_l^i \otimes u_{l'}^j) \equiv Q^{ll'} \) is a vector of length \( n \), which can be conveniently calculated numerically for any given system. Its multiplication with \( \tilde{u}_l^i \) can also be computed, and we have

\[
\tilde{u}_l^i Q(V) = \tilde{u}_l^i Q V^{(2)} = \sum_{ll'} \xi_l \xi_{l'} \tilde{u}_l^i Q^{ll'}.
\]

The same procedure applies to polynomials of any order. In particular, for the cubic term we have

\[
\tilde{u}_l^i K(V) = \sum_{ll'l''} \xi_l \xi_{l'} \xi_{l''} \tilde{u}_l^i K^{ll'l''},
\]

where \( K^{ll'l''} = K(u_l^i \otimes u_{l'}^j \otimes u_{l''}^k) \), and \( u_l^i \), \( u_{l'}^j \), \( u_{l''}^k \) are modes.
This leads to an explicit amplitude equation set:

$$\dot{\xi}_i = \lambda_i \xi_i + \sum_{ll'} \xi_i \xi_{l'} \tilde{u}^i Q^{ll'} + \sum_{ll''} \xi_i \xi_{l''} \tilde{u}^i K^{ll''}. \quad (17)$$

Notice that in the literature, the term amplitude equations is reserved for the dynamics of principal modes. In this paper, we loosen the term to refer also the dynamics of the amplitudes of all modes. These amplitude equations are valid in all region of the state space, as they are only a projection of the original dynamics to a different coordinate system. We refer the amplitude equations for principal modes explicitly as amplitude equations after adiabatic elimination. In the Häussler system, the coefficients in amplitude equations (17) can be established straightforwardly, after the matrices $Q$ and $K$ being obtained from Eqs. (6) and (7), respectively.

3.3 Adiabatic elimination

The amplitude equations for principal modes are obtained by adiabatic elimination of the ancillary modes. We now perform the adiabatic elimination up to the third order. For ancillary modes indexed by $s$, we have

$$\dot{\xi}_s \approx \lambda_s \xi_s + \sum_{pp'} \xi_p \xi_{p'} \tilde{u}^s Q^{pp'}, \quad (18)$$

where $p$ and $p'$ are indices of principal modes. Only relevant terms for an approximation up to the third order are shown here. By setting $\dot{\xi}_s = 0$ and solving for $\xi_s$, we get

$$\xi_s = -\frac{1}{\lambda_s} \sum_{pp'} \xi_p \xi_{p'} \tilde{u}^s Q^{pp'}. \quad (19)$$

When we substitute this into the amplitude equations (17) for the principal modes, we get the amplitude equations after adiabatic elimination:

$$\dot{\xi}_i = \lambda_i \xi_i + \sum_{pp'} \xi_p \xi_{p'} \tilde{u}^i Q^{pp'}$$

$$+ \sum_{pp' p''} \left[ \xi_p \xi_{p'} \xi_{p''} \tilde{u}^i \left( K^{pp' p''} - \sum_s \frac{1}{\lambda_s} Q^{ps} \tilde{u}^s Q^{p' p''} - \sum_s \frac{1}{\lambda_s} Q^{sp} \tilde{u}^s Q^{pp''} \right) \right]. \quad (20)$$

Here, $i$ runs over the principal modes only, and so do $p$, $p'$ and $p''$. Compared to the full set of amplitude equations (17), the adiabatic elimination generates a correction in the cubic terms. The quadratic terms remain the same. Again all the coefficients can be computed numerically.
3.4 Coexistence or competition of modes

After obtaining the amplitude equations, the next question is how to investigate the nonlinear interactions between the principal modes. The simplest question is whether the modes compete or coexist. In the analytical treatment of the Häussler system [13], inspection of Eq. (10) shows that modes in one relative orientation (\( \xi_c \) and \( \xi_s \)) compete with modes in the other (\( \eta_c \) and \( \eta_s \)). We here present a numerical method to determine if the modes in a set \( G \) compete with each other or can coexist. This is a problem of mode selection which can be addressed by examining the linear stability of the nonlinear steady-state solution of the amplitude equations [7]. The method can be described as follows.

Let \( G \) be any subset of principal modes

- set \( \xi_i = 0 \) for principal modes that are not in \( G \);
- find nonzero roots \( R \) of the amplitude equations;
- if there exists a root \( R \) at which the system is stable, the modes in \( G \) coexist;
- if for all \( R \) the system is unstable, the modes in \( G \) compete.

The stability at fixed point \( R \) can be established by linear stability analysis. Find the maximum eigenvalue \( \lambda \) of the Jacobian of the amplitude equations evaluated at \( R \). \( R \) is stable if \( \lambda < 0 \), and unstable if \( \lambda > 0 \). We illustrate this method using the amplitude equations (10) of the four principal modes \( \xi_c, \xi_s, \eta_c, \eta_s \).

**Example 1** \( G = \{ \xi_c, \eta_c \} \).

We set \( \xi_s = 0, \eta_s = 0 \), solve the equation, and get \( \xi_c^2 = \eta_c^2 = \frac{4}{\gamma' + \gamma} \equiv d^2 \). At one of the roots, \((d, 0, d, 0)^T\), we obtain the Jacobian

\[
J = \begin{pmatrix}
-\frac{\gamma}{2} 2'd^2 & 0 & -\frac{\gamma}{2} 4'd^2 & 0 \\
0 & 0 & 0 & 0 \\
-\frac{\gamma}{2} 4'd^2 & 0 & -\frac{\gamma}{2} 2'd^2 & 0 \\
0 & 0 & 0 & 0
\end{pmatrix}
\]

The eigenvalues are \( 4' - 2', -4' - 2', 0, 0 \). If \( 4' - 2' > 0 \), a condition which was shown to hold in the analytical treatment, this state is unstable. The other three roots give the same result. We can conclude that modes \( \xi_c \) and \( \eta_c \) compete, which is in agreement with the analytical result.

**Example 2** \( G = \{ \xi_c, \xi_s \} \).

We set \( \eta_c = 0, \eta_s = 0 \), solve the equation, and get \( \xi_c^2 + \xi_s^2 = \frac{4}{\gamma} \). There are infinitely many roots, if \( 2' > 0 \). At one of the roots, \( \xi_c = \xi_s = \sqrt{\frac{2}{\gamma}} \equiv d \), the Jacobian is:

\[
J = \begin{pmatrix}
-\frac{\gamma}{2} 2'd^2 & -\frac{\gamma}{2} 2'd^2 & 0 & 0 \\
-\frac{\gamma}{2} 2'd^2 & -\frac{\gamma}{2} 2'd^2 & 0 & 0 \\
0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0
\end{pmatrix}
\]
The eigenvalues are $-2\gamma, 0, 0, 0$. Because the maximum eigenvalue is 0, linear stability is undetermined. It can be shown that all other roots are also marginally stable. Consequently, modes $\xi_c$ and $\xi_s$ coexist.

This procedure is constructive, and a stable root stands for an instance of mode coexistence. The same method was used analytically in other studies [16]. It can be readily implemented numerically. A problem with numerical calculation could be that when there is degeneracy at the amplitude equations, there might exist infinitely many roots. In this case, a few examples may suffice.

3.5 Excited ancillary modes

The surviving principal modes excite ancillary modes, which together contribute to the final pattern. Without exact values of the modes amplitude, all possibly excited ancillary modes can be identified numerically as follows. We first determine all modes that are excited by (a subset of) principal modes via the quadratic term $Q$. Given a set of principal modes $P_m$, the set of $Q$-excited modes, i.e., the set of modes that are excited via the $Q$ terms is denoted by $S_q(P_m)$, or $S_q$ for short, and defined recursively:

- initially $S_q = P_m$;
- excited($S_q$) = {modes excited by pairs of modes in $S_q$}, indicated by corresponding nonzero coefficients in the amplitude equations before adiabatic elimination;
- $S_q = S_q \cup$ excited($S_q$);
- Repeat until no more modes can be added to $S_q$.

All modes that are excited by $Q$-excited modes via the $K$ terms, $S_k(S_q(P_m))$, are obtained by the same procedure.

4 Experiments

4.1 System setup

In the following examples, we apply the numerical normal mode analysis method described in the last section to the Häussler system, with $N = 8$. All experiments are performed in Matlab.

We experiment with different coupling functions. The function $C(\tau, \tau', \rho, \rho') = C(\tau - \tau', \rho - \rho')$ is modeled by an isotropic Gaussian $C(\tau, \tau', \rho, \rho') = C(\tau - \tau', \rho - \rho') = \frac{1}{2\pi\sigma_1\sigma_2} \exp\left(-\frac{(\tau - \tau')^2}{2\sigma_1^2} - \frac{(\rho - \rho')^2}{2\sigma_2^2}\right)$ with $\sigma_1 = \sigma_2$. An example of an isotropic $C$ function is shown in Fig. 1a, which has $\sigma_1 = \sigma_2 = 1$ and support size $7 \times 7$. The function $T(\tau, \tau', \rho, \rho') = T(\tau - \tau', \rho - \rho')$ is modeled by a Gaussian of different aspect ratio of the two axes, with the direction of the principal axis at $\pi/4$. By $T3$ we refer to the function with aspect ratio 3 ($\sigma_1 = 1, \sigma_2 = 3$), by $T5$ to that with aspect ratio 5 ($\sigma_1 = 1, \sigma_2 = 5$), shown in Fig. 1b and c, respectively.

4.2 Fourier modes

As has been pointed out, the eigenfunctions of the Häussler system under periodic boundary condition are the Fourier basis $e^{ikl}$ (see Eq. 8). A few examples of the
Coupling functions in the form of 2D Gaussian.

(a) $C$ function; (b) $T$ function with aspect ratio 3; (c) $T$ function with aspect ratio 5

Fourier modes are shown in Fig. 2. The left eigenfunction corresponding to mode $e^{ikl}$ is $\frac{1}{N^2} (e^{ikl})^H$, where $H$ denotes the conjugate transpose. As a first step, we directly use Fourier modes to derive the amplitude equations. The equations obtained numerically will be compared to the analytical results of [13], serving as a verification of our numerical method.

The eigenvalues of the Fourier modes are calculated numerically from the linear term. For the coupling function $C$, the modes $e^{\pm 1 \pm 1}$ all have the same, maximal, eigenvalue. The control parameter $\alpha$ can be set such that only this eigenvalue is positive, so that these are the only principal modes. In the following examples, $\alpha$ is chosen such that the real parts of the largest and second largest eigenvalues are of the same magnitude but different sign.

The amplitude equations obtained numerically have the same form as those derived analytically:

\begin{align}
\dot{\xi}_{11} &= (\lambda + a\xi_{11}\xi_{-1-1} + b\xi_{1-1}\xi_{-11})\xi_{11} \\
\dot{\xi}_{-1-1} &= (\lambda + a\xi_{11}\xi_{-1-1} + b\xi_{1-1}\xi_{-11})\xi_{-1-1} \\
\dot{\xi}_{1-1} &= (\lambda + b\xi_{11}\xi_{-1-1} + a\xi_{1-1}\xi_{-11})\xi_{1-1} \\
\dot{\xi}_{-11} &= (\lambda + b\xi_{11}\xi_{-1-1} + a\xi_{1-1}\xi_{-11})\xi_{-11}.
\end{align}

(21)

For $\alpha = 0.6363$, we obtain $\lambda = 0.1257$ and coefficients $a = -1.5240$, $b = -3.0480$ when setting ancillary amplitudes to zero, and $a = 1.3368$, $b = -2.0466$.
after adiabatic approximation and elimination of those amplitudes from Eq. (17), resulting in Eq. (20). These coefficients match precisely the theoretical results in [13].

For the coupling function $T$, the largest eigenvalue has multiplicity of only 2 (modes $e^{11}$ and $e^{-1-1}$). By setting $\alpha$ such that only these two modes grow, we obtain the amplitude equations

$$\dot{\xi}_{11} = (\lambda + a\xi_{11}\xi_{-1-1})\xi_{11}$$
$$\dot{\xi}_{-1-1} = (\lambda + a\xi_{11}\xi_{-1-1})\xi_{-1-1}.$$  \hspace{1cm} (22)

This form is the same for both coupling functions $T3$ and $T5$. For this case there are no theoretical results given in [13] as the theory deals only with separable coupling functions that have certain properties which the $T$ functions do not. For $T3$ (Fig. 1b), when $\alpha = 0.8874$, we get $\lambda = 0.0615$, $a = -1.8978$ with zero ancillary amplitudes, and $a = 25.4743$ after adiabatic elimination. For $T5$ (Fig. 1c), when $\alpha = 0.8922$, we get $\lambda = 0.0589$, $a = -1.9022$ (0 ancillary amplitudes) and $a = 26.9021$ (adiabatic approximation).

4.3 Numerical modes

4.3.1 Modes

Now we determine the modes numerically, by calculating the Jacobian matrix evaluated at $W = 1$, and calculate its (right and left) eigenvectors and corresponding eigenvalues. Parameter $\alpha$ is set to be the same as in the corresponding Fourier mode case. The eigenvectors together with their eigenvalues are shown in Fig. 3, for the coupling function $C$.

4.3.2 Amplitude equations

The first four modes have the same positive eigenvalues. Denoting their amplitudes as $\xi_i$, with $i = 1, 2, 3, 4$, we numerically obtain the amplitude equations

$$\dot{\xi}_1 = \left(\lambda + a(\xi_1^2 + \xi_2^2) + b(\xi_3^2 + \xi_4^2)\right)\xi_1$$
$$\dot{\xi}_2 = \left(\lambda + a(\xi_1^2 + \xi_2^2) + b(\xi_3^2 + \xi_4^2)\right)\xi_2$$
$$\dot{\xi}_3 = \left(\lambda + b(\xi_1^2 + \xi_2^2) + a(\xi_3^2 + \xi_4^2)\right)\xi_3$$
$$\dot{\xi}_4 = \left(\lambda + b(\xi_1^2 + \xi_2^2) + a(\xi_3^2 + \xi_4^2)\right)\xi_4.$$  \hspace{1cm} (23)

The form of these equations is the same as that of their analytical counterpart (see Eq. 10). The coefficients obtained are $\lambda = 0.1257$, $a = -0.7620$, $b = -1.5240$ (0 ancillary amplitudes) and $a = 0.6684$, $b = -1.0233$ (adiabatic approximation). Note that the coefficients computed here are exactly half of their respective value computed using Fourier modes. This is due to the different normalization of the eigenmodes.
4.3.3 Excited ancillary modes

The amplitude equations describe the evolution of principal modes, from which the winners can be obtained. The winning principal modes excite ancillary modes, which can be obtained following the procedure in Sect. 3.5. As an example, we assume that the two principal modes of the left orientation, as shown in Fig. 4a, win, and obtain all modes excited by them. All those that are excited via the quadratic term are shown in Fig. 4b. There are seven such $Q$-excited modes, forming set $S_q$. All modes that are excited by modes in $S_q$ via the $K$ term are exactly the same modes as in $S_q$. This indicates that these seven modes are all modes that are excited by the two principal modes in Fig. 4a.

Note that these seven modes are only a small subset of all $N^2 = 64$ modes, indicating a system with much reduced degrees of freedom. If all four principal modes are active, there are 32 excited modes altogether (not shown).

4.3.4 $T$ coupling function

The numerically determined modes for the coupling function $T3$ are shown in Fig. 5. The first two modes have the same positive eigenvalue. Denoting their amplitudes as $\xi_i$, with $i = 1, 2$, we numerically obtain the amplitude equations.
Fig. 4  All modes that are excited by principal modes. a Winning principal modes $P_m$; b excited modes via the $Q$ terms $S_q(P_m)$, which is the same set as modes further excited via the $K$ terms $S_k(S_q(P_m))$.

Fig. 5  Numerically obtained modes and their eigenvalues for coupling function $T3$. Shown are the 16 modes with the largest eigenvalues.
\[
\begin{align*}
\dot{\xi}_1 &= (\lambda + a(\xi_1^2 + \xi_2^2))\xi_1 \\
\dot{\xi}_2 &= (\lambda + a(\xi_1^2 + \xi_2^2))\xi_2.
\end{align*}
\] (24)

The coefficients obtained are \( \lambda = 0.0615 \) (same as Fourier modes), \( a = -0.9489 \) (0 ancillary amplitudes) and \( a = 12.7342 \) (after adiabatic elimination). Again there is no analytical result in [13] to compare with. Note that \( a \) becomes positive after adiabatic elimination. A positive \( a \) makes the system unbounded, with 0 being the only, unstable, root. In this case, a higher-order approximation is needed.

5 Conclusion

5.1 Summary and computational issues

We here present a method for the analysis of dynamical systems with the help of a numerically performed normal mode extraction, to open the way to the treatment of realistic systems of lower symmetry. The formulation presented here for obtaining amplitude equations is not new in principle, following closely the treatment given in [12]. Our point is rather that whereas the approach lay essentially dormant for decades, as due to its complications in detail it was restricted to unrealistically idealized model cases, it now can be developed into a routine tool for realistic systems on the basis of automated numerical implementation.

We have applied this method to a system for the ontogenesis of retinotopy, the Häussler system [13] where an analytical treatment exists, and obtained identical results, verifying the correctness of our method. Without any adjustment, we have also obtained results for the case of a less symmetrical coupling function. The same method applies to inhomogeneous boundary conditions, and the results will be presented in a separate paper.

Our method has been formulated on dynamical systems with third-order polynomial dynamics. Higher order polynomials can be handled analogously. The method can be applied to more general systems through polynomial expansion. Of polynomial dynamical systems, this method is particularly suitable to those in which the nonlinear terms are expressed in matrix form, i.e., where the matrices \( Q \) and \( K \) are given explicitly. In the Häussler system that we analyzed as an example, these matrices have to be calculated from the corresponding functions \( Q(V) \) and \( K(V) \). In this case, if the system size is large, there may not be memory big enough to even store these matrices directly. A solution to this problem is to modify our procedure such that entries are stored only when needed. We are currently working on this formulation.

There are other issues in numerical calculation that need to be addressed as they arise. One of the difficulties we encountered is the orientation of eigenvectors with degenerate eigenvalues. As any linear combinations of eigenvectors sharing a same eigenvalue will also be eigenvectors of this eigenvalue, the numerical procedure may give out a basis not adapted to the structure of the system’s nonlinearities. This is not an issue, however, for less symmetrical systems, which are exactly the target of our methods. The modes in Fig. 3 were actually computed from the \( T \)
coupling function, as this results in the same eigenspace and suppresses mixtures of the diagonal modes that eventually prevail in the $C$ system due to nonlinear competition.

5.2 Mode interactions in self-organizing systems

Our analysis of the Häussler system furthered our understanding of mode interactions in self-organizing systems. A partial answer to our initial question as to why the system with task-adapted coupling function $T$ is faster than that with the isotropic function $C$ can be read from their amplitude equations (Eq. 23 vs. 24). Compared to $C$, $T$ does not need to break the symmetry between diagonals in the two orientations. As in general symmetry breaking of this kind is very time consuming, this is one of the reasons that the $T$ system is faster than the $C$ system.

The contribution of excited ancillary modes to the final state has been largely ignored. Presumably after the competition among principal modes, only a small number of ancillary modes will be excited so that analyzing their dynamics is possible. The Häussler system may in this context be an instructive example. Once the competition between principal modes has been decided, the surviving principal modes excite only a very sparse subset of the ancillary modes. All in all, out of the $N^2$ modes only the less than $N$ modes that agree in orientation and phase with the winning principal mode pair are thus excited, see Fig. 4. All of these conspire to sharpen the diagonal such that finally a one-to-one mapping between retina and tectum develops.

In the context of organizing systems, the general aspect of this is that early symmetry-breaking decisions are followed by the gradual excitation of finer-scale modes that lead to system differentiation. What may be less typical in the Häussler system is that there is only one (early) symmetry breaking event. Other systems are likely to come again and again to decision points, so that the Häussler system can be a model only for a single lap from one decision point to the next. In organismic ontogenesis, genetic regulation determines those decisions; in other systems they may be determined by chance. This involves the study of secondary instability [4].

With the framework to analyze general systems, our next step is to analyze other dynamical systems in biology. Note that for systems with attractor dynamics, such as Hopfield networks [15], the analysis shows that all modes decay exponentially to their stable state, which, in a sense, is an uninteresting behavior. By analyzing and comparing various self-organizing biological systems, we can hope to reveal principles of their organization.

References