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PATTERN FORMING INSTABILITIES DRIVEN BY NON-DIFFUSIVE INTERACTIONS

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Abstract. In analogy to the analysis of minimal conditions for the formation of diffusion driven instabilities in the sense of Turing, in this paper minimal conditions for a class of kinetic equations with mass conservation are discussed, whose solutions show patterns with a characteristic wavelength. The related linearized systems are analyzed, and the minimal number of equations is derived, which is needed for specific patterns to occur.

1. **Introduction.** Pattern formation is ubiquitous in biological and chemical systems. Being able to distinguish between the possible underlying mechanisms driving these patterns and their related function, is an important aim for a better understanding and for experimental control. Patterns generated by diffusive instabilities are quite well understood. In his pioneering work (cf. [27]) Turing proved, that for chemical reactions diffusion can drive an otherwise stable system towards pattern formation with a characteristic wavelength or characteristic time period. This idea of diffusive morphogens, has later been applied to many pattern forming biological systems (cf. [12], [18], [19]), only to name a few of the many references on this topic.

A main part of Turing's analysis was devoted to linearized reaction-diffusion systems. This is often sufficient in order to obtain estimates on the basic quantitative features of the observed patterns, like their characteristic wavelength; or in the case of dynamic patterns, their speed of propagation. The linear analysis, of

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course, only predicts exponential growth of the chemical, respectively morphogen concentrations.

There are, however, structure forming processes in biology, where diffusive signals do not seem to play the major role. An example for this are the counter migrating rippling waves in populations of myxobacteria which occur before their final aggregation and fruiting body formation, [6]. These waves are assumed to result from a local, i.e. cell-cell contact induced, exchange of a so-called C-signal. Also in a number of other signaling processes, e.g. within cellular tissues a localized/non-diffusive exchange of signals between cells seems to play an important role. This is one main reason to have a closer look at the pattern forming behavior of such systems. Further, the aggregation process of myxobacteria happens during a state without cell division, so mass is conserved. Interestingly it is not obvious how to obtain nontrivial patterns for the resulting type of models, in particular if no delay terms are included into the equations. These systems differ from the before mentioned reaction-diffusion systems and their approximations. The systems considered in the present paper have a dispersion relation which asymptotically is a horizontal line in the complex plane for large wavenumbers. So the fastest growing mode could in principle be infinity. To find patterns in our case, we start from a situation where the most unstable branch of the dispersion relation is a line with constant real part in the complex plane. Then we perturb suitably - which is not trivial - such, that the slowest rate of growth in the dispersion relation happens for small and for large values of the wavenumber, i.e. the maximal rate of growth is achieved for a finite, positive wavenumber. With such arguments we do not only obtain a positive real part for the wavelength but also a maximum which is not infinity.

From a mathematical point of view examples for systems, where pattern formation results from non-diffusive signaling, are kinetic equations of the following type

$$\partial_t f(t,x,c) + U(c) \cdot \partial_x f(t,x,c) + \partial_c [K[f(t,x,c)]] = 0. \tag{1}$$

Here $\{c\}$ denotes a set of internal variables characterizing the state of the cells. Further the total mass of the cells is conserved. For cell movement in one spatial dimension $\{c\}$ would also include the direction of motion (right or left), in higher spatial dimensions the cell orientations. Variables like chemical concentrations and the fraction of occupied cell surface receptors could also be included. The set $\{c\}$ can be continuous or discrete. In the discrete case the operator ∂_c must be replaced by a suitable "discrete divergence operator", which we will specify later.

The function $f(t,x,c)$ can be thought of as the cell density, and $K[f(t,x,c)]$ is an additive or an integral operator, in general non-linear, which describes the transitions of the cells w.r.t. the internal variables $\{c\}$. This operator acts on the densities $f(t,x,\cdot)$ locally, i.e. $K[f(t,x,\cdot)]$ depends on $f(t,x,\cdot)$ at point x only. Examples for equations of type (1) as models for pattern formation in biology can be found for instance in [8], [9], [10], [11], [15], [17], [20], and [23].

As we have indicated above, model (1) is quite different from the parabolic systems considered by Turing. Further, linearization around a homogeneous state does not provide any specific wavelength, in case $\{c\}$ contains only two elements (cf. [17])). Systems close to, but more general than (1), which do yield specific wavelengths on the linearized level have been discussed in the literature. In [14] systems with a structure similar to (1) are considered, which contain additional diffusion for the cell densities and which exhibit nontrivial patterns. Further, the cell states are characterized by a continuous variable in this case, which is additionally affected by a noise term. In [2] examples are discussed, where next to the terms like in (1), an additional delay term occurs, which also produces nontrivial patterns near homogeneous states. It is natural to ask, if there exist examples for systems of type (1), which yield non trivial patterns near homogeneous solutions, where neither diffusion nor explicit delays are responsible for pattern formation.

In this paper we will provide sufficient conditions for examples of equations of type (1), such that suitable linearizations show an instability with a characteristic wavelength. In order to obtain the onset of nontrivial patterns on the linearized level a minimal complexity of the model is needed. In case of Turing's systems at least two different species are necessary. In our case at least three equations are needed.

A paper close to our setting is [13], where

$$a_t + \Gamma a_x = M\,(b-a) + \frac{1}{2} f\,(a+b)\ \ ,\ b_t - \Gamma b_x = M\,(a-b) + \frac{1}{2} f\,(a+b) \qquad (2)$$

was studied, with $a = (\alpha_1, \alpha_2)^t$, $b = (\beta_1, \beta_2)^t$, $f\,(u) = (f_1(u_1, u_2), f_2(u_1, u_2))^t$ and diagonal matrices Γ, M with diagonal entries γ_1, γ_2 and μ_1, μ_2. A key feature of (2) is that the reactions between the species generally change the total concentration $\int \sum_{i=1}^{2} (\alpha_i + \beta_i)\ dx$.
This is different in (1) where $\int\int f\,(t,x,c)\,dxdc$ is preserved. This crucially influences the dispersion relation.

In [13] a number of instabilities for (2) are considered. Among them a kind of hyperbolic version of Turing's instability. For an intuitive explanation of this consider $\|M\| \to \infty$, $\|\Gamma\| \to \infty$, $\Gamma^2/(2M) \to \tilde{D}$, where $\|\cdot\|$ denotes a matrix norm and $\tilde{D}$ is a diagonal matrix with diagonal entries $\tilde{d}_1, \tilde{d}_2 > 0$. Formally, solutions which have a characteristic wavelength larger than $1/\sqrt{\|M\|}$ can be approximated by solutions of the parabolic system

$$u_t = \tilde{D} u_{xx} + f\,(u) \quad \text{with} \quad u = a + b\ . \qquad (3)$$

Solutions of a linearization of this model near a homogeneous steady state yield pattern formation with a specific wavelength of order one. So for large enough wavelengths and under suitable assumptions on M and $\tilde{D}$ one can expect analogous instabilities for (2) as the ones obtained by Turing for (3) even though the dispersion relations associated to (2) are different from the ones for (3) for very large wavelengths, due to the change of character of the problem from hyperbolic to parabolic.
The instabilities considered in this paper for conservation laws of type (1) differ from this and the resulting patterns are traveling waves with a characteristic wavelength and wave velocity.

Further, in [13] sets of parameters are studied which yield Hopf bifurcations for (2). A characteristic wavelength for solutions associated to such bifurcations has still to be proved.

The plan of this paper is as follows. In Section 2 we give a precise definition of what we call a pattern forming system in the present context. In Section 3 we briefly discuss some of Turing's results. In Section 4 we study the pattern forming properties of equations of type (1). In Subsection 4.1 we recall a situation for which pattern formation can not be decided by linear analysis. In Subsection 4.2 and the following subsections, necessary conditions for patterns with a defined wavelength on the linearized level are given. In Section 5 minimal models for rippling of myxobacteria are discussed, without assuming the existence of an internal clock or of delays. Further on, the validity of this model is checked by means of a biological test experiment and interpreted.

2. **Pattern forming equations.**

We will restrict our analysis to linearized equations. So we are interested in problems of the form

$$u_t = Bu \ , \tag{4}$$

where B is a linear operator, invariant under translations, i.e. $B[u(\cdot + a)] = B[u](\cdot + a)$, $a \in \mathbb{R}^N$.

The function $y \to u(y,t)$ maps $\mathbb{R}^N$ into a suitable function space X, describing the variables needed to characterize a "macroscopic" region $[y, y+dy]$. Typically X will include chemical concentrations, internal cell variables, cell orientations and others. It is well known that this type of operators can be analyzed by Fourier analysis. This amounts to consider the action of B on modes $\exp(ikx)$ for $k \in \mathbb{R}^N$ i.e.

$$B\left(e^{iky}V\right) = \left[\tilde{B}(k)\,V\right] e^{iky} \ \ , \ \ V \in X \ ,$$

where $\tilde{B}(k)$ is a linear operator acting on X. We can then look for solutions of (4) of the form $u = e^{\omega t + iky}V$, where V is a eigenfunction of

$$\omega V = \tilde{B}(k) \cdot V \ . \tag{5}$$

Under some general compactness assumptions, the eigenvalues of (5) are a discrete set $\{\omega_1(k), \omega_2(k), ...\}$ for each $k \in \mathbb{R}^N$. For a perturbation $u(y,0) = u_0(y) = V_0 e^{iky}$ with wavenumber k we aim to calculate its corresponding growth rate. The shortest way to do so is to calculate

$$\Omega(k) \equiv \max_j \{\mathrm{Re}(\omega_j(k))\} \ . \tag{6}$$

So we use the following definition for a pattern generating system:

Definition 2.1. Equation (4) is said to generate patterns, if $\Omega = \Omega(k)$ in (6) achieves a global maximum at a finite number of nonzero values $k_{0,i}, \ i = 1, ..., \ell$. In this case solutions of (4) with suitable initial data develop patterns with wavelength $\lambda_i = \frac{2\pi}{k_{0,i}}$.

If $\mathrm{Im}(\omega_j(k_{0,i})) \neq 0$ for some $i \in \{1, ..., \ell\}$, then we will say that (4) generates oscillatory patterns.

If $\mathrm{Im}(\omega_j(k_{0,i})) = 0$ for every $i \in \{1, ..., \ell\}$ we will say that (4) generates stationary patterns.

If for every $\delta > 0$, $\Omega(k)$ achieves a global maximum in $\mathbb{R}^N \setminus B_\delta(0)$ at a finite number of points, then we will say that equation (4) generates patterns for wavelengths smaller than $2\pi/\delta$.

3. **Turing's instabilities.**

Let us briefly recall the instability results derived by Turing in [27] for reaction-diffusion systems within the above mentioned framework. Here we restrict ourselves to one dimension. For this case in [27] the pattern-forming properties of equations of type

$$\partial_t u = \tilde{D}\partial_x^2 u + Au \ . \tag{7}$$

were studied, where $u = u(x,t)$ has values in $\mathbb{R}^N$ and $\tilde{D}, A \in M_N(\mathbb{R})$ which is the set of real $N \times N$ matrices, $\tilde{D}$ is a diagonal matrix with diagonal entries $\tilde{D}_i > 0$ for $i = 1, ..., N$, and $A = (a_{ij})_{i,j}$. System (7) can be obtained from the linearization of a reaction-diffusion system without cross-diffusion terms near a homogeneous state.

Theorem 3.1. *(Turing, cf. [27]).*

- *For $N = 1$ equation (7) does not generate patterns for any $A \in \mathbb{R}$ in the sense of Definition 2.1.*
- *For $N = 2$, system (7) generates stationary patterns in the sense of Definition 2.1 if*

$$a_{11} + a_{22} < 0 \ , \ detA > 0 \ , \ a_{11}\tilde{D}_2 + a_{22}\tilde{D}_1 > 2\sqrt{\tilde{D}_1\tilde{D}_2 detA} > 0 \ . \tag{8}$$

  On the other hand, (7) does not generate oscillatory patterns for any choice of $A \in M_2(\mathbb{R})$ in the sense of Definition 2.1.
- *For $N = 3$ there exists an open set of matrices $A \in M_3(\mathbb{R})$ such that (7) generates oscillatory patterns in the sense of Definition 2.1.*

Remark 1. Several results for Turing-type instabilities, also by Turing himself, were derived for bounded domains with periodic or with Neumann boundary conditions. Here we consider the whole space. Thus the discrete character of the spectrum of the operators does not have to be taken into account.

This means, that linear reaction-diffusion equations can generate nontrivial patterns with specific wavelengths, if at least two species are involved. Moreover, patterns in the sense of Definition 2.1 with nontrivial characteristic length and time scales can be generated, if at least three species are involved. It is well known that conditions (8) can be interpreted as the interplay between a short range acting chemical activator and a long range acting chemical inhibitor, with the diffusion coefficient of the inhibitor being larger than the one of the activator, cf. [12].

4. Patterns without diffusive interaction.

First we define the general framework for our analysis, since to our opinion there are more interesting points to explore in the future for the given setting, than we can present here. Later we will deal with specific cases, some of which are also relevant for biological applications. The equations we are finally dealing with in this paper are of type (14), (15).

We suggest to study the pattern forming properties of linear equations of type

$$\partial_t f(t,x,c) + U(c) \cdot \partial_x f(t,x,c) + \partial_c [L[f]](t,x,c) = 0 \ , \tag{9}$$

where f is the concentration of "cells" in the state $\{c\}$ at a given time t at point $x \in \mathbb{R}$, which in this section is one-dimensional, and where L is the linearization of K, acting on f as explained in the introduction. Let the space of states be measurable and $\mu(\cdot)$ be the related measure. Equations of type (9) naturally arise when systems of type (1) are linearized around a spatially homogeneous (patternless) state. If the set $\{c\}$ is discrete, then the differential operator ∂_c has to be replaced by a suitable discrete derivative. In general, we will assume that the operator ∂_c is a flux in the space of states, which means

$$\partial_c g(t,x,c) = -\int F(c,c')\, g(t,x,c')\, d\mu(c') + \int F(c',c)\, g(t,x,c)\, d\mu(c') \ .$$

In the discrete case such operators reduce to finite sums. Their most relevant property is

$$\int \partial_c g(t,x,c)\, d\mu(c) = -\int\int F(c,c')\, g(t,x,c')\, d\mu(c')\, d\mu(c) + \int\int F(c',c)\, g(t,x,c)\, d\mu(c')\, d\mu(c) = 0\ .$$

Therefore, these interactions locally conserve $\int f(t,x,c)\, d\mu(c)$. As an example suppose that the space of internal states $\{c\}$ is the real line and let μ be the Lebesgue measure $d\mu(c) = dc$. Let

$$F(c,c') = \delta_0(c - c' - h)/h\ ,$$

where δ_0 is the Dirac measure in order to describe transition rates, which transfer state c to state $c+h$. Then

$$\partial_c g(t,x,c) = [-g(t,x,c-h) + g(t,x,c)]/h\ .$$

$$\text{Let}\quad L[f](t,x,c) = a(c)\, f(t,x,c) \tag{10}$$

for a suitable function $a(c)$ and

$$\partial_c(L[f](t,x,c)) = [-a(c-h)\, f(t,x,c-h) + a(c)\, f(t,x,c)]/h\ .$$

For $h \to 0$ we obtain

$$\partial_c g(t,x,c) = \frac{\partial}{\partial c}\Big[a(c)\, f(t,x,c)\Big]\ .$$

Therefore (9) becomes

$$\partial_t f(t,x,c) + U(c)\cdot \partial_x f(t,x,c) + \frac{\partial}{\partial c}[a(c)\, f(t,x,c)] = 0\ .$$

This equation naturally arises, when studying stage structured population models with spatial dynamics. See for instance in [7], [8]. Some general references for modeling and analysis of stage/age structured populations are e.g. [4], [5] [21], [26], and [24].

Another typical choice of internal variables is a discrete set $\{c\} = \{s_1, s_2, s_3, ..., s_N\}$. Define the shift operator: $\tau_+(s_k) = s_{k+1}$ for $k = 1, ..., N$ with $s_{N+1} := s_1$ and τ_- analogously. The discrete derivative $\tilde{\partial}_c$ describes the sequential change between states and is defined by

$$\tilde{\partial}_c g(x,c) \equiv g(x,c) - g\Big(x, \tau_-(c)\Big)\ . \tag{11}$$

With $L[f]$ given as in (10) equation (9) becomes

$$\partial_t f(t,x,c) + U(c)\cdot \partial_x f(t,x,c) + a(\tau_+(c))\, f(t,x,\tau_+(c)) - a(c)\, f(t,x,c) = 0\ .$$

This is a finite dimensional system for N variables, namely $f(t,x,s_1), f(t,x,s_2), ..., f(t,x,s_N)$. Equations of type (1) and (9) arise for instance when modeling systems of cells which interact with each other via direct cell-cell contact and not by means of any diffusive chemical. The transport of information in space in this context is purely due to motion/drift of the cells themselves. An interesting example for pattern formation due to such processes are the rippling patterns of myxobacteria which we will discuss in the last section of the paper.

Also in [13] equations without diffusive interactions were studied, where mass was not conserved and stationary patterns were obtained. In our present context additionally the number of "cells" which are involved is preserved. Therefore pattern formation occurs solely due to cell interaction and transitions between cell states, and does not related to natural growth and death processes. Due to this assumption the dispersion relation becomes crucially different.

4.1. **A case without pattern formation.** First we relate some of the results in [17] to the case $N = 1$ in Theorem 3.1. Consider a system with two internal variables $\{c\}$ denoted by $+$ and $-$. To connect with the notation in [17], let

$$f(x,+,t) = u_+(x,t) \ , \ f(x,-,t) = u_-(x,t) \ , \ U(+) = U_+ \ , \ U(-) = U_- \ .$$

The most general local operator $L[f]$ in (9) and the "discrete derivative" operator (11) then read

$$\begin{pmatrix} L[f]_+ \\ L[f]_- \end{pmatrix} = \begin{pmatrix} a_{1,1} & a_{1,2} \\ a_{2,1} & a_{2,2} \end{pmatrix} \begin{pmatrix} u_+ \\ u_- \end{pmatrix} \quad , \quad \begin{pmatrix} (\partial_c g)_+ \\ (\partial_c g)_- \end{pmatrix} = \begin{pmatrix} (g)_+ - (g)_- \\ (g)_- - (g)_+ \end{pmatrix} .$$

with $a_{i,j} \in \mathbb{R}$ for $i,j \in \{1,2\}$. Therefore, (9) reduces to

$$\begin{pmatrix} \partial_t u_+ \\ \partial_t u_- \end{pmatrix} + \begin{pmatrix} U_+\partial_x u_+ \\ U_-\partial_x u_- \end{pmatrix} = \begin{pmatrix} a_{11}u_+ + a_{12}u_- - (a_{21}u_+ + a_{22}u_-) \\ a_{21}u_+ + a_{22}u_- - (a_{11}u_+ + a_{12}u_-) \end{pmatrix} \tag{12}$$

With the change of variables $x \to x - \frac{U_+ + U_-}{2}t$, we can assume w.l.o.g. that $U_+ = -U_- =: U$. This transformation does not change the non-pattern or pattern forming behavior of the system. Also, the characteristic wavelength of the patterns, if existent, does not change. However, any standing pattern could change to a traveling wave type of pattern or vice versa. Systems of type (12) were obtained in [17] from

$$\begin{pmatrix} \partial_t u_+ \\ \partial_t u_- \end{pmatrix} + \begin{pmatrix} U\partial_x u_+ \\ -U\partial_x u_- \end{pmatrix} = \begin{pmatrix} -\lambda(u_+,u_-)\,u_+ + \lambda(u_-,u_+)\,u_- \\ -\lambda(u_-,u_+)\,u_- + \lambda(u_+,u_-)\,u_+ \end{pmatrix} \tag{13}$$

for general functions λ by linearization around homogeneous stationary solutions. Let us restate some results obtained in [17] in the above given terminology.

Theorem 4.1. *([17]) The linear system (12) with $U_+ = -U_- \equiv U$ does not generate patterns in the sense of Definition 2.1 for any choice of $U \in \mathbb{R}$,*
$T = -a_{11} + a_{21}$, $S = -a_{22} + a_{12}$.

Proof. W.l.o.g. assume $U \neq 0$, otherwise $\omega = \omega(k)$ in (6) is independent on k. The dispersion relation associated to (12) with $U_+ = -U_- \equiv U$ can be computed by

$$\det \begin{pmatrix} \omega + ikU + T & -S \\ -T & \omega - ikU + S \end{pmatrix} = 0 \ .$$

$$\text{Then} \quad \omega_\pm = \frac{1}{2}\left[-(T+S) \pm \left[(T+S)^2 - 4\left(ikU(S-T) + k^2U^2\right)\right]^{\frac{1}{2}}\right] \ .$$

The behavior of $\Omega(k) = \max\{\mathrm{Re}(\omega_+(k)), \mathrm{Re}(\omega_-(k))\}$ is analyzed by studying

$$h(k) \equiv \mathrm{Re}\left\{\left[(T+S)^2 - 4\left(ikU(S-T) + k^2U^2\right)\right]^{\frac{1}{2}}\right\} = \mathrm{Re}\sqrt{(a^2 - b^2k^2) + cik}$$

with $a^2 \equiv (T+S)^2$, $b^2 \equiv 4U^2$, $c = -4U(S-T) = 4U(T-S)$, and $\sqrt{\cdot}$ being the complex root with positive real part. By symmetry $h(k) = h(-k)$. Now we show that $h(k)$ is monotone in $[0,\infty)$. Using again symmetry, we can restrict our analysis to the case $c \geq 0$. Since $U \neq 0$ we have $b^2 > 0$ and

$$h(k) = \sqrt[4]{(a^2 - b^2k^2)^2 + c^2k^2}\sqrt{\left[1 + \cos\left(\arctan\left(\frac{ck}{(a^2 - b^2k^2)}\right)\right)\right]\Big/2} \ \geq 0 \ ,$$

where $\arctan(\cdot) \in [0,\pi]$, $\cos(\cdot) \in [0,\pi]$. After some computations we obtain

$$h(k) = \frac{1}{\sqrt{2}}\sqrt{H(k)}\ , \text{ where } H(k) \equiv \sqrt{\left(a^2 - b^2k^2\right)^2 + c^2k^2} + \left(a^2 - b^2k^2\right)\ .$$

We have that

$$\frac{dH(k)}{dk} = \frac{k\left(c^2 - 2b^2H(k)\right)}{\sqrt{\left(a^2 - b^2k^2\right)^2 + c^2k^2}}\ , \text{ and } H(0) = 2a^2\ .$$

So $H(k)$ is increasing if $4a^2b^2 < c^2$, and decreasing if $4a^2b^2 > c^2$. If $4a^2b^2 = c^2$, $H(k)$ is constant. Thus $H(\cdot)$ and $h(k)$ are monotone, and our theorem follows. □

4.2. **The pattern forming case.** Here and in the following we study a particular class of equations of type (9), namely

$$\partial_t f + U\cdot\partial_x f + DAf = 0\ , \text{ where} \tag{14}$$

$$D = \begin{pmatrix} 1 & 0 & ... & -1 \\ -1 & 1 & ... & 0 \\ & ... & ... & \\ 0 & ... & -1 & 1 \end{pmatrix}\ ,\ U = \begin{pmatrix} U_1 & 0 & ... & 0 \\ 0 & U_2 & ... & 0 \\ & ... & ... & \\ 0 & ... & 0 & U_N \end{pmatrix}\ . \tag{15}$$

Here D describes the transition from state to state analogous to (11), and A is a square matrix in $M_N(\mathbb{R})$. The space of "internal cell states" $\{c\}$ is the set $\{1,2,...,N\}$. First we begin our analysis with a generic matrix A. The dispersion relation associated to (14) solves

$$zw + ikU\cdot w + DAw = 0 \tag{16}$$

Here and in the following we often omit the identity matrix in arithmetic expressions with scalar quantities and matrices.

In the subsequent arguments the following properties of the matrix DA will be relevant.

Proposition 1. *Let D be given as in (15). Then, the matrix DA has a zero eigenvalue. Moreover*

$$b := (1,\cdots,1)^t \tag{17}$$

is an element of the kernel of $(DA)^t$, which is the transposed matrix of DA.

Proof. We have $\det(DA) = \det(D)\det(A) = 0$ since $\det D = 0$. Therefore 0 is an element of the spectrum of DA. Since $D^t b = 0$,

$$(DA)^t b = A^t D^t b = A^t(0) = 0\ . \tag{18}$$

Thus $b \in \ker((DA)^t)$. □

4.3. **Nondegenerate U, non-symmetric A.**

Definition 4.2. We call U in (15) nondegenerate, if $U_i \neq U_j$ for any $i \neq j$.

In this subsection we show how to obtain a class of matrices A for which (14) exhibits nontrivial patterns when U is nondegenerate. The key idea is to choose $A = A_0 + \varepsilon M$, where A_0 yields a "hyperbolic" dispersion relation for (14). By this we mean that the most unstable part of the spectrum of A_0 lies on the imaginary axis. Notice, that for a pure transport equation/first order hyperbolic equation the spectrum is the imaginary axis. The matrix εM will then be chosen as a small perturbation of A_0 that will deform that part of the spectrum into a curve which yields pattern formation in the sense of Definition 2.1. So pattern forming solutions

bifurcate from the non-pattern forming state $\varepsilon = 0$.
More precisely, we assume

Assumption 1. *The set of eigenvectors of DA_0 with zero eigenvalue is the linear subspace generated by $e_1 = (1, 0, \cdots, 0)^t \in \mathbb{R}^N$. Moreover $U_1 \neq 0$.*

As a consequence, the spectrum of the set of solutions of the family of eigenvalue problems

$$zw + ikU \cdot w + DA_0 w = 0 \ , \quad k \in \mathbb{R} \tag{19}$$

contains the line $\{z = -ikU_1\}$, i.e. the spectrum associated to A_0 is "hyperbolic".

Assumption 2. *All solutions of (19) which are different from $-ikU_1$ are located in the half-plane $\{\mathrm{Re}\,(z) < -\nu_0\}$ for some $\nu_0 > 0$.*

Remark 2. For convenience we have chosen e_1 as a distinguished eigenvector for DA_0. But e_1 cannot be rotated without modifying the matrix U. Thus we do not consider the most general choice of matrices A_0 yielding hyperbolic behavior. But the main goal of this paper is to find examples for instabilities. It would be interesting though to classify the matrices A_0 in general, which yield hyperbolic behavior for the spectrum. A first attempt to do so is given in the Diploma-thesis by Julian Scheuer [25].
The condition $U_1 \neq 0$ is essential, since without a characteristic speed it would not be possible to obtain a characteristic wavelength. W.l.o.g. let $U_1 > 0$.

Now we analyze the dispersion relation associated to (14) for $A = A_0 + \varepsilon M$ where $\varepsilon > 0$ is small. The spectrum of (16) can be computed in a perturbative manner and the following lemma yields a preliminary estimate of its location.

Lemma 4.3. *Let A_0 satisfy Assumptions 1 and 2. Let $A = A_0 + \varepsilon M$. Then, there exist positive constants $C = C\,(A_0, M)$, β and ε_0, independent of ε, such that for each $k \in \mathbb{R}$ and $|\varepsilon| \leq \varepsilon_0$ the spectrum associated to (16) consists of*
(i) an eigenvalue $z_1 = z_1\,(k)$ satisfying $|\mathrm{Re}\,(z_1)| \leq C\varepsilon^\beta$.
(ii) and $(N-1)$ eigenvalues, counted with multiplicity, which are located in the half-plane $\left\{\mathrm{Re}\,(z) \leq -\frac{\nu_0}{2} + C\varepsilon^\beta\right\}$.

Proof. Let $|\varepsilon| < \varepsilon_0 < 1$. Then if $|z| > |k|\|U\| + \|D\|\|A_0\| + \|D\|\|M\|$ we have $\det(zI + ikU + DA) = \det(zI + ikU + DA_0 + \varepsilon DM) \neq 0$. Therefore we can assume that $|z| \leq |k|\|U\| + \|D\|\|A_0\| + \|D\|\|M\|$ and then

$$\|Adj(zI + ikU + DA_0)\| \leq C(|k|^{N-1} + 1)\,,$$

where C is a constant depending only on D, A_0 and M.
Let $\zeta_1 = -ikU_1, \zeta_2, \ldots, \zeta_N \in \mathbb{C}$ be the eigenvalues of $-ikU - DA_0$, then

$$\det(zI + ikU + DA_0) = \prod_{k=1}^{N}(z - \zeta_k) = (z + ikU_1)\prod_{k=2}^{N}(z - \zeta_k)\,.$$

Due to Assumption 2, $\zeta_2, \ldots, \zeta_N$ lie in the half-plane $\mathrm{Re}(z) < -\frac{\nu_0}{2} < 0$. Therefore there exists a constant $C = C(\nu_0)$ such that

$$|\det(zI + ikU + DA_0)| \geq C(\nu_0)\,|z + ikU_1|$$

for all $z \in \mathbb{C}$ with $\mathrm{Re}(z) \geq -\nu_0$. Then for all $z \in \mathbb{C}$ with $\mathrm{Re}(z) \geq -\frac{\nu_0}{2}$ and $|z| \leq |k|\|U\| + \|D\|\|A_0\| + \|D\|\|M\|$ we can write

$$\|(zI + ikU + DA_0)^{-1}\| = \left\|\frac{Adj(zI + ikU + DA_0)}{\det(zI + ikU + DA_0)}\right\| \leq C\frac{|k|^{N-1} + 1}{|z + ikU_1|}\ ,$$

where $C = C(D, A_0, M, \nu_0) > 0$.

Now let $z \in \mathbb{C}$ with $|z| \leq |k|\|U\| + \|D\|\|A_0\| + \|D\|\|M\|$ and either $\mathrm{Re}(z) > Q|\varepsilon|^\beta$ or $-\frac{\nu_0}{2} + Q|\varepsilon|^\beta < \mathrm{Re}(z) < -Q|\varepsilon|^\beta$, with $\beta = 1/N \in (0,1)$ and $Q \geq 1$ to be determined.

Up to a change of ε_0, it is always possible to assume that $-\frac{\nu_0}{2} + Q|\varepsilon|^\beta < -Q|\varepsilon|^\beta$. From the previous inequality it follows that $zI + ikU + DA_0$ is invertible and

$$\|(zI + ikU + DA_0)^{-1}\| \leq C(|k|^{N-1} + 1)|\varepsilon|^{-\beta}\,. \tag{20}$$

By Neumann series we have that $(zI + ikU + DA)^{-1}$ equals

$$\left(\sum_{n=0}^{\infty}(-1)^n \left[\varepsilon(zI + ikU + DA_0)^{-1} D\, M\right]^n\right)(zI + ikU + DA_0)^{-1}$$

thus $\det(zI + ikU + DA) \neq 0$ if $\|\varepsilon(zI + ikU + DA_0)^{-1}D\,M\| < 1$. In view of (20), this is true if $C\|DM\|\,(|k|^{N-1} + 1)|\varepsilon|^{1-\beta} < 1$. Up to choosing ε_0 smaller, we have $C\|DM\|\,|\varepsilon|^{1-\beta} < 1/2$. Therefore we obtain the simpler sufficient condition $C\|DM\|\,|k|^{N-1}\,|\varepsilon|^{1-\beta} < 1/2$. Now we distinguish two cases.

$$\text{If}\ \ C\|DM\|\,|k|^{N-1}\,|\varepsilon|^{1-\beta} < 1/2 \quad \text{i.e.} \quad |k| < \left(2C\,\|DM\||\varepsilon|^{1-\beta}\right)^{\frac{-1}{N-1}}$$

then $\det(zI + ikU + DA) \neq 0$.

$$\text{If}\ \ |k| \geq \left(2C\,\|DM\||\varepsilon|^{1-\beta}\right)^{\frac{-1}{N-1}}$$

then, up to choosing ε_0 very small, we have $|k| \gg 1$ and it is sufficient to study the eigenvalue problem

$$Uw + \frac{1}{ik}DAw = \lambda\, w \quad w \neq 0\ ,\ \lambda = -\frac{z}{ik}$$

as a perturbation of the eigenvalue problem for U. The eigenvalues $U_1, \ldots, U_N$ of U are all semisimple and, according to [16], Theorem 2.3, page 82, if U_j is an eigenvalue with multiplicity m_j and eigenprojection P_j, one can compute the corrections of U_j to order $1/|k|$ by computing the spectrum of P_jDAP_j with respect to the invariant subspace $P_j(\mathbb{R}^N)$. This gives a $m_j \times m_j$ matrix whose eigenvalues are the first order corrections we wanted to obtain. Thus

$$\det(zI + ikU + DA) = 0 \ \Rightarrow\ \frac{-z}{ik} = U_j + \frac{\lambda_j(DA)}{ik} + \mathcal{O}\left(\frac{1}{k^2}\right)$$

for some $j \in \{1, ..., N\}$, where $\lambda_j(DA)$ is an eigenvalue of P_jDAP_j w.r.t. the invariant subspace $P_j(\mathbb{R}^N)$. We have $P_jDAP_j = P_jDA_0P_j + \varepsilon P_jDMP_j$ and $\lambda_j(DA) = \lambda_j(DA_0) + \mathcal{O}(\varepsilon^\gamma)$ with $\gamma \geq 1/m_j \geq 1/N = \beta$. From

$$\frac{-z}{ik} = U_j + \frac{\lambda_j(DA)}{ik} + \mathcal{O}\left(\frac{1}{k^2}\right)$$

it follows that $z = -ikU_j - \lambda_j(DA_0) + \mathcal{O}\left(\varepsilon^\gamma\right) + \mathcal{O}\left(1/|k|\right)$. For $\varepsilon = 0$ we obtain an approximation for the solution of $\det(zI + ikU + DA_0) = 0$ in the neighborhood of $-ikU_j$. Due to Assumption 2, it follows that either $\lambda_j(DA_0) = 0$, which is the case for $j = 1$, or

$$\mathrm{Re}\left(-ikU_j - \lambda_j(DA_0) + \mathcal{O}\left(1/|k|\right)\right) < -\nu_0\,.$$

Since $\beta = 1/N$ we have $\frac{1-\beta}{N-1} = \beta$ and $|k|^{-1} \leq \mathcal{O}\left(|\varepsilon|^{\beta}\right)$. Therefore for $\varepsilon \neq 0$ if

$$\begin{gathered} \det(zI + ikU + DA) = 0 \\ \Rightarrow z = -ikU_j - \lambda_j(DA_0) + \mathcal{O}\left(\varepsilon^{\gamma}\right) + \mathcal{O}\left(\tfrac{1}{|k|}\right) \text{ for some } j \in \{1, \ldots, N\} \\ \Rightarrow \operatorname{Re}(z) = \operatorname{Re}\left(-ikU_j - \lambda_j(DA_0) + \mathcal{O}\left(\tfrac{1}{|k|}\right)\right) + \mathcal{O}\left(\varepsilon^{\gamma}\right) + \mathcal{O}\left(\tfrac{1}{|k|}\right) \\ \Rightarrow \operatorname{Re}(z) \leq -\nu_0 + \mathcal{O}(|\varepsilon|^{\beta}) \text{ or } |\operatorname{Re}(z)| \leq \mathcal{O}(|\varepsilon|^{\beta}) \end{gathered}$$

Here $|\mathcal{O}(|\varepsilon|^{\beta})| \leq G|\varepsilon|^{\beta}$ with $G = G(D, M)$. Up to choosing $Q = G(D, M)$, $\det(zI + ikU + D(A)) = 0$ implies that $|\operatorname{Re}(z)| \leq Q|\varepsilon|^{\beta}$ or $\operatorname{Re}(z) \leq -\nu_0 + Q|\varepsilon|^{\beta}$ for any $\varepsilon \in (-\varepsilon_0, \varepsilon_0)$, which is a contradiction. ◻

Due to Lemma 4.3 we have, for small ε, that the only eigenvalue relevant for the pattern forming properties of (14) is contained in the strip $|\operatorname{Re}(z_1)| \leq C\varepsilon^{\beta}$. This eigenvalue can be obtained as a perturbation of the eigenvalue $z = -ikU_1$ of problem (16). To compute its asymptotics for $\varepsilon \to 0$ we will use classical perturbation methods for eigenvalue problems, cf. [16].

First we introduce some notation. Let $\langle \cdot, \cdot \rangle$ denote the scalar product in $\mathbb{R}^N$, let B^t denote the transposed matrix of B and let span $\{a, b, ..., z\}$ denote the linear subspace of $\mathbb{R}^N$ generated by the vectors $a, b, ..., z$.

Lemma 4.4. *Let A_0 satisfy Assumptions 1 and 2. Then, for each $k \in \mathbb{R}$ there exists a unique vector $e_1^T = e_1^T(k) \in \mathbb{C}^N$, which solves the linear system*

$$\left[-ikU_1 + ikU + (DA_0)^t\right] e_1^T = 0 \tag{21}$$

$$\text{and fulfills} \quad \left\langle e_1^T, e_1 \right\rangle = 1 \, . \tag{22}$$

Proof. Assumption 1 and since U is not degenerate imply that for each $k \in \mathbb{R}$ we have $\ker(-ikU_1 + ikU + D_0) = \operatorname{span}(e_1)$. Therefore

$$\operatorname{rank}(-ikU_1 + ikU + DA_0) = \operatorname{rank}\left(-ikU_1 + ikU + (DA_0)^t\right) = N - 1 \, ,$$

and there exists $w = w(k) \in \mathbb{C}^N$ with $\ker\left(-ikU_1 + ikU + (DA_0)^t\right) = \operatorname{span}(w)$. To obtain a unique e_1^T solving (21), (22) with $e_1^T = Cw$ for some $C \in \mathbb{R}$ and $\langle w, e_1 \rangle \neq 0$, we notice due to Assumption 1 that $-ikU_1 + ikU + DA_0$ is a matrix with coefficients $t_{i,j} = t_{i,j}(k)$, where $t_{11} = t_{21} = ... = t_{N1} = 0$. Since $\ker(-ikU_1 + ikU + DA_0) = \operatorname{span}(e_1)$ the characteristic polynomial of this matrix has a simple root at $\zeta = 0$. Therefore

$$\det(t_{ij})_{i,j=2,\ldots,N} \neq 0 \, . \tag{23}$$

Thus when solving $\left[-ikU_1 + ikU + (DA_0)^t\right] w = 0$ the first component of w can be chosen as a free parameter w_1. In particular, for $w_1 = 1$ and $e_1^T = w$ we obtain the desired solution of problem (21), (22). ◻

Now we can compute the asymptotics of the eigenvalues of (16) as a perturbation of $z = -ikU_1$.

Proposition 2. *Let A_0 satisfy Assumptions 1 and 2. Let $A = A_0 + \varepsilon M$ and $e_1^T = e_1^T(k)$ be as in Lemma 4.4. Then, there exist positive constants C, ε_0 which depend on $\|A_0\|, \|M\|$ but are independent of k and ε, such that for each $0 \leq \varepsilon \leq \varepsilon_0$ the spectrum associated to problem (16) consists of one eigenvalue $z_1 = z_1(k)$ satisfying*

$$\left|z_1 + ikU_1 + \varepsilon \left\langle e_1^T, DMe_1 \right\rangle\right| \leq C\varepsilon^2/(1 + |k|) \tag{24}$$

and $(N-1)$ *eigenvalues, counted with multiplicity, which are contained in the half-plane* $\mathrm{Re}(z) \leq -\nu_0/4$ *.*

Proof. The last estimate is a consequence of Lemma 4.3, (ii). To obtain (24) suppose that $|k| \leq R$ for some constant $R > 0$. General perturbation theory for eigenvalues of matrices ensures that

$$z = -ikU_1 + \theta \quad , \quad w = e_1 + r \ , \tag{25}$$

where $\theta = \theta(k, \varepsilon)$ and $r = r(k, \varepsilon)$ are small for $\varepsilon \to 0$. Plugging this into (16) and using Assumption 1 we obtain

$$-ikU_1 r + \theta e_1 + \theta r + ikUr + DA_0 r + \varepsilon DMe_1 + \varepsilon DMr = 0 \ . \tag{26}$$

Assume, w.l.o.g. that the eigenvector w satisfies $\left\langle e_1^T, w \right\rangle = 1$. Then (22) and (25) yield that $\left\langle e_1^T, r \right\rangle = 0$. Therefore, multiplying (26) by e_1^T and using (21) it follows that

$$\theta + \varepsilon \left\langle e_1^T, DMe_1 \right\rangle + \varepsilon \left\langle e_1^T, DMr \right\rangle = 0. \tag{27}$$

Neglecting quadratic terms we obtain the following approximation

$$\theta \sim -\varepsilon \left\langle e_1^T, DMe_1 \right\rangle \quad \text{as} \quad \varepsilon \to 0 \ . \tag{28}$$

This gives the leading order term in the asymptotic expansion of (24). The error term for $|k| \leq R$ can be obtained by classical perturbation theory for eigenvalue problems (cf. [16]). To obtain (24) for $|k| \geq R$ we rewrite (16) as

$$\frac{z}{ik} w + \left(U + \frac{DA_0}{ik} \right) \cdot w + \frac{\varepsilon}{ik} DM \cdot w = 0 \ . \tag{29}$$

The correction of the eigenvalue of problem (29) for $\varepsilon = 0$, $\frac{z}{ik} = -U_1$ can be computed perturbatively, similar as above. Arguing like in the proof of Lemma 4.3 it follows that

$$\frac{z}{ik} = -U_1 - \frac{\varepsilon}{ik} \left\langle e_1^T, DMe_1 \right\rangle + O\left(\frac{\varepsilon^2}{|k|^2} \right)$$

for $\varepsilon \to 0$, uniformly for $|k| \geq 1$. Thus (24) follows. □

To understand the pattern forming properties of (14) for $A = A_0 + \varepsilon M$ with small ε we use Proposition 2 and study $\eta(k) \equiv -\left\langle e_1^T, DMe_1 \right\rangle$. To prove pattern formation in the sense of Definition 2.1, we show that $\eta(k)$ reaches its maximum at a discrete set of values $k_{0,i} \neq 0$. Since $\eta(k)$ is analytic, this property is a consequence of

Proposition 3. *Let Assumptions 1 and 2 hold. Then the asymptotics of* $\eta(k) \equiv -\left\langle e_1^T, DMe_1 \right\rangle$ *with* e_1^T *as in Lemma 4.4 are given by*

$$\eta(k) \sim -\langle e_1, DMe_1 \rangle \quad \textit{for} \quad |k| \to \infty \tag{30}$$

$$\eta(k) \sim -ik \langle \psi_0, DMe_1 \rangle - k^2 \langle \psi_1, DMe_1 \rangle + ... \quad \textit{for} \quad |k| \to 0. \tag{31}$$

Here ψ_0 *and* ψ_1 *are unique solutions of*

$$(U - U_1) b + (DA_0)^t \psi_0 = 0 \quad , \quad \langle \psi_0, e_1 \rangle = 0 \tag{32}$$

$$-(U - U_1) \psi_0 + (DA_0)^t \psi_1 = 0 \quad , \quad \langle \psi_1, e_1 \rangle = 0 \tag{33}$$

with b *as in (17).*

Proof. The problem reduces to deriving the asymptotics for e_1^T. To show (30) we can approximate the solutions of (21), (22) by the solutions of

$$[-iU_1 + iU]\, e_1^T = 0 \quad , \quad \left\langle e_1^T, e_1 \right\rangle = 1 \; , \tag{34}$$

since under suitable normalization conditions solutions of linear systems of equations depend continuously on their parameters. Since U is diagonal and nondegenerate, both equations in (34) are solved for $e_1^T = e_1$. Therefore $\lim_{|k|\to\infty} e_1^T = e_1$ and (30) follows.

For $k \to 0$ the asymptotics of $\eta(k)$ can again be computed by perturbative methods. Consider (21), (22) as perturbation of $(DA_0)^t\, e_1^T = 0$, $\left\langle e_1^T, e_1 \right\rangle = 1$, which are solved, due to (18), by $e_1^T = b$. Assume

$$e_1^T = b + ik\psi_0 + k^2\psi_1 + ... \;\; \text{with} \;\; \langle \psi_0, e_1 \rangle = \langle \psi_1, e_1 \rangle = ... = 0 \tag{35}$$

where $\psi_0,\ \psi_1, ...$ will be determined later. Plugging (35) into (21) and separating terms with the same powers of k we obtain

$$(DA_0)^t\, \psi_0 + (U - U_1)\, b = 0 \quad , \quad (DA_0)^t\, \psi_1 - (U - U_1)\, \psi_0 = 0 \; . \tag{36}$$

Equations (36) combined with the normalization conditions in (35) can be solved due to (23) and because $\langle b, (U - U_1)e_1 \rangle = 0$. Plugging (35) into $\eta(k) \equiv -\left\langle e_1^T, DMe_1 \right\rangle$ we obtain (31), since $D^t b = 0$. Therefore

$$\langle b, DMe_1 \rangle = \left\langle D^t b, Me_1 \right\rangle = 0 \; . \tag{37}$$

The convergence of the series in (35) can be shown by using (23) and standard perturbation theory, [16] □

Now we can formulate the main result of this subsection.

Theorem 4.5. *Let A_0 satisfy Assumptions 1 and 2. Let $A = A_0 + \varepsilon M$ with $M \in M_N(\mathbb{R})$ satisfying*

$$\langle e_1, DMe_1 \rangle \geq 0 \quad , \quad \langle \psi_1, DMe_1 \rangle < 0 \; , \tag{38}$$

where ψ_1 is as in (32), (33). Then, for $\varepsilon > 0$ small enough, system (14) generates oscillatory patterns in the sense of Definition 2.1.

Proof. The asymptotics (30), (31) as well as (38) imply that $\operatorname{Re}(\eta(k))$ has a global maximum in $\mathbb{R}$ for some bounded set of values $k_{0,i} \in \mathbb{R}\backslash \{0\}$. Further, $\eta(k)$ is analytic w.r.t. k and therefore the set of points where $\operatorname{Re}(\eta(k))$ achieves its maximum is finite. With (24), it follows that $\operatorname{Re}(z_1(k))$ reaches its maximum for some set of values $\tilde{k}_{0,i} \in \mathbb{R}\backslash \{0\}$, if $\varepsilon > 0$ is small enough. Since $z_1(k)$ is contained in the set of zeros of an analytic function, this maximum is achieved in a finite number of points. Since for such a point $\tilde{k}_{0,i} \neq 0$, it follows from (24) that $\operatorname{Im}\left(z_1\left(\tilde{k}_{0,i}\right)\right) \neq 0$, if ε is small enough. Thus the result follows. □

The key problem now is to show the existence of matrices A_0, M which satisfy the properties of Theorem 4.5.

The case $N = 3$. First we describe the assumptions for 3×3 matrices U, A_0, M in Theorem 4.5 when the set of internal variables contains three elements. Let the diagonal entries of U all be different, let D be like in (15), and let $A_0 = (a_{ij})_{i,j}$ and $M = (m_{ij})_{i,j}$. Calculate DA_0, then the assumption $DA_0 e_1 = 0$ implies that

$$a_{11} - a_{31} = a_{11} - a_{21} = a_{21} - a_{31} = 0\ ,\ \text{thus } a_{11} = a_{21} = a_{31}\ . \tag{39}$$

In order to fulfill the second condition of Assumption 1 the sub-matrix

$$B = \begin{pmatrix} -a_{12} + a_{22} & -a_{13} + a_{23} \\ -a_{22} + a_{32} & -a_{23} + a_{33} \end{pmatrix} \tag{40}$$

of DA_0 must be diagonalizable. A sufficient condition for this is that B has different eigenvalues. This is the case if

$$(a_{12} + a_{23} - a_{22} - a_{33})^2 \\ -4\,(a_{12}a_{23} - a_{12}a_{33} - a_{23}a_{32} + a_{22}a_{33} - a_{13}a_{22} + a_{13}a_{32}) \neq 0 \tag{41}$$

$$a_{12}a_{23} - a_{12}a_{33} - a_{23}a_{32} + a_{22}a_{33} - a_{13}a_{22} + a_{13}a_{32} \neq 0 \tag{42}$$

Therefore, Assumption 1 reduces to (39), (41), (42). Assumption 2 reduces to the following. Let B be given as in (40). Then

$$\text{the roots of }\ \det\left(zI + ik\begin{pmatrix} U_2 & 0 \\ 0 & U_3 \end{pmatrix} + B\right) = 0\ \text{ are located} \\ \text{in the half-plane }\ \{\operatorname{Re}(z) \leq -\nu_0\}\ \text{ for some } \nu_0 > 0. \tag{43}$$

Choose M such that (37), (38) hold. Due to (35) we have $\psi_1 = (0, \psi_{12}, \psi_{13})^t$ for suitable numbers ψ_{12}, ψ_{13}. Calculate DM, then (38) reduces to

$$\begin{aligned} m_{11} - m_{31} &\geq 0 \quad \text{and} \\ \langle \psi_1, DMe_1 \rangle &= [\psi_{12} - \psi_{13}]\,(m_{21} - m_{11}) + \psi_{13}\,(m_{31} - m_{11}) < 0\ . \end{aligned} \tag{44}$$

In order to show the existence of a matrix M satisfying conditions (44), we only need to have $\psi_{12} \neq \psi_{13}$. The vector ψ_1 is defined by (35), (36) and can be expressed in terms of the matrices U and A. The result is not giving too much insight though. Therefore it is more convenient to look for specific values of U, A_0 and M satisfying (39), (41), (42), (43), (44).

Let D be given as before, $U_1 = 1$, $U_2 = 2$, $U_3 = 3$ and for arbitrary $a > 0$ let

$$A_0 = \begin{pmatrix} a & 1 & 0 \\ a & 2 & 1 \\ a & 0 & 2 \end{pmatrix}\ ,\ \text{ then }\ DA_0 = \begin{pmatrix} 0 & 1 & -2 \\ 0 & 1 & 1 \\ 0 & -2 & 1 \end{pmatrix} \tag{45}$$

and (36) reduces to

$$\begin{pmatrix} 1 & -2 \\ 1 & 1 \end{pmatrix}\begin{pmatrix} \psi_{02} \\ \psi_{03} \end{pmatrix} + \begin{pmatrix} 1 \\ 2 \end{pmatrix} = 0 = \begin{pmatrix} 1 & -2 \\ 1 & 1 \end{pmatrix}\begin{pmatrix} \psi_{12} \\ \psi_{13} \end{pmatrix} - \begin{pmatrix} \psi_{02} \\ 2\psi_{03} \end{pmatrix}\ .$$

Therefore

$$(\psi_{02}, \psi_{03}) = (-5/3, -1/3) \quad , \quad (\psi_{12}, \psi_{13}) = (-1, 1/3)\ . \tag{46}$$

Using (44) these conditions further reduce to $4\,(m_{11} - m_{21}) < (m_{11} - m_{31})$ and $m_{11} - m_{31} \geq 0$. There are infinitely many choices for M which yield these inequalities.

If A_0 is given by (45), then the characteristic polynomial of B equals $P(x) = x^2 - 2x + 3$. Therefore (41) and (42) are satisfied. It remains to check (43). We have

$$\det\left(z\begin{pmatrix}1 & 0\\ 0 & 1\end{pmatrix} + ik\begin{pmatrix}2 & 0\\ 0 & 3\end{pmatrix} + \begin{pmatrix}1 & 1\\ -2 & 1\end{pmatrix}\right)$$
$$= z^2 + 2z - 6k^2 + 3 + i(5zk + 5k) \equiv Q(z,k)$$

and the roots of $Q(z,k)$ are given by$z = -1 - \frac{5}{2}ik \pm \frac{1}{2}\sqrt{(-8-k^2)}$ with real parts -1. Thus we obtain (43). Let

$$M = \begin{pmatrix}2 & 0 & 0\\ 1.95 & 0 & 0\\ 1 & 0 & 0\end{pmatrix} \tag{47}$$

Then the dispersion relation consists in finding the roots of the polynomial

$$\det(z + ikU + DA) = 0 \tag{48}$$

for D as in (15), U, A_0 as in (45) with $a = 0.5$, and $A = A_0 + \varepsilon M$ for $\varepsilon = 0.01$. These are calculated numerically for given $k \in \mathbb{R}$ w.r.t. the variable z. Figure 1 shows the branch with the largest real part. All other roots have negative real parts.

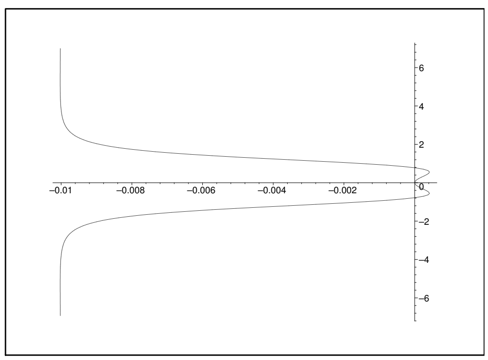

FIGURE 1. Root with largest real part of (48) for D as in (15), U, A_0 as in (45), $a = 0.5$, M as in (47), $A = A_0 + \varepsilon M$, $\varepsilon = 0.01$. Horizontal: $\mathrm{Re}(z(k))$, vertical: $\mathrm{Im}(z(k))$.

The case $N = 2$. In this case Assumptions 1 and 2 as well as (38) cannot be satisfied as expected from the results in [17], (cf. Theorem 4.1). To obtain $DA_0e_1 = 0$, we need that $a_{11} = a_{21}$. Conditions (38) imply that $m_{11} - m_{21} \geq 0$ and

$$(U_2 - U_1)^2(a_{12} - a_{22})^{-2}(m_{11} - m_{21}) < 0$$

by using (32), (33). Therefore, $(m_{11} - m_{21}) < 0$, which is a contradiction. Thus the inequalities required impose a minimal degree of complexity on system (14), or, more precisely, the need for at least three different state variables.

4.4. **Reflection-symmetry, nondegenerate matrix U.** Here we study systems of type (14) which fulfill some symmetry properties, which naturally arise in models for pattern formation in myxobacteria, as we will discuss later. Assume that $N = 2n$ and that f in (14) is of the form

$$f = \begin{pmatrix}\varphi\\ \psi\end{pmatrix} =: (\varphi,\psi)^t \quad , \quad \varphi,\ \psi \in \mathbb{R}^n \ .$$

Further assume that system (14) is invariant under the transformation

$$(x,\varphi,\psi)\to(-x,\psi,\varphi) \tag{49}$$

Due to this invariance and by explicit calculations we can see that

$$U=\begin{pmatrix} V & 0\\ 0 & -V\end{pmatrix} \quad \text{and} \quad A=\begin{pmatrix} Y_1 & Z_1\\ Z_2 & Y_2\end{pmatrix}=\begin{pmatrix} Y & Z\\ Z & Y\end{pmatrix} \tag{50}$$

where $V, Y_1, Y_2, Y, Z_1, Z_2, Z$ are $n\times n$ matrices and V is a diagonal matrix. To see the last formula, let D be as in (15) and use

$$\mathcal{I}:=\begin{pmatrix} 0 & I\\ I & 0\end{pmatrix} \quad , \quad \mathcal{I}\begin{pmatrix} \psi\\ \varphi\end{pmatrix}=\begin{pmatrix} \varphi\\ \psi\end{pmatrix} \quad , \quad \mathcal{I}U=-U\mathcal{I} \tag{51}$$

$$\mathcal{I}\begin{pmatrix} Y_1 & Z_1\\ Z_2 & Y_2\end{pmatrix}=\begin{pmatrix} Y_2 & Z_2\\ Z_1 & Y_1\end{pmatrix}\mathcal{I}\ , \tag{52}$$

We can rewrite D as

$$D=\begin{pmatrix} \sigma & \lambda\\ \lambda & \sigma\end{pmatrix} \tag{53}$$

where $\sigma=(\sigma_{ij})_{i,j}$ and $\lambda=(\lambda_{ij})_{i,j}$ are $n\times n$ matrices with $\sigma_{11}=...=\sigma_{nn}=1$, $\sigma_{21}=\sigma_{32}=...=\sigma_{n(n-1)}=-1$, just $\lambda_{1n}=-1$ and all other σ_{ij}, λ_{ij} being zero. Then

$$\mathcal{I}D=\mathcal{I}\begin{pmatrix} \sigma & \lambda\\ \lambda & \sigma\end{pmatrix}=\begin{pmatrix} \sigma & \lambda\\ \lambda & \sigma\end{pmatrix}\mathcal{I}=D\mathcal{I}\ . \tag{54}$$

Applying transformation (49) to system (14) and then multiplying the obtained formula by $\mathcal{I}$ and using (51)-(54) we get

$$\partial_t\begin{pmatrix} \varphi\\ \psi\end{pmatrix}+\begin{pmatrix} V & 0\\ 0 & -V\end{pmatrix}\cdot\partial_x\begin{pmatrix} \varphi\\ \psi\end{pmatrix}+D\begin{pmatrix} Y_2 & Z_2\\ Z_1 & Y_1\end{pmatrix}\begin{pmatrix} \varphi\\ \psi\end{pmatrix}=0\ .$$

This equation is equivalent to (14) if

$$D\begin{pmatrix} Y_1 & Z_1\\ Z_2 & Y_2\end{pmatrix}=D\begin{pmatrix} Y_2 & Z_2\\ Z_1 & Y_1\end{pmatrix}\ ,$$

respectively $Y_2=Y_1+G$, $Z_2=Z_1+H$, where

$$D\begin{pmatrix} G & H\\ -H & -G\end{pmatrix}=\begin{pmatrix} \sigma & \lambda\\ \lambda & \sigma\end{pmatrix}\begin{pmatrix} G & H\\ -H & -G\end{pmatrix}=0\ .$$

Since under this assumption the matrices G and H do not appear in the equation, we can assume $Y_2=Y_1\equiv Y$, $Z_2=Z_1\equiv Z$, which yields the second equation of (50). Further on, we assume in this subsection that the matrix V is non degenerate. Under the symmetry assumptions (16) reduces to

$$z\begin{pmatrix} w_1\\ w_2\end{pmatrix}+ik\begin{pmatrix} V & 0\\ 0 & -V\end{pmatrix}\begin{pmatrix} w_1\\ w_2\end{pmatrix}+\begin{pmatrix} P & Q\\ Q & P\end{pmatrix}\begin{pmatrix} w_1\\ w_2\end{pmatrix}=0\ , \tag{55}$$

where $P=\sigma Y+\lambda Z$, $Q=\sigma Z+\lambda Y$. Our goal is to study the eigenvalue problem (55) as a perturbation of a problem which is "as hyperbolic as possible". Let

$$A=A_0+\varepsilon M \quad , \quad M=\begin{pmatrix} m & n\\ n & m\end{pmatrix} \quad , \quad \begin{pmatrix} \Theta & \Lambda\\ \Lambda & \Theta\end{pmatrix}=DM \tag{56}$$

$$A_0=\begin{pmatrix} Y_0 & Z_0\\ Z_0 & Y_0\end{pmatrix} \quad , \quad \begin{pmatrix} P_0 & Q_0\\ Q_0 & P_0\end{pmatrix}=DA_0\ .$$

For $\varepsilon = 0$, (55) reads

$$z\begin{pmatrix} w_1 \\ w_2 \end{pmatrix} + ik\begin{pmatrix} V & 0 \\ 0 & -V \end{pmatrix}\begin{pmatrix} w_1 \\ w_2 \end{pmatrix} + \begin{pmatrix} P_0 & Q_0 \\ Q_0 & P_0 \end{pmatrix}\begin{pmatrix} w_1 \\ w_2 \end{pmatrix} = 0 \ . \tag{57}$$

Notice that Assumptions 1 and 2 in Subsection 4.3 cannot be satisfied for the eigenvalue problem (57), since due to the symmetry assumptions, some of the eigenvalues are degenerate. Indeed, suppose that DA_0 has an eigenvector with eigenvalue zero, namely $(e_1, 0)^t$, or equivalently $P_0 e_1 = 0$, $Q_0 e_1 = 0$. Due to the symmetry of DA_0 we have$DA_0\,(0, e_1)^t = 0$. So the kernel of DA_0 has at least dimension 2. Therefore, if A satisfies the symmetry conditions above, the assumptions defining the "hyperbolic" character of problem (14) with $A = A_0$ have to be modified. Instead of Assumptions 1 and 2 we need in this case

Assumption 3. *The kernel of DA_0 is the subspace generated by the vectors $(e_1, 0)^t$, $(0, e_1)^t$. In particular $P_0 e_1 = Q_0 e_1 = 0$.*

As a consequence the set of solutions of the eigenvalue problem (57) contains the lines $\{z = -ikV_1\ ,\ z = ikV_1\ ,\ k \in \mathbb{R}\}$.

Assumption 4. *All other solutions of the eigenvalue problem (57) are included in the half-plane $\{\mathrm{Re}\,(z) \le -\nu_0\}$ for some $\nu_0 > 0$.*

Now we can study the spectrum of (57). Then the analog of Lemma 4.3 is

Lemma 4.6. *Let A_0 satisfy Assumptions 3 and 4. Let A, M be given by (56). Then there exist positive constants $C = C\,(A_0, M)$, β and ε_0 independent of ε such that for each $k \in \mathbb{R}$ and $|\varepsilon| \le \varepsilon_0$ the spectrum associated to problem (55) consists of*

(i) Two eigenvalues $z_1 = z_1\,(k)$, $z_2 = z_2\,(k)$ satisfying $|\mathrm{Re}\,(z_1)| \le C\varepsilon^\beta$.

(ii) and $(N-2)$ eigenvalues, counted with multiplicity, contained in the half-plane $\left\{\mathrm{Re}\,(z) < -\nu_0 + C\varepsilon^\beta\right\}$.

Proof. The proof is the same as for Lemma 4.3, since the arguments given there do not use the non-degeneracy of the matrix U. □

Using perturbative methods, we now compute the changes of the part of the spectrum of (57) contained in the lines $\{z = -ikV_1\ ,\ z = ikV_1\ ,\ \ k \in \mathbb{R}\}$ for $\varepsilon \to 0$. Due to the multiplicity of these eigenvalues for $k = 0$, this computation has to be done slightly different in comparison to the case for matrices with multiple eigenvalues for $k = 0$. The following analog of Lemma 4.4 holds

Lemma 4.7. *Let A_0 satisfies Assumptions 3 and 4. Then, for each $k \in \mathbb{R}$ there exist vectors $v_1^T\,(k)$, $v_2^T\,(k)$ solving the adjoint problems*

$$\left[z + ik\begin{pmatrix} V & 0 \\ 0 & -V \end{pmatrix} + \begin{pmatrix} P_0^t & Q_0^t \\ Q_0^t & P_0^t \end{pmatrix}\right]_{z=-ikV_1} v_l^T\,(k) = 0, \quad l = 1, 2 \tag{58}$$

and satisfying the normalization conditions

$$\left\langle v_1^T\,(k)\,, (e_1, 0)^t \right\rangle = \left\langle v_2^T\,(k)\,, (0, e_1)^t \right\rangle = 1\ . \tag{59}$$

Proof. The proof is similar to the one of Lemma 4.4. The only essential difference is, that for $k = 0$ the subspace of solutions that solve the eigenvalue problem (57) with $z = 0$ is of dimension two. Therefore, the solution of the adjoint problem is two dimensional, and with arguments as in Lemma 4.4, the basis of eigenfunctions

$v_1^T(0)$, $v_2^T(0)$ can be chosen such that they satisfy the normalization conditions (59). ☐

Arguing as in the proof of Proposition 2, we can now compute the changes of the eigenvalues $\{z = \pm ikV_1\}$.

Proposition 4. *Let A_0 satisfy Assumptions 3 and 4. Let A be given as in (56) and $v_1^T(k)$, $v_2^T(k)$ be given as in Lemma 4.4. Let $|k| \geq \delta > 0$. Then, there exist positive constants C, ε_0 depending on $\|A_0\|$, $\|M\|$, δ but independent of k and ε, such that for each $0 \leq \varepsilon \leq \varepsilon_0$ the spectrum associated to problem (55) consists of two eigenvalues $z_1 = z_1(k)$, $z_2 = z_2(k)$ satisfying*

$$|z_1 + ikV_1 - \varepsilon\theta_1| + |z_2 - ikV_1 - \varepsilon\theta_2| \leq C\varepsilon^2(1+|k|)^{-1} , \tag{60}$$

$$\text{where} \quad \theta_l = -\left\langle v_l^T(k), DM\, E_l\right\rangle \quad , \quad l = 1,2 , \tag{61}$$

$$\text{with} \quad E_1 = (e_1, 0)^t \quad \text{and} \quad E_2 = (0, e_1)^t , \tag{62}$$

and $(N-2)$ eigenvalues, counted with multiplicity, which are contained in the half-plane $\operatorname{Re}(z) \leq -\frac{\nu_0}{2}$.

Proof. Consider solutions of (55) in the perturbative form

$$z_1 = -ikV_1 + \varepsilon\theta_1 + ... \quad , \quad z_2 = ikV_1 + \varepsilon\theta_2 + ...$$

with eigenvectors $v_1 = (e_1, 0)^t + \varepsilon Z_1 + ...$, $v_2 = (0, e_1)^t + \varepsilon Z_2 + ...$. Plugging these formulas into (55), using $P_0 e_1 = Q_0 e_1 = 0$, and neglecting quadratic and higher order terms w.r.t. ε we obtain

$$\theta_l E_l + (-1)^l ikV_1 Z_l + ikUZ_l + DA_0\, Z_l + DM\, E_l = 0 , \quad l = 1,2 . \tag{63}$$

Taking the scalar product of (63) with v_1^T, respectively with v_2^T, as given in Lemma 4.7, we obtain $z_1 \sim -ikV_1 + \varepsilon\theta_1$, $z_2 \sim ikV_1 + \varepsilon\theta_2$ with θ_1, θ_2 as given in (61). This provides the terms of leading order in (60). The error terms can be estimated as in the proof of Proposition 2. Finally $\operatorname{Re}(z) \leq -\frac{\nu_0}{2}$ follows from Lemma 4.6. ☐

To obtain sufficient conditions for pattern formation, we analyze the asymptotics for $|k| \to 0$ and $|k| \to \infty$ for the functions θ_1 and θ_2. For this we need

Lemma 4.8. *Let A_0 satisfy Assumption 3. Then, there exists a basis of* $\ker\left((DA_0)^t\right)$ *given by two vectors $\{b_1, b_2\}$, which satisfy*

$$\langle E_1, b_1\rangle = \langle E_2, b_2\rangle = 1 \quad , \quad \langle E_1, b_2\rangle = \langle E_2, b_1\rangle = 0 \quad , \quad b_2 = \mathcal{I} b_1 \tag{64}$$

Proof. Assumption 3 implies $\dim\ker\left((DA_0)^t\right) = \dim\ker(DA_0) = 2$. The two unique vectors b_1, b_2 satisfying (64) can be found like in the proof of Lemma 4.4. The last identity in (64) follows from

$$\begin{pmatrix} 0 & I \\ I & 0 \end{pmatrix}\begin{pmatrix} P_0^t & Q_0^t \\ Q_0^t & P_0^t \end{pmatrix}\begin{pmatrix} 0 & I \\ I & 0 \end{pmatrix} = \begin{pmatrix} P_0^t & Q_0^t \\ Q_0^t & P_0^t \end{pmatrix}. \tag{65}$$

☐

Proposition 5. *Under Assumptions 3 and 4 the asymptotics of $\theta_1(k)$ and $\theta_2(k)$ defined in (61)*

$$\theta_1 \sim -\langle e_1, \Theta e_1\rangle \quad , \quad \theta_2 \sim -\langle e_1, \Theta e_1\rangle \quad \text{for} \quad |k| \to \infty . \tag{66}$$

For $k \to 0$ we have

$$\theta_1 = -\left\langle \left[b_1 + ik\psi_{1,0} + k^2\psi_{1,1}\right], DM\, E_1 \right\rangle \tag{67}$$
$$= -\left\langle b_1, (\Theta e_1, \Lambda e_1)^t \right\rangle - ik\left\langle \psi_{1,0}, (\Theta e_1, \Lambda e_1)^t \right\rangle - k^2\left\langle \psi_{1,1}, (\Theta e_1, \Lambda e_1)^t \right\rangle + ...$$

$$\theta_2 = -\left\langle b_1, (\Theta e_1, \Lambda e_1)^t \right\rangle + ik\left\langle \psi_{1,0}, (\Theta e_1, \Lambda e_1)^t \right\rangle - k^2\left\langle \psi_{1,1}, (\Theta e_1, \Lambda e_1)^t \right\rangle + ... \tag{68}$$

where $\psi_{1,0}$, and $\psi_{1,1}$ are the unique solutions of

$$-V_1 b_1 + U b_1 + \begin{pmatrix} P_0^t & Q_0^t \\ Q_0^t & P_0^t \end{pmatrix} \psi_{1,0} = 0 \tag{69}$$

$$V_1\psi_{1,0} - U\psi_{1,0} + \begin{pmatrix} P_0^t & Q_0^t \\ Q_0^t & P_0^t \end{pmatrix} \psi_{1,1} = 0 \tag{70}$$

$$\langle E_1, \psi_{1,0}\rangle = \langle E_2, \psi_{1,0}\rangle = 0 \tag{71}$$

$$\langle E_1, \psi_{1,1}\rangle = \langle E_2, \psi_{1,1}\rangle = 0 \tag{72}$$

and b_1 is as in Lemma 4.8.

Proof. Arguing similarly as in the proof of Proposition 3, we obtain

$$v_1^T(k) \sim (e_1, 0)^t = E_1 \ \text{ for } \ |k| \to \infty \quad , \quad v_2^T(k) \sim (0, e_1)^t = E_2 \ \text{ for } \ |k| \to \infty \ .$$

Thus (66) follows. To compute the asymptotics of θ_1, θ_2 for $|k| \to 0$ we expand $v_1^T(k)$, $v_2^T(k)$ which solve (58) as power series

$$v_1^T(k) = \alpha_{11} b_1 + \alpha_{12} b_2 + ik\psi_{1,0} + k^2\psi_{1,1} + ... \tag{73}$$

$$v_2^T(k) = \alpha_{21} b_1 + \alpha_{22} b_2 + ik\psi_{2,0} + k^2\psi_{2,1} + ... \tag{74}$$

where the coefficients α_{ij} must be determined. Plugging (73) into (58) for $l = 1$ and using that $z = -ikV_1$ we obtain

$$- ikV_1(\alpha_{11} b_1 + \alpha_{12} b_2) + k^2 V_1 \psi_{1,0} + ikU(\alpha_{11} b_1 + \alpha_{12} b_2)$$
$$- k^2 U\psi_{1,0} + \begin{pmatrix} P_0^t & Q_0^t \\ Q_0^t & P_0^t \end{pmatrix}\left(ik\psi_{1,0} + k^2\psi_{1,1}\right) = O\left(k^3\right)$$

Separating the terms with powers k and multiplying them by E_1, E_2 we obtain a set of compatibility conditions.

$$-V_1(\alpha_{11}\langle E_1, b_1\rangle + \alpha_{12}\langle E_1, b_2\rangle) + (e_1, 0)\, U(\alpha_{11} b_1 + \alpha_{12} b_2) = 0$$
$$-V_1(\alpha_{11}\langle E_2, b_1\rangle + \alpha_{12}\langle E_2, b_2\rangle) + (0, e_1)\, U(\alpha_{11} b_1 + \alpha_{12} b_2) = 0\ .$$

Using the normalization conditions (64) as well as $V^t = V$ and $V_1 \neq 0$, it follows that

$$-\alpha_{11} V_1 + V_1\langle E_1, (\alpha_{11} b_1 + \alpha_{12} b_2)\rangle = -\alpha_{11} V_1 + \alpha_{11} V_1 = 0$$
$$-\alpha_{12} V_1 - V_1\langle E_2, (\alpha_{11} b_1 + \alpha_{12} b_2)\rangle = -\alpha_{12} V_1 - \alpha_{12} V_1 = 0\ .$$

From the second condition it follows that $\alpha_{12} = 0$. Taking the limit $k \to 0$ in (59) we obtain $\alpha_{11} = 1$. Imposing the additional normalization conditions (71) we have a unique solution for (69). The compatibility conditions required for solving (70) are satisfied, namely

$$\langle E_1, V_1\psi_{1,0} - U\psi_{1,0}\rangle = \langle E_2, V_1\psi_{1,0} - U\psi_{1,0}\rangle = 0\ .$$

Imposing the compatibility conditions (72) we can solve (70) uniquely.

In a similar manner, plugging (74) into (58) for $l = 2$ we obtain

$$V_1\left[\alpha_{21}b_1 + \alpha_{22}b_2\right] + U\left[\alpha_{21}b_1 + \alpha_{22}b_2\right] + \begin{pmatrix} P_0^t & Q_0^t \\ Q_0^t & P_0^t \end{pmatrix}\psi_{2,0} = 0 \tag{75}$$

$$-V_1\psi_{2,0} - U\psi_{2,0} + \begin{pmatrix} P_0^t & Q_0^t \\ Q_0^t & P_0^t \end{pmatrix}\psi_{2,1} = 0 \tag{76}$$

Multiplying(75) by $(e_1, 0)^t$ and using (59) we obtain, as in the previous case, that $\alpha_{21} = 0$, $\alpha_{22} = 1$. Thus we can uniquely solve systems (75), (76) by imposing the normalization conditions$\langle E_1, \psi_{2,0}\rangle = \langle E_2, \psi_{2,0}\rangle = 0$, $\langle E_1, \psi_{2,1}\rangle = \langle E_2, \psi_{2,1}\rangle = 0$. So for $|k| \to \infty$ we obtained the asymptotics (66). Using (61), (73) we obtain the asymptotics (67) for $|k| \to 0$ and with a similar argument that

$$\begin{aligned} \theta_2 &= -\left\langle\left[b_2 + ik\psi_{2,0} + k^2\psi_{2,1}\right], DM\ E_2\right\rangle \\ &= -\left\langle b_2, (\Lambda e_1, \Theta e_1)^t\right\rangle - ik\left\langle \psi_{2,0}, (\Lambda e_1, \Theta e_1)^t\right\rangle - k^2\left\langle \psi_{2,1}, (\Lambda e_1, \Theta e_1)^t\right\rangle + \dots . \end{aligned} \tag{77}$$

Using $b_2 = \mathcal{I}b_1$ we get $\psi_{2,0} = -\mathcal{I}\psi_{1,0}$ and $\psi_{2,1} = \mathcal{I}\psi_{1,1}$. With this expression we can transform (77) into (68). □

Remark 3. The crucial difference between the asymptotics (67), (68) in Proposition 5 and the asymptotics (31) in Proposition 3 is that the zero's order term in the expansion (31) vanishes due to (37). In Proposition 5 the term $\left\langle b_1, (\Theta e_1, \Lambda e_1)^t\right\rangle$ does not necessarily vanish.

Now we can formulate some sufficient conditions for pattern formation under the symmetry assumption (49).

Theorem 4.9. *Let $\delta > 0$. Let U, A satisfy (50) and A_0 satisfy Assumptions 3 and 4. Let A be given as in (56) with $\varepsilon > 0$ sufficiently small. Let $\psi_{1,0}$, $\psi_{1,1}$ be the unique solutions of (69)-(72) and b_1 be given as in Lemma 4.8. Then, system (14) has oscillatory patterns with wavelength smaller than $\frac{2\pi}{\delta}$ in the sense of Definition 2.1, if the following conditions are fulfilled*

$$\left\langle b_1, (\Theta e_1, \Lambda e_1)^t\right\rangle = 0\ ,\ \ \langle e_1, \Theta e_1\rangle \geq 0\ ,\ \ \left\langle \psi_{1,1}, (\Theta e_1, \Lambda e_1)^t\right\rangle < 0\ . \tag{78}$$

Example: $N = 4$, $n = 2$. Consider matrices U, A satisfying (50). Let V be a diagonal matrix with diagonal entries $V_1 \neq V_2$. Then also U is a diagonal matrix with diagonal entries $U_1 = V_1 = -U_3$, $U_2 = V_2 = -U_4$. Let D be like in (15) and to simplify the notation denote the entries of A_0 in (56) by y_{ij} and z_{ij}. Then calculate DA_0. Assumption 3 implies that $y_{11} = y_{21} = z_{11} = z_{21}$ and therefore the entries of the matrix DA_0 in the first and third row are all zero. Now we can compute b_1, b_2 as in Lemma 4.8. These vectors solve

$$\begin{aligned} &(y_{12} - z_{22})\,b_{i,1} + (-y_{12} + y_{22})\,b_{i,2} + (z_{12} - y_{22})\,b_{i,3} + (-z_{12} + z_{22})\,b_{i,4} = 0 \\ &(z_{12} - y_{22})\,b_{i,1} + (-z_{12} + z_{22})\,b_{i,2} + (y_{12} - z_{22})\,b_{i,3} + (-y_{12} + y_{22})\,b_{i,4} = 0\ , \end{aligned}$$

where $b_i = (b_{i,1}, b_{i,2}, b_{i,3}, b_{i,4})^t$, $i = 1, 2$. Let

$$L \equiv \begin{pmatrix} -y_{12} + y_{22} & -z_{12} + z_{22} \\ -z_{12} + z_{22} & -y_{12} + y_{22} \end{pmatrix}$$

Now (64) yields $b_{1,1} = 1$, $b_{1,3} = 0$, $b_{2,3} = 1$, $b_{2,1} = 0$. Further $b_{2,2} = b_{1,4}$, $b_{2,4} = b_{1,2}$. So the system of four equations above reduces to two equations

$$(-y_{12} + y_{22})\, b_{1,2} + (-z_{12} + z_{22})\, b_{1,4} = -\,(y_{12} - z_{22}) \tag{79}$$

$$(-z_{12} + z_{22})\, b_{1,2} + (-y_{12} + y_{22})\, b_{1,4} = -\,(z_{12} - y_{22}) \tag{80}$$

In order to solve system (79), (80) we have to assume $(-y_{12} + y_{22})^2 \neq (-z_{12} + z_{22})^2$. Then $b_1 = (1, b_{1,2}, 0, b_{1,4})^t$, $b_2 = (0, b_{1,4}, 1, b_{1,2})^t$. Due to the normalization conditions (71) we have $\psi_{1,0} = (0, \psi_{1,0,2}, 0, \psi_{1,0,4})^t$, $\psi_{1,1} = (0, \psi_{1,1,2}, 0, \psi_{1,1,4})$ and

$$L \begin{pmatrix} \psi_{1,0,2} \\ \psi_{1,0,4} \end{pmatrix} + \begin{pmatrix} V_2 - V_1 & 0 \\ 0 & -\,(V_1 + V_2) \end{pmatrix} \begin{pmatrix} b_{1,2} \\ b_{1,4} \end{pmatrix} = 0$$

$$L \begin{pmatrix} \psi_{1,1,2} \\ \psi_{1,1,4} \end{pmatrix} - \begin{pmatrix} V_2 - V_1 & 0 \\ 0 & -\,(V_1 + V_2) \end{pmatrix} \begin{pmatrix} \psi_{1,0,2} \\ \psi_{1,0,4} \end{pmatrix} = 0\ .$$

Let M be as in (56). Calculate

$$DM = \begin{pmatrix} \Theta & \Lambda \\ \Lambda & \Theta \end{pmatrix}\ ,\ \text{then}\ \Theta e_1 = \begin{pmatrix} m_{11} - n_{21} \\ -m_{11} + m_{21} \end{pmatrix}\ ,\ \Lambda e_1 = \begin{pmatrix} n_{11} - m_{21} \\ -n_{11} + n_{21} \end{pmatrix}\ .$$

The sufficient conditions for oscillatory pattern formation, (78), then reduce to

$$(m_{11} - n_{21}) + b_{1,2}\,(-m_{11} + m_{21}) + b_{1,4}\,(-n_{11} + n_{21}) = 0\ ,\ m_{11} - n_{21} \geq 0$$

$$\psi_{1,1,2}\,(-m_{11} + m_{21}) + \psi_{1,1,4}\,(-n_{11} + n_{21}) < 0$$

Therefore, as in the previous case, we need the linear independence of $(b_{1,2}, b_{1,4})^t$, $(\psi_{1,1,2}, \psi_{1,1,4})^t$. As a specific example we can choose

$$L = \begin{pmatrix} 2 & -1 \\ -1 & 2 \end{pmatrix}\ .$$

So $y_{12} - y_{22} = -2$, $z_{12} - z_{22} = 1$. Let $z_{22} - y_{12} =: a$. Then $z_{12} - y_{12} = 1 + a$, $z_{12} - y_{22} = -1 + a$. And with $V_1 = 2$, $V_2 = 1$ we have

$$w = \begin{pmatrix} a \\ 1 - a \end{pmatrix}\quad ,\quad R := \begin{pmatrix} -1 & 0 \\ 0 & -3 \end{pmatrix} = \begin{pmatrix} V_2 - V_1 & 0 \\ 0 & -\,(V_1 + V_2) \end{pmatrix}$$

$$(b_{1,2}, b_{1,4})^t = L^{-1} w = \left(\frac{1}{3}a + \frac{1}{3}\ ,\ -\frac{1}{3}a + \frac{2}{3}\right)^t$$

$$(\psi_{1,1,2}, \psi_{1,1,4})^t = -L^{-1} R L^{-1} R L^{-1} w = \left(\frac{17}{27}a - \frac{55}{27}\ ,\ \frac{31}{27}a - \frac{86}{27}\right)^t$$

and the desired condition is satisfied.

Assumption 4 requires that the rest of the spectrum of $zw + ikU \cdot w + DA_0 w = 0$, $k \in \mathbb{R}$ is left from a half-plane contained in $\{\mathrm{Re}\,(z) < 0\}$. The spectrum consists of the roots of

$$\det \begin{pmatrix} z + ikV_1 & y_{12} - z_{22} & 0 & z_{12} - y_{22} \\ 0 & -y_{12} + y_{22} + (z + ikV_2) & 0 & -z_{12} + z_{22} \\ 0 & z_{12} - y_{22} & z - ikV_1 & y_{12} - z_{22} \\ 0 & -z_{12} + z_{22} & 0 & -y_{12} + y_{22} + (z - ikV_2) \end{pmatrix}$$

$$= (z + ikV_1)\,(z - ikV_1)\,\det \begin{pmatrix} y_{22} - y_{12} + z + ikV_2 & z_{22} - z_{12} \\ z_{22} - z_{12} & y_{22} - y_{12} + z - ikV_2 \end{pmatrix}$$

$= 0$. Therefore we have to solve

$$(y_{22} - y_{12})^2 + 2\,(y_{22} - y_{12})\, z + z^2 + k^2 V_2^2 - (z_{22} - z_{12})^2 = 0\ ,$$

whose solutions are $z = -\left(y_{22} - y_{12}\right) \pm \sqrt{\left(z_{22} - z_{12}\right)^2 - k^2 V_2^2}$. Then, if $|z_{22} - z_{12}| < (y_{22} - y_{12})$ we obtain the desired condition.
For $y_{22} = 2.5$, $y_{12} = 0.5$, $z_{22} = 0.5 + a$, $z_{12} = 1.5 + a$ and for $a = 0$ we obtain

$$y_{22} = 2.5\ ,\ y_{12} = 0.5\ ,\ z_{22} = 0.5\ ,\ z_{12} = 1.5\ ,\ y_{11} = y_{21} = z_{11} = z_{21} = c \tag{81}$$

Then $(b_{1,2}, b_{1,4}) = (\frac{1}{3}, \frac{2}{3})$, $(\psi_{1,1,2}, \psi_{1,1,4}) = (-\frac{55}{27}, -\frac{86}{27})$. And the conditions for m, n become: $m_{21} = n_{21} - 2m_{11} + 2n_{11}$, $86\,(n_{21} - n_{11}) > -55\,(m_{21} - m_{11})$, $m_{11} - n_{21} \geq 0$. This holds for

$$m_{11} = 1.1\quad ,\quad m_{21} = 2.8\quad ,\quad n_{11} = 2\quad ,\quad n_{21} = 1 \tag{82}$$

with all other entries of M being zero.

The root with the largest real part of (55) for this choice of data and with $\varepsilon = 0.001$ can be seen in Figure 2

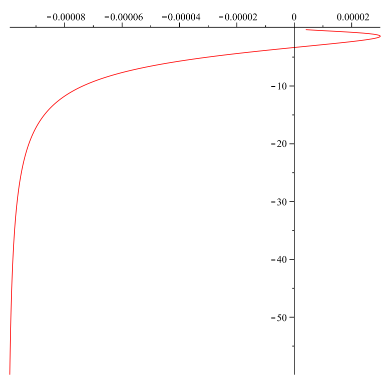

FIGURE 2. $N = 4$. Root with largest real part of (55) for U as in (50), $V_1 = 2, V_2 = 1$, D as in (15), A_0 as in (81) and M as in (82), $\varepsilon = 0.001$. Horizontal: $\mathrm{Re}(z(k))$, vertical: $\mathrm{Im}(z(k))$.

5. **Rippling dynamics of myxobacteria.** In this section we describe a specific class of models whose linearization yields problems of type (9). These problems are motivated by the intriguing counter migrating wave-like patterns observed before the final aggregation of and self-organization of myxobacteria (cf. [6]), which happens under starvation conditions. During their alignment and before their final self-organization takes place, the bacteria move in opposite directions in a quasi one-dimensional fashion and reverse their direction of motion, mainly due to contact and exchange of a so-called C-signal with counter migrating cells. As a result, counter-migrating population waves with a characteristic wavelength occur. A major question is, if the local exchange of C-signal and the resulting change of direction of motion is the main underlying mechanism for these waves or rather not.
The instabilities we described in the following can of course also arise in other biological or physical contexts. But here we want to stick with the basic phenomenon of rippling in myxobacteria.

From [17] we know already, that one cell state for each direction of motion is not sufficient to decide about pattern formation on the linearized level. Therefore we introduce 4 states. Consider bacteria, which exist in two different states 1 and 2, Let u_i, v_i denote the densities of cells which move towards the right, respectively the left, with internal state $i = 1, 2$. First, the bacteria change their state from 1 to 2, e.g. from a non-excited state to an excited state. Then, in a second step, they reverse their direction of motion. So we assume that there exists an intermediate state for the cells before they reorient. This can be interpreted e.g. by the local transfer of the so-called C-signal during cell-cell contact, which excites the bacterium and/or prepares it to switch the location of its molecular motor for movement, before it reverses its direction. So the four cellular states evolve according to the following transition: $u_1 \to u_2 \to v_1 \to v_2 \to u_1$.

Translating the previously described kinetics into a system of differential equations, we obtain

$$(u_1)_t + (u_1)_x = S_2(u_1, u_2, v_1, v_2) - T_1(u_1, u_2, v_1, v_2) \tag{83}$$

$$(u_2)_t + (u_2)_x = T_1(u_1, u_2, v_1, v_2) - T_2(u_1, u_2, v_1, v_2) \tag{84}$$

$$(v_1)_t - (v_1)_x = T_2(u_1, u_2, v_1, v_2) - S_1(u_1, u_2, v_1, v_2) \tag{85}$$

$$(v_2)_t - (v_2)_x = S_1(u_1, u_2, v_1, v_2) - S_2(u_1, u_2, v_1, v_2)\ . \tag{86}$$

To further simplify, we assume that the system is invariant under the change of variables $(x, u_i, v_i) \to (-x, v_i, u_i)$, $i = 1, 2$. Therefore $T_i(u_1, u_2, v_1, v_2) = S_i(v_1, v_2, u_1, u_2)$ for $i = 1, 2$. And (83)-(86) can be rewritten just in terms of T_1, T_2 accordingly. Due to this invariance assumption we study systems of type (9), which are obtained by linearizing systems of the above given type around a homogeneous equilibrium, with $u_1 = v_1$ and $u_2 = v_2$. Thus there exists a solution for the algebraic system

$$T_1(u_{1,0}, u_{2,0}, u_{1,0}, u_{2,0}) = T_2(u_{1,0}, u_{2,0}, u_{1,0}, u_{2,0})\ . \tag{87}$$

For general functions $T_1,\ T_2$ a curve/continuum of stationary states which solve (87) is to be expected. This is a major difference in comparison with Turing's instabilities. This continuum of steady states relates to the fact that different total cell densities are allowed. When prescribing $\sigma \equiv (u_1 + u_2 + v_1 + v_2)$ we obtain $u_{1,0} + u_{2,0} = \frac{\sigma}{2}$ and the homogeneous steady state can be determined uniquely. Under our symmetry condition we have

$$\sigma = 2(u_{1,0} + u_{2,0})\ . \tag{88}$$

If σ is fixed we must solve (87) with the constraint (88). For generic functions $T_1,\ T_2$ we can expect this problem to have a unique solution, at least locally near $u_{1,0} = u_{2,0}$. The stationary values for $u_1,\ u_2,\ v_1,\ v_2$ are assumed to fulfill $u_1 = v_1 = u_{1,0},\ u_2 = v_2 = u_{2,0}$.

Define $T_{\ell,j} \equiv \partial_j T_\ell(u_{1,0}, u_{2,0}, u_{1,0}, u_{2,0})$, where $j = 1, 2$ denotes derivatives with respect to u_1, u_2 and $j = 3, 4$ denotes derivatives with respect to v_1, v_2. Then the linearization of (83)-(86), including the invariance condition becomes

$$(\varphi_1)_t + (\varphi_1)_x = \sum_{j=1}^2 (T_{2,j+1} - T_{1,j})\varphi_j + (T_{2,j} - T_{1,j+2})\psi_j \tag{89}$$

$$(\varphi_2)_t + (\varphi_2)_x = \sum_{j=1}^2 (T_{1,j} - T_{2,j})\varphi_j + (T_{1,j+2} - T_{2,j+2})\psi_j \tag{90}$$

$$(\psi_1)_t - (\psi_1)_x = \sum_{j=1}^2 (T_{2,j} - T_{1,j+2})\varphi_j + (T_{2,j+2} - T_{1,j})\psi_j \tag{91}$$

$$(\psi_2)_t - (\psi_2)_x = \sum_{j=1}^2 (T_{1,j+2} - T_{2,j+2})\varphi_j + (T_{1,j} - T_{2,j})\psi_j \tag{92}$$

with $u_i = u_{i,0} + \varphi_i$, $v_i = v_{i,0} + \psi_i$, $i = 1, 2$, and $|\varphi_i| << u_{i,0},\ |\psi_i| << v_{i,0}$. Problem (89)-(92) is of type (9), with a point measure $d\mu(c)$ containing four elements $\{c\} \equiv \{(1,+)^t, (2,+)^t, (1,-)^t, (2,-)^t\}$. In the following we analyze systems of type (89)-(92) and respective variations, which yield oscillatory patterns in the sense of Definition 2.1.

Systems having some analogies with (83)-(86) but which include time-delays have been considered in [2], where

$$(u_1)_t + (u_1)_x = f_l(x,t) - f_l(x-\nu\tau, t-\tau) \quad (93)$$
$$(u_2)_t + (u_2)_x = f_l(x-\nu\tau, t-\tau) - f_r(x,t) \quad (94)$$
$$(v_1)_t - (v_1)_x = f_r(x,t) - f_r(x+\nu\tau, t-\tau) \quad (95)$$
$$(v_2)_t - (v_2)_x = f_r(x+\nu\tau, t-\tau) - f_l(x,t) \quad (96)$$

were studied, with suitable functions f_l, f_r depending on u_1, u_2, v_1, v_2. In [2] it was shown that the linearization of (93)-(96) around an homogeneous solution generates oscillatory patterns in the sense of Definition 2.1. One major difference between systems (83)-(86) and (93)-(96) is the delay τ in the second model, that could be interpreted as an "internal clock" or refractory time. The main result of our paper is to show that the structure of the nonlinearities in (83)-(86) is rich enough to generate oscillatory patterns without including delay terms in the equation. Further mathematical models for pattern formation in myxobacteria can be found in [1], [3], [14], and in [11], [22], to only name a few references.

Now system (89)-(92) is in the form of (14), (15) with the invariance condition (49) thus with the symmetry condition (50). In the following subsections we will first prove that if the bacteria in the excited state move with the same speed as the non-excited ones, then no solutions with oscillatory patterns bifurcate from "hyperbolic" matrices. Second we assume that the cells in the excited state move with slower speed than the non-excited cells. In a third model the excited cells are not moving at all. Similar pattern forming properties can be derived if the speed of the excited cells is larger than the speed of the non-excited cells. For this we have to construct suitable conditions for the nonlinearities, i.e. the specific exchange between the different cell states, since the combination of both pattern forming effects is by no means a general effect, but rather specifies the nonlinear behavior of the model crucially.

5.1. **Degenerate U, reflection symmetry, 4D, no pattern.** Here we show that under suitably generic conditions on the coefficients, system (14) with 4×4 matrices cannot yield oscillatory patterns in the proximity of "hyperbolic" matrices, if U contains only two opposite velocities and (14) is invariant under the transformation $(x,\varphi,\psi)\to(-x,\psi,\varphi)$. Let $A = A_0 + \varepsilon M$ and M as in (56), where by notational convenience the entries of A_0 are denoted by y_{ij} and z_{ij}. Let D be like in (15) and the diagonal matrix U with diagonal entries $U_1 = U_2 = V_1 = -U_3 = -U_4$, where $V_1 \in \mathbb{R}$, $V_1 \neq 0$ and $\varepsilon > 0$ is small. By rescaling we can assume w.l.o.g. that $V_1 = 1$.

First we precise the meaning of a p-hyperbolic matrix.

Definition 5.1. The matrix A_0 in (56) is a p-hyperbolic matrix if the vectors $(y_{11}, y_{21}, z_{11}, z_{21})^t$, $(y_{12}, y_{22}, z_{12}, z_{22})^t$ generate a linear subspace of dimension one and

$$\Delta_1'(0) \neq 0\ ,\ \text{ where} \quad (97)$$

$$\Delta_1(k) \equiv \det \begin{pmatrix} 2ik + y_{11} - z_{21} & y_{12} - z_{22} & z_{11} - y_{21} \\ -y_{11} + y_{21} & 2ik - y_{12} + y_{22} & -z_{11} + z_{21} \\ z_{11} - y_{21} & z_{12} - y_{22} & y_{11} - z_{21} \end{pmatrix}$$

$$+\det\begin{pmatrix} 2ik+y_{11}-z_{21} & y_{12}-z_{22} & z_{12}-y_{22} \\ -y_{11}+y_{21} & 2ik-y_{12}+y_{22} & -z_{12}+z_{22} \\ -z_{11}+z_{21} & -z_{12}+z_{22} & -y_{12}+y_{22} \end{pmatrix}$$

The set of matrices fulfilling (97) is open.

Remark 4. (97) is a technical condition which ensures that the dispersion relation associated to (14) can be computed perturbatively for $\varepsilon \to 0$. It is generically satisfied.

Proposition 6. *Let A_0 be a p-hyperbolic matrix in the sense of Definition 5.1. Then there exist $\alpha_1,\ \alpha_2 \in \mathbb{R}$ with $(\alpha_1)^2+(\alpha_2)^2 \neq 0$ and*

$$DA_0\,(\alpha_1,\alpha_2,0,0)^t = 0 = DA_0\,(0,0,\alpha_1,\alpha_2)^t \tag{98}$$

Here $\alpha_1,\ \alpha_2$ are uniquely determined, up to multiplication by $C \neq 0$. Moreover, for each $k \in \mathbb{R}$ the spectrum of the matrix $-(ikU+DA_0)$ contains the eigenvalues $-ik$ and ik.

Proof. Due Definition 5.1 there exist $\alpha_1,\ \alpha_2$ as stated with

$$\alpha_1\,(y_{11},y_{21},z_{11},z_{21})^t + \alpha_2\,(y_{12},y_{22},z_{12},z_{22})^t = 0\ . \tag{99}$$

Now calculate DA_0. Formula (98) then follows from (99). Since $U\,(\alpha_1,\alpha_2,0,0)^t = (\alpha_1,\alpha_2,0,0)^t$ and $U\,(0,0,\alpha_1,\alpha_2)^t = -(0,0,\alpha_1,\alpha_2)^t$, the mentioned properties about the spectrum of $-(ikU+DA_0)$ follow immediately. □

So an additional technical assumption on the matrix A_0 is needed in order to obtain the desired pattern forming properties.

Definition 5.2. A matrix A_0 is a stable p-hyperbolic matrix, if it is p-hyperbolic and if for each $k \in \mathbb{R}$ the spectrum of $-ikU - DA_0$ consists of the eigenvalues $-ik,\ ik$ and two more eigenvalues contained in the half-plane $\operatorname{Re}(z) < 0$.

Now we can state the main result of this section

Theorem 5.3. *Let A_0 be a stable p-hyperbolic matrix in the sense of Definition 5.2. Let $A = A_0 + \varepsilon M$. Let $\Delta_1(k)$ be as in Definition 5.1 and $\Delta_2(k) \equiv$*

$$\det\begin{pmatrix} 2ik+y_{11}-z_{21} & y_{12}-z_{22} & z_{11}-y_{21} & n_{12}-m_{22} \\ -y_{11}+y_{21} & 2ik-y_{12}+y_{22} & -z_{11}+z_{21} & -n_{12}+n_{22} \\ z_{11}-y_{21} & z_{12}-y_{22} & y_{11}-z_{21} & m_{12}-n_{22} \\ -z_{11}+z_{21} & -z_{12}+z_{22} & -y_{11}+y_{21} & -m_{12}+m_{22} \end{pmatrix}$$

$$+\det\begin{pmatrix} 2ik+y_{11}-z_{21} & y_{12}-z_{22} & n_{11}-m_{21} & z_{12}-y_{22} \\ -y_{11}+y_{21} & 2ik-y_{12}+y_{22} & -n_{11}+n_{21} & -z_{12}+z_{22} \\ z_{11}-y_{21} & z_{12}-y_{22} & m_{11}-n_{21} & y_{12}-z_{22} \\ -z_{11}+z_{21} & -z_{12}+z_{22} & -m_{11}+m_{21} & -y_{12}+y_{22} \end{pmatrix}$$

Define functions $P_0(k,a),\ P_1(k,a)$ by

$$\det\left((ik+a\varepsilon)+ikU+DA_0+\varepsilon DM\right) = P_0(k,a)+P_1(k,a)\,\varepsilon + O\left(\varepsilon^2\right)\ . \tag{100}$$

We can write

$$\Delta_1(k) = 2ik\,(\mu_1 ki+\nu_1)\ \ ,\ \ \Delta_2(k) = 2ik\,(\mu_2 ki+\nu_2)\ . \tag{101}$$

$$\textit{Then}\ \ P_0(k,a)+P_1(k,a)\,\varepsilon = 0 \tag{102}$$

defines a monotone function $r(k) = \operatorname{Re}(a)$ in case μ_1,μ_2,ν_1,ν_2 as defined in (101) satisfy

$$\mu_1\nu_2 - \mu_2\nu_1 \neq 0\ . \tag{103}$$

Remark 5. For $\varepsilon = 0$ the dispersion relation contains the solution $z = ik$. Now the derivative of z w.r.t. ε is $-\Delta_2/\Delta_1$. Due to (97) we have $\nu_1 \neq 0$ and (101) implies that $\Delta_2(0) = 0$. Therefore we obtain that Δ_2/Δ_1 is finite.

Remark 6. The function $\zeta = ik + a\varepsilon$ with $a = a(k)$ defined by (102) provides a linear approximation in ε of the eigenvalue $z = z(k, \varepsilon)$ of

$$(z + ikU + DA_0 + \varepsilon DM)\, v = 0 \ , \tag{104}$$

such that $z = ik$ for $\varepsilon = 0$. The monotonicity of $r(k)$ does not imply monotonicity of $\mathrm{Re}\,(z(k, \varepsilon))$, because classical perturbation theory for eigenvalue problems (cf. [16]) just implies $z(k, \varepsilon) = ik + a\varepsilon + O(\varepsilon^2)$ as $\varepsilon \to 0$. The uniformity of this approximation breaks down in general for $k \to 0$, since $z(0, 0)$ is a double eigenvalue. Some care is required to show uniformity of the approximation as $k \to \infty$. Therefore, from Theorem 5.3 we can only conclude that for the eigenvalue problem (104) patterns with wavelengths of order one for ε small are absent, if condition (103) holds. However, this Theorem does not rule out the onset of patterns with very large wavelengths for $\varepsilon \to 0$ under condition (103). Moreover, if (103) does not hold, there could be patterns with wavelengths of order one arising from quadratic terms in ε. The analysis of such higher order pattern would require methods different from the ones presented here.

Proof. The left hand side of (100) can be expanded as

$$\det \begin{pmatrix} 2ikI + E & F \\ F & E \end{pmatrix} + O(\varepsilon^2) \ , \quad \text{where} \tag{105}$$

$$E = \begin{pmatrix} y_{11} - z_{21} + \varepsilon m_{11} - \varepsilon n_{21} + a\varepsilon & y_{12} - z_{22} + \varepsilon m_{12} - \varepsilon n_{22} \\ -y_{11} + y_{21} - \varepsilon m_{11} + \varepsilon m_{21} & -y_{12} + y_{22} - \varepsilon m_{12} + \varepsilon m_{22} + a\varepsilon \end{pmatrix}$$

$$F = \begin{pmatrix} z_{11} - y_{21} + \varepsilon n_{11} - \varepsilon m_{21} & z_{12} - y_{22} + \varepsilon n_{12} - \varepsilon m_{22} \\ -z_{11} + z_{21} - \varepsilon n_{11} + \varepsilon n_{21} & -z_{12} + z_{22} - \varepsilon n_{12} + \varepsilon n_{22} \end{pmatrix} .$$

The first term in (105) can be expanded w.r.t. ε. Arguing as in the proof of Proposition 6 it follows that if $\varepsilon = 0$ the last two columns of the matrix in (105) are linearly dependent, so the determinant vanishes. Using the multilinearity of the determinant we can rewrite $P_0(k, a) = 0$, $P_1(k, a) = \Delta_1(k)\, a + \Delta_2(k)$. Then, the solution of (102) yields $a = -\Delta_2/\Delta_1$. Formulas (101) are a consequence of the linear dependence of the vectors $(y_{11}, y_{21}, z_{11}, z_{21})^t, (y_{12}, y_{22}, z_{12}, z_{22})^t$. Due to (97) we have $\nu_1 \neq 0$ and to the leading order

$$a = -(\mu_2 ki + \nu_2)/(\mu_1 ki + \nu_1) \text{ and } \mathrm{Re}\,(a) = (\alpha_2 + \beta_2 k^2)/(\alpha_1 + \beta_1 k^2) \tag{106}$$

for some $\alpha_1, \beta_1, \alpha_2, \beta_2 \in \mathbb{R}$, $\alpha_1 \neq 0$. The right hand side of (106) is monotone w.r.t. k, if (103) is satisfied. Thus our theorem follows. □

5.2. **Reduced motility of bacteria in the excited state.** Here we need that the diagonal matrix U contains more than two opposite velocities, so we assume

$$U_1 = 2 \ , \ U_2 = 1 \ , \ U_3 = -2 \ , \ U_4 = -1 \tag{107}$$

We obtain (14) by linearizing (83)-(86) with A given by

$$A = \begin{pmatrix} T_{1,1} & T_{1,2} & T_{1,3} & T_{1,4} \\ T_{2,1} & T_{2,2} & T_{2,3} & T_{2,4} \\ T_{1,3} & T_{1,4} & T_{1,1} & T_{1,2} \\ T_{2,3} & T_{2,4} & T_{2,1} & T_{2,2} \end{pmatrix} = A_0 + \varepsilon M \ .$$

Further, we will make the following assumptions

$$T_1 = T_1\left(u_1 + u_2 + v_1 + v_2, u_1, v_1 + v_2\right) \quad , \quad T_2 = T_2\left(u_2\right) \ . \tag{108}$$

The bacteria change through the states in the following way: $u_1 \to u_2 \to v_1 \to v_2$. Thus cells of non-excited type u_1 get excited (i.e. prepare for turning) in dependence of the total cell density, the collisions with counter-migrating cells and by the cell density of their own kind. Turning is then automatic and depends on the distribution u_2 itself. Assume, as above, that the eigenvector associated to the eigenvalue $(-2ik)$ for the unperturbed problem $z + ikU + DA_0 = 0$ is $(1, 0, 0, 0)^t$. Then, again denoting the entries of the matrix A_0 in (56) by y_{ij}, z_{ij}, we have $y_{11} = y_{21} = z_{11} = z_{21} = c$, (cf. Assumption 3), for some constant $c \in \mathbb{R}$. In order to obtain a particular example which fulfills the constraints (108) we choose $c = 0$ and $z_{1,2} = z_{2,2} = 0$. Then, due to (108) we must have

$$A_0 = \begin{pmatrix} 0 & y_{12} & 0 & 0 \\ 0 & y_{22} & 0 & 0 \\ 0 & 0 & 0 & y_{12} \\ 0 & 0 & 0 & y_{22} \end{pmatrix} \quad , \quad M = \begin{pmatrix} m_{11} & m_{12} & n_{11} & n_{11} \\ 0 & m_{22} & 0 & 0 \\ n_{11} & n_{11} & m_{11} & m_{12} \\ 0 & 0 & 0 & m_{22} \end{pmatrix} \ .$$

Since we are interested in $A = A_0 + \varepsilon M$ the values of m_{12}, m_{22} can be absorbed in the respective entries in A_0, namely in y_{12}, y_{22}. So we chose $m_{12} = m_{22} = 0$. The corresponding dispersion relation associated to (14) can then be computed by solving $\det\left(z + ikU + DA_0 + \varepsilon DM\right) = 0$. We compute solutions of this equation near the "hyperbolic line" $z = -2ik$ perturbatively. To do so we take an expansion, which is uniform on the whole line $k \in \mathbb{R}$, i.e. $z = -2ik + a\varepsilon + \ldots$. Keeping only terms of linear order in ε we obtain

$$a = -m_{11}\,\frac{iy_{22}y_{12} - 5y_{22}k + 4ik^2 + y_{12}k - iy_{22}^2}{5y_{12}k - iy_{12}^2 - 5y_{22}k + 4ik^2 - iy_{22}^2 + 2iy_{22}y_{12}} \ .$$

To have the remaining part of the spectrum in the region $\mathrm{Re}(z) < 0$ we need $y_{12} - y_{22} < 0$. Then we get the following asymptotics

$$\mathrm{Re}\,(a) \sim (m_{11} - n_{11})\,\frac{y_{22}}{y_{12} - y_{22}} - \frac{m_{11}y_{12} - 9n_{11}y_{22}}{\left(y_{12} - y_{22}\right)^3}k^2 + \ldots$$

for $k \to 0$ and $\lim_{k\to\infty} a = -m_{11}$. The following conditions ensure oscillatory pattern formation for (14) in sense of Definition 2.1

$$m_{11} = n_{11} \ , \ m_{11}y_{12} - 9n_{11}y_{22} > 0 \ , \ m_{11} > 0 \ .$$

W.l.o.g. assume that $m_{11} = n_{11} = 1$. Taking into account $y_{12} - y_{22} < 0$, a sufficient condition for oscillatory pattern formation for small $\varepsilon > 0$ is

$$y_{12} - 9y_{22} > 0 \ , \ y_{22} - y_{12} > 0 \ .$$

One possible choice for A_0 is taking $y_{12} = -1$, $y_{22} = -0.5$, for M taking $m_{11} = n_{11} = n_{12} = 1$ and all other entries being zero. Then with $\varepsilon > 0$ we obtain oscillatory patterns for (14). The root with the largest real part corresponding to the dispersion relation for this choice of matrices is shown in Figure 3. To summarize

Theorem 5.4. *The differential equation (14) with $A = A_0 + \varepsilon M$ where $y_{12} = -1$, $y_{22} = -0.5$, $m_{11} = n_{11} = n_{12} = 1$ and all other entries are zero, with U as in (107) and $\varepsilon > 0$ sufficiently small generates oscillatory patterns in the sense of Definition 2.1.*

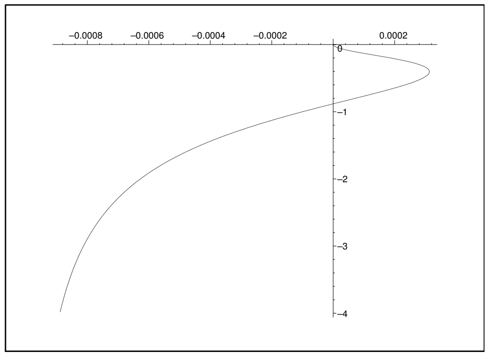

FIGURE 3. Root with the largest real part of the dispersion relation for the situation in Theorem 5.4 with $\varepsilon = 0.001$. Horizontal: $\mathrm{Re}(z(k))$, vertical: $\mathrm{Im}(z(k))$.

The roles of the entries 1 and 2 in U can be exchanged with the same conclusion, including the signs of the coefficients. In all situations found, the functions show an inhibitory character for some interactions, which is untypical for the behavior known of myxobacteria.

5.3. **Bacteria in the excited state do not move.** For the diagonal matrix U we now assume

$$U_1 = 1 = -U_3 \ , \ U_2 = U_4 = 0 \ . \tag{109}$$

In this case it is not possible to obtain oscillatory patterns with functional dependences as given in (108) for the transition functions. But with different dependencies for T_2 we can obtain oscillatory pattern formation without inhibitory effects, which is more realistic in the context of movement of myxobacteria. A first natural generalization of the previous case, namely $T_1 = T_1(u_1 + u_2 + v_1 + v_2, u_1, v_1 + v_2)$, $T_2 = T_2(u_1 + u_2 + v_1 + v_2, u_2)$ does not give oscillatory patters at the linearized level for ε. Instead we assume

$$T_1 = T_1(u_1 + u_2 + v_1 + v_2, u_1, v_1, v_2) \quad , \quad T_2 = T_2(u_1 + u_2 + v_1 + v_2) \ .$$

A set of matrices A_0, M, $A = A_0 + \varepsilon M$ consistent with this are

$$A_0 \text{ with constant entries } c \text{ everywhere, apart from } y_{12} \text{ and } z_{12} \ , \tag{110}$$

$$M \text{ with zero entries everywhere, apart from } m_{11} \text{ and } n_{11} \ . \tag{111}$$

We then solve

$$\det(z + ikU + DA_0 + \varepsilon DM) = 0 \tag{112}$$

near the line of hyperbolicity $z = -ik$, i.e. we expand $z = -ik + a\varepsilon + \ldots$. The solution of order ε yields

$$a = -k\ \frac{n_{11}c + m_{11}y_{12} - m_{11}c - n_{11}z_{12} + im_{11}k}{-2ck + 2iy_{12}c + iz_{12}^2 + ik^2 + 2y_{12}k - iy_{12}^2 - 2iz_{12}c} \ .$$

Then we have the following asymptotic formula

$$\mathrm{Re}(a) \sim \frac{-1}{(2cy_{12} + z_{12}^2 - y_{12}^2 - 2z_{12}c)^2} \big(-2m_{11}cy_{12} + m_{11}z_{12}^2 + m_{11}y_{12}^2 \\ -2m_{11}z_{12}c + 2n_{11}cy_{12} - 2n_{11}c^2 + 2m_{11}c^2 - 2n_{11}z_{12}y_{12} + 2n_{11}z_{12}c\big)\, k^2$$

for $k \to 0$, and $\lim_{k\to\infty} a = -m_{11}$. The part of the spectrum of $-(ikU + DA_0)$ not contained in the line $\mathrm{Re}\,(z) = 0$ is given by $z = y_{12} - 2c + z_{12}$, $z = -z_{12} + y_{12}$. Therefore the following conditions ensure the existence of oscillatory patterns in the sense of Definition 2.1 for $\varepsilon > 0$ sufficiently small

$$\begin{aligned} -2m_{11}y_{12}c + m_{11}z_{12}^2 + m_{11}y_{12}^2 - 2m_{11}z_{12}c + 2n_{11}y_{12}c - 2n_{11}c^2 \\ +2m_{11}c^2 - 2n_{11}z_{12}y_{12} + 2n_{11}z_{12}c \quad < 0 \\ m_{11} > 0 \ , \ y_{12} - 2c + z_{12} < 0 \ , \ -z_{12} + y_{12} < 0 \end{aligned}$$

With the following choice in (111) all these inequalities are satisfied

$$c = 1.5 \ , \ y_{12} = 0.5 \ , \ z_{12} = 1 \ , \ m_{11} = 1 \ , \ n_{11} = 2 \ . \tag{113}$$

The form of the root of the dispersion relation with largest real part for this choice of matrices is given in Figure 4. In summary we have

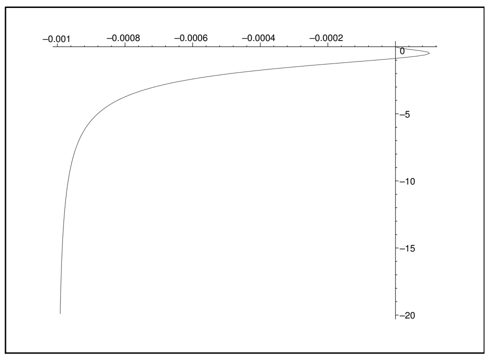

FIGURE 4. Root with largest real part of (112) with conditions as given in Theorem 5.5 for $\varepsilon = 0.01$. Horizontal: $\mathrm{Re}(z(k))$, vertical: $\mathrm{Im}(z(k))$.

Theorem 5.5. *The differential equation (14) with $A = A_0 + \varepsilon M$, and A_0, M as given in (111) with coefficients as in (113), U given as in (109), and $\varepsilon > 0$ sufficiently small, generates oscillatory patterns in the sense of Definition 2.1.*

5.4. **A symmetric** 6×6 **System with degenerate** U**.** We have seen before that a generic 4×4 system cannot yield oscillatory patterns near hyperbolic settings if the matrix U contains only two opposite velocities. In this section we give an example of a 6×6 system, which is invariant under the transformation $(x, \varphi, \psi) \to (-x, \psi, \varphi)$ and yields oscillatory pattern formation. Let the diagonal matrix U be such, that

$$U_1 = U_2 = U_3 = 1 \ , \ U_4 = U_5 = U_6 = -1 \tag{114}$$

and D be like in (15). We consider linearizations of systems like (83)-(86) which contain two additional variables (u_3, v_3). Let $\tilde{\sigma} = u_1 + u_2 + u_3 + v_1 + v_2 + v_3$. Assume that the transition functions are

$$T_1 = T_1\,(u_1, v_1 + v_2 + v_3) \quad , \quad T_2 = T_2\,(u_2, \tilde{\sigma}) \quad , \quad T_3 = T_3\,(u_3) \tag{115}$$

with $T_i > 0$ for $u_i > 0$, $i = 1, 2, 3$. Even after intensive and well designed trials we were unable to find simpler functional dependencies than (115). In particular replacing $T_2(u_2, \tilde{\sigma})$ by $T_2(u_2)$ is too simple to generate oscillatory patterns with our method. The linearized matrix A compatible with (115) has the form

$$A = \begin{pmatrix} y_{11} & 0 & 0 & z_{11} & z_{11} & z_{11} \\ y_{21} & y_{22} & y_{21} & y_{21} & y_{21} & y_{21} \\ 0 & 0 & y_{33} & 0 & 0 & 0 \\ z_{11} & z_{11} & z_{11} & y_{11} & 0 & 0 \\ y_{21} & y_{21} & y_{21} & y_{21} & y_{22} & y_{21} \\ 0 & 0 & 0 & 0 & 0 & y_{33} \end{pmatrix} , \tag{116}$$

with $A = A_0 + \varepsilon M$ where A_0 is "hyperbolic". We assume a particular form of "hyperbolic" behavior, namely $DA_0 (1,0,0,0,0,0)^t = DA_0 (0,0,0,1,0,0)^t = 0$, which is satisfied if $y_{11} = y_{21} = z_{11} = 0$. Let A_0 be a diagonal matrix with

$$a_{0,11} = a_{0,44} = 0 \ , \ a_{0,22} = a_{0,55} = y_{22} \ , \ a_{0,33} = a_{0,66} = y_{33} \tag{117}$$

Then $A = A_0 + \varepsilon M$ is of the form (116) in case

$$M = \begin{pmatrix} m_{11} & 0 & 0 & n_{11} & n_{11} & n_{11} \\ m_{21} & 0 & m_{21} & m_{21} & m_{21} & m_{21} \\ 0 & 0 & 0 & 0 & 0 & 0 \\ n_{11} & n_{11} & n_{11} & m_{11} & 0 & 0 \\ m_{21} & m_{21} & m_{21} & m_{21} & 0 & m_{21} \\ 0 & 0 & 0 & 0 & 0 & 0 \end{pmatrix} . \tag{118}$$

The spectrum of $-(ikU + DA_0)$ is given by the eigenvalues

$$\{-ik, -ik - y_{22}, -ik - y_{33}, ik, ik - y_{22}, ik - y_{33}\} \ .$$

Therefore, to obtain that the most unstable branch of the dispersion relation for small ε is a perturbation of $\pm ik$ we have to assume $y_{2,2} > 0$, $y_{3,3} > 0$. As before, the dispersion relation associated to (14) is given by the roots of

$$\det (z + ikU + DA_0 + \varepsilon DM) = 0 \ , \tag{119}$$

and we can look for perturbative solutions of (119) of the form $z = ik + a\varepsilon + \ldots$. Solving (119) to the leading order in ε we obtain

$$a = -\frac{2km_{11}(y_{33} + y_{22}) + iy_{22}y_{33}(n_{11} - m_{11}) + 4ik^2 m_{11} - 2km_{21}y_{33}}{-iy_{22}y_{33} + 2ky_{22} + 2ky_{33} + 4ik^2} \ .$$

The real part of a has the following asymptotics

$$Re(a(k)) \sim (n_{11} - m_{11}) \\ - 4\frac{(n_{11} - m_{21})y_{22}y_{33} + n_{11}y_{22}^2 + (n_{11} - m_{21})y_{33}^2}{y_{22}^2 y_{33}^2} k^2 + \ldots \ .$$

for $k \to 0$ and $a(k) \to -m_{1,1}$ for $k \to \infty$. A sufficient condition for oscillatory patterns in the sense of Definition 2.1 is then

$$n_{11} = m_{11} > 0 \ , \ -4 \ \frac{(n_{11} - m_{21})y_{22}y_{33} + (n_{11} - m_{21})y_{33}^2 + n_{11}y_{22}^2}{y_{22}^2 y_{33}^2} > 0 \ .$$

A variety of coefficients y_{ij}, n_{ij} satisfy these inequalities, e.g.

$$m_{11} = n_{11} = 1 \ , \ y_{22} = y_{33} = 1 \ , \ m_{21} = 4 \ . \tag{120}$$

The form of the most unstable branch of the dispersion relation associated to these coefficients is given in Figure 5. To summarize

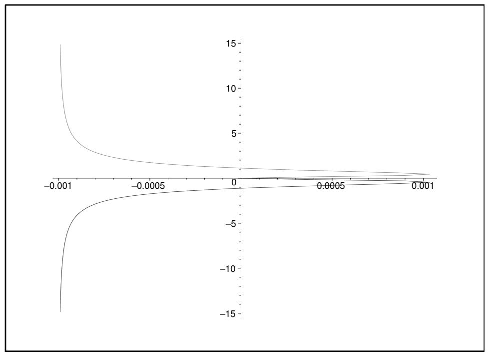

FIGURE 5. Root of (119) with the largest real part for conditions as given in Theorem 5.6 with $\varepsilon = 0.001$. Horizontal: $\mathrm{Re}(z(k))$, vertical: $\mathrm{Im}(z(k))$.

Theorem 5.6. *The differential equation (14) with $A = A_0 + \varepsilon M$, and A_0, M as in (117), (118), (120), U as in (114) and $\varepsilon > 0$ sufficiently small, generates oscillatory patterns in the sense of Definition 2.1.*

5.5. **Test of the model - wildtype and mutants.** Pattern formation in biology often relates to certain functional mechanisms. In myxobacteria there is a peculiar phenomenon, that allows to test models for rippling on their reliability. There exist mutants which can be mixed with wildtype populations, moving the way the wildtype does, but which do not produce the C-signal, which upon contact with counter-migrating bacteria make these bacteria change their orientation. The mutants themselves can receive the signal and thus turn, but they do not send the signal and thus cannot induce turning for other bacteria. When mixing these two types of bacteria still rippling patterns occur, but with an increasing fraction of mutants the wavelength of the ripples increases too. For a large enough fraction of mutants in the total population, the rippling pattern is finally lost.

We can see all these effects of rippling, increasing of the wavelength of the rippling pattern, and the loss of the rippling phenomenon in the following basic 6×6 model for the wildtype and its naturally extended version for the wildtype-mutant situation. In the wildtype and mutant system a critical value of the mutant fraction exists, at which the pattern is lost. For this to happen, we need to exchange the roles of the dependencies of T_1 and T_2, in comparison to the model discussed before. We intentionally introduced both dependencies in this paper to stress, that oscillatory patterns in this model do not occur generically, but need peculiar nonlinearities.

Assume that the bacteria are given in 3 states which can move in opposite spatial directions. So we have the sequence of states

$$u_1 \to u_2 \to u_3 \to v_1 \to v_2 \to v_3 \to u_1 \ .$$

Then the following set of transition functions (if mutants are absent) can generate oscillatory patterns as before and additionally is able to produce the desired bifurcations in the population, when mutants are present

$$T_1 = T_1\left(\tilde{\sigma}, u_1\right) \ \ , \ \ T_2 = \lambda_2\left(v_1 + v_2 + v_3\right) u_2 \ \ , \ \ T_3 = \lambda_3 u_3 \ , \qquad (121)$$

So the right moving bacteria of type 1 become excited at rate T_1/u_1, respectively become able to receive or send the C-signal to induce turning in other bacteria - in dependence of the total cell density and their own density, for instance, when the total population density is high enough. The bacteria of type 2 receive the C-signal upon contact with counter migrating cells v_i, $i = 1, 2, 3$ at rate $\lambda_2(v_1+v_2+v_3)$. The bacteria of type 3 then turn with rate λ_3. These dependencies and their biological interpretation fit very well to what is known about myxobacteria and C-signaling.

For the model with mutants and wildtype cells we have the following. Since the counter-migrating mutants do not produce the signal, they do not occur in the collision term associated to T_2. Only wildtype cells produce the C-signal upon collision, which makes the counter-migrating cells, which receive the signal, turn. Here and in the following we define

$$\sigma = u_1 + u_2 + u_3 + v_1 + v_2 + v_3 + \bar{u}_1 + \bar{u}_2 + \bar{u}_3 + \bar{v}_1 + \bar{v}_2 + \bar{v}_3 \ ,$$

where $\bar{u}_i, \bar{v}_i$ denote the corresponding concentrations of mutants. Let
$q = v_1+v_2+v_3$ and let us further assume $T_1 = T_1(\sigma, u_1)$, $T_2 = \lambda_2(q)\, u_2$, $T_3 = \lambda_3 u_3$ as before, and $\bar{T}_1 = T_1(\sigma, \bar{u}_1)$, $\bar{T}_2 = \lambda_2(q)\, \bar{u}_2$, $\bar{T}_3 = \lambda_3 \bar{u}_3$. Given that T_1 and $\bar{T}_1$ are the transition functions we need

$$T_1(\sigma, 0) = \bar{T}_1(\sigma, 0) = 0 \ . \tag{122}$$

This also guarantees, that this larger model reduces to the smaller wildtype only model, in case the mutants are absent.
Using our usual approach to derive coefficients, which yield bifurcations near "hyperbolic" matrices, for functional dependences as in (121), we obtain the following choice of coefficients

$$T_{1,\sigma} + T_{1,u} = \varepsilon m_{11},\ T_{1,\sigma} = \varepsilon m_{12},\ T_{2,u} = y_{22},\ T_{3,u} = y_{33},\ T_{2,\xi} = \varepsilon n_{12}. \tag{123}$$

We obtain oscillatory patterns for the following choice of coefficients

$$m_{1,2} = m_{1,1} = 1 \tag{124}$$

$$-y_{22}y_{33} + n_{21}y_{33}y_{22} + n_{21}y_{33}^2 - y_{22}^2 - y_{33}^2 > 0\ ,\ y_{22} > 0\ ,\ y_{33} > 0 \tag{125}$$

and ε sufficiently small.

The fraction of wildtype cells in the total population will now be denoted by α, which means $\alpha = 1$ in the previous considerations.

Condition (124) is not strictly needed to generate oscillatory patterns. However, it is convenient, because with this choice the most unstable branch of the dispersion relation associated to the linearization of (121) contains the origin for $k = 0$ to the leading order in ε and for arbitrary values of α. Therefore, with the choice in (124) the analysis of the bifurcation w.r.t. α reduces to proving that a local minimum for the dispersion relation at $k = 0$ becomes a local maximum for changing α.

If we assume (123) and (124) to hold in an open subset of $\{(u_i, v_i, \bar{u}_i, \bar{v}_i), i = 1, 2, 3\}$ which intersects $(\{u_1 = 0\} \cup \{\bar{u}_1 = 0\})$ we obtain $T_{1,u} = 0$. This contradicts (122).

In order to avoid this problem we will assume that $T_{1,u} = 0 = \bar{T}_{1,\bar{u}}$ only holds approximatively in case $u_1, \bar{u}_1$ are sufficiently large. For this to hold we will assume that $T_1 = \lambda_1(\sigma)\, \Psi\left(u_1/\sigma^\beta\right)$, where the total cell concentration σ is large and $0 < \beta < 1$. We assume that $\lambda_1(\sigma)$ is a function of order one and that $\Psi(\xi) \sim \xi$ for $\xi \to 0$ and $\Psi(\xi) \sim 1$ for $\xi \to \infty$ and similar laws for $\bar{T}_1$. Then the approximation $T_{1,u}$ only holds for $u_1 >> \sigma^\beta$. For generic T_1, T_2, T_3 and under our assumptions (123), (124) we have that $u_1, \bar{u}_1$ are of order σ and our approximation conditions would be justified. The concentration of mutants will be of order $(1-\alpha)\,\sigma$ and then, the function T_1 will approximately be given by

$$T_1 = \lambda_1(\sigma) \qquad \text{for} \qquad (1-\alpha) >> \sigma^{\beta-1} \ . \tag{126}$$

In case $(1-\alpha)$ is small, also u_1 is small and we would need to compute $T_1 = \lambda_1(\sigma)\Psi(u_1/\sigma^{\beta})$. This would result in steady state concentrations remaining positive for all α. The bifurcation phenomenon for α also happens in this case. But from here on will restrict our analysis to the situation (126). The homogeneous equilibria for the concentrations of wildtype cells and mutants are characterized by $T_1 = T_2 = T_3$, $\bar{T}_1 = \bar{T}_2 = \bar{T}_3$, and $u_i = v_i$, $\bar{u}_i = \bar{v}_i$ for $i = 1,2,3$, and $u_1 + u_2 + u_3 = \alpha\sigma/2$, $\bar{u}_1+\bar{u}_2+\bar{u}_3 = (1-\alpha)\sigma/2$. The solutions of these equations under the approximation (126) are

$$\begin{aligned}
u_2 &= \frac{\lambda_1(\sigma)}{\lambda_2\left(\frac{\alpha\sigma}{2}\right)} \ , \ u_3 = \frac{\lambda_1(\sigma)}{\lambda_3} \ , \ \bar{u}_2 = \frac{\lambda_1(\sigma)}{\lambda_2\left(\frac{\alpha\sigma}{2}\right)} \ , \ \bar{u}_3 = \frac{\lambda_1(\sigma)}{\lambda_3} \\
u_1 &= \frac{\alpha\sigma}{2} - (u_2+u_3) = \frac{\alpha\sigma}{2} - \frac{\lambda_1(\sigma)}{\lambda_2\left(\frac{\alpha\sigma}{2}\right)} - \frac{\lambda_1(\sigma)}{\lambda_3} \\
\bar{u}_1 &= \frac{(1-\alpha)\sigma}{2} - (\bar{u}_2+\bar{u}_3) = \frac{(1-\alpha)\sigma}{2} - \frac{\lambda_1(\sigma)}{\lambda_2\left(\frac{\alpha\sigma}{2}\right)} - \frac{\lambda_1(\sigma)}{\lambda_3} \ .
\end{aligned}$$

The linearized problem near the homogeneous states is of the form

$$\partial_t f + \begin{pmatrix} U & 0 \\ 0 & U \end{pmatrix} \partial_x f + \begin{pmatrix} D & 0 \\ 0 & D \end{pmatrix} A f = 0 \ , \tag{127}$$

where for the diagonal matrix U we have $U_1 = U_2 = U_3 = 1$, $U_4 = U_5 = U_6 = -1$, D is like in (15) and

$$A = \begin{pmatrix} A_1 & A_2 & A_3 & A_3 \\ A_2 & A_1 & A_3 & A_3 \\ \bar{A}_3 & \bar{A}_2 & \bar{A}_1 & \bar{A}_3 \\ \bar{A}_2 & \bar{A}_3 & \bar{A}_3 & \bar{A}_1 \end{pmatrix} \qquad \text{with } A_1 = \begin{pmatrix} T_{1,\sigma} & T_{1,\sigma} & T_{1,\sigma} \\ 0 & T_{2,u} & 0 \\ 0 & 0 & T_{3,u} \end{pmatrix}$$

$$A_2 = \begin{pmatrix} T_{1,\sigma} & T_{1,\sigma} & T_{1,\sigma} \\ T_{2,\xi} & T_{2,\xi} & T_{2,\xi} \\ 0 & 0 & 0 \end{pmatrix} \quad , \quad A_3 = \begin{pmatrix} T_{1,\sigma} & T_{1,\sigma} & T_{1,\sigma} \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix}$$

and $\bar{A}_1, \bar{A}_2, \bar{A}_3$ analogously with the respective $\bar{T}_{i,q}$ instead of $T_{i,q}$. Using the transition functions (121), (126) we obtain the following linearized coefficients at the homogeneous states

$$\begin{aligned}
&T_{1,\sigma} = \bar{T}_{1,\sigma} = T^0_{1,\sigma} \ , \ T_{1,u} = \bar{T}_{1,u} = 0 \quad , \quad T_{3,u} = \bar{T}_{3,u} = T^0_{3,u} \\
&T_{2,u} = \bar{T}_{2,u} = \frac{\lambda_2(\alpha\sigma/2)}{\lambda_2(\sigma/2)} T^0_{2,u} \ , \ T_{2,\xi} = \bar{T}_{2,\xi} = \frac{\lambda_2'(\alpha\sigma/2)}{\lambda_2'(\sigma/2)} \frac{\lambda_2(\sigma/2)}{\lambda_2(\alpha\sigma/2)} T^0_{2,\xi} \ .
\end{aligned}$$

Where $T^0_{i,w}$ denotes $T_{i,w}$ for $\alpha = 1$ and σ being fixed.

The transition between functions, which yield oscillatory patterns, and functions which do not, is characterized by $(-y_{22}y_{33} + n_{21}y_{33}y_{22} + n_{21}y_{33}^2 - y_{22}^2 - y_{33}^2) < 0$ in difference to (125). To obtain such a switch we choose

$$\lambda_2(\alpha\sigma/2) \Big/ \lambda_2(\sigma/2) = \phi(\alpha) \quad \text{with} \quad \phi(\alpha) = e^{\alpha^2-1} \ .$$

The superexponential growth of ϕ seems to be crucial to obtain the desired bifurcation with this scheme. Such type of superexponential growth is known e.g. in chemical reactions and can result for instance from a threshold activation energy

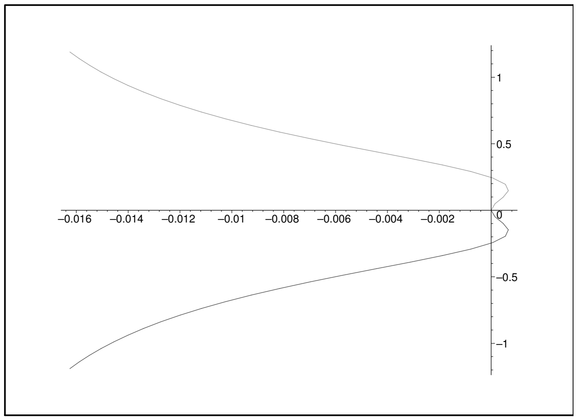

FIGURE 6. $\alpha = 0.7$

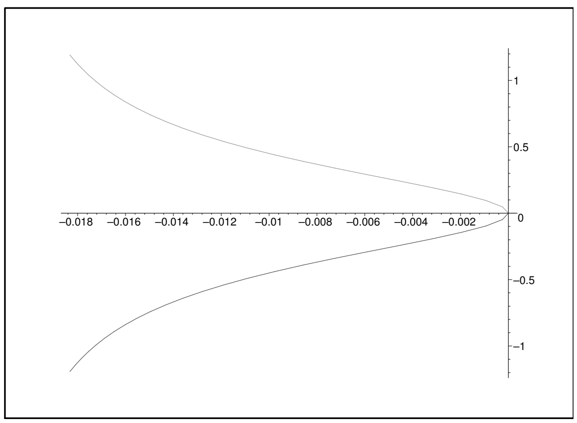

FIGURE 7. $\alpha = 0.5$

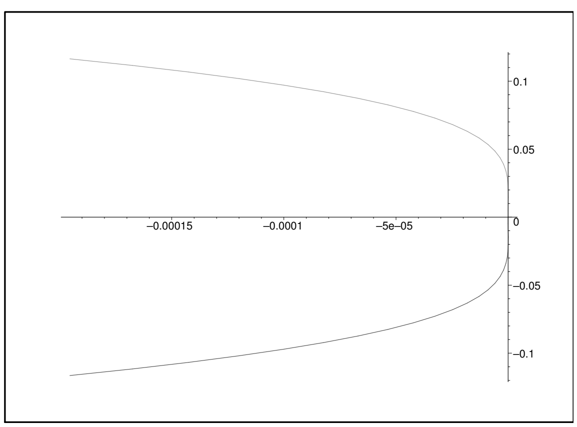

FIGURE 8. Magnified scale in comparison with figures 6, 7. $\alpha = 0.6$

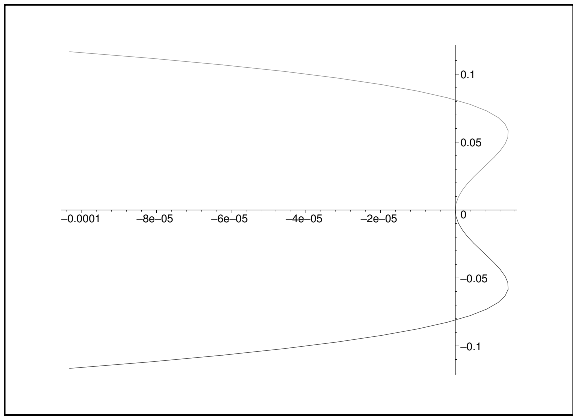

FIGURE 9. Magnified scale in comparison with figures 6, 7. $\alpha = 0.61$

that is able to produce exponential dependences. With this functional choices we have

$$T_{1,\sigma} = \bar{T}_{1,\sigma} = T^0_{1,\sigma} \ , \ T_{1,u} = \bar{T}_{1,u} = 0 \quad , \quad T_{3,u} = \bar{T}_{3,u} = T^0_{3,u} \ ,$$
$$T_{2,u} = \bar{T}_{2,u} = e^{\alpha^2-1} T^0_{2,u} \ , \ T_{2,\xi} = \bar{T}_{2,\xi} = \alpha e^{\alpha^2-1} T_{2,\xi} / e^{\alpha^2-1^0} = \alpha T^0_{2,\xi} \ .$$

We choose the coefficients for "small" mutant concentrations as in (123).

The figures show the branch with the root with the largest real part for the dispersion relation corresponding to (127) for different values of α. For arbitrary α it contains a "neutral" bifurcation branch given by the values $z = \pm ik$, $k \in \mathbb{R}$. Calculating the dispersion relation reduces to solving a polynomial equation of degree ten. Figures 6, ..., 9 show the parametrization of the most unstable branch for $\alpha = 0.7, \ 0.5$ and in a magnified scale near the bifurcation value for $\alpha = 0.6, \ 0.61$.

With this we have obtained a model for the one-dimensional motion of myxobacteria which shows the following behavior. The model for the wildtype population shows rippling patterns with a defined wavelength. The same is true for the natural extension of the model for mixtures of wildtype and mutants, only the wavelength of the rippling pattern increases with an increasing fraction of mutants. If the fraction of mutants within the population is too large, the rippling pattern vanishes, as it is observed in experiments. So the model passes the known experimental tests so far.

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REFERENCES

[1] M. S. Alber, M. A. Kiskowski and Y. Jing, *Lattice gas cellular automaton model for rippling and aggregation in myxobacteria*, Physica D, **191** (2004), 343–358.

[2] U. Börner and M. Bär, *Pattern formation in a reaction-advection model with delay: A continuum approach to myxobacterial rippling*, Annalen der Physik, **13** (2004), 432–441.

[3] U. Börner, A. Deutsch, H. Reichenbach and M. Bär, *Rippling patterns in aggregates of myxobacteria arise from cell-cell collisions*, Physical Review Letters, **89** (2002), 078101.

[4] O. Diekmann, M. Gyllenberg, J. A. J. Metz and H. R. Thieme, *On the formulation and analysis of general deterministic structured population models I. Linear Theory*, J. Math. Biol., **36** (1998), 349–388.

[5] O. Diekmann, M. Gyllenberg, H. Huang, M. Kirkilionis, J. A. J. Metz and H. R. Thieme, *On the formulation and analysis of general deterministic structured population models II. Nonlinear theory*, J. Math. Biol., **43** (2001), 157–189.

[6] M. Dworkin and D. Kaiser eds., "Myxobacteria II," American Society for Microbiology (AMS) Press, 1993.

[7] R. Erban and H. J. Hwang, *Global existence results for complex hyperbolic models of bacterial chemotaxis*, DCDS-B, **6** (2006), 1239–1260.

[8] R. Erban and H. Othmer, *From signal transduction to spatial pattern formation in E.coli : A paradigm for multi-scale modeling in biology*, Multiscale Modeling and Simulation, **3** (2005), 362–394.

[9] E. Geigant, "Nichtlineare Integro-Differential-Gleichungen zur Modellierung interaktiver Musterbildungsprozesse auf S^1," (German) [Nonlinear Integro-Differential Equations for the Modelling of Interactive Pattern Formation Processes on S^1], Bonner Mathematische Schriften **323** Ph.D thesis, University of Bonn, 1999.

[10] E. Geigant, *On peak and periodic solutions of an integro-differential equation on* S^1, in "Geometric Analysis and Nonlinear Partial Differential Equations", Springer-Verlag, Berlin, (2003), 463–474.

[11] E. Geigant and M. Stoll, *Bifurcation analysis of an orientational aggregation model*, J. Math. Biol., **46** (2003), 537–563.

[12] A. Gierer and H. Meinhardt, *A theory of biological pattern formation*, Kybernetik, **12**, (1972), 30–39.

[13] T. Hillen, *A Turing model with correlated random walk*, J. Math. Biol., **35** (1996), 49–72.

[14] O. Igoshin, J. Neu and G. Oster, *Developmental waves in Myxobacteria: A novel pattern formation mechanism*, Phys. Rev. E, **7** (2004), 1–11.

[15] K. Kang, B. Perthame, A. Stevens and J. J. L. Velázquez, *An Integro-differential equation model for alignment and orientational aggregation*, J. of Differential Equations, **246** (2009), 1387–1421.

[16] T. Kato, "Perturbation Theory for Linear Operators," Springer-Verlag, Berlin, 1980.

[17] F. Lutscher and A. Stevens, *Emerging patterns in a hyperbolic model for locally interacting cell systems*, J. Nonlinear Science, **12** (2002), 619–640.

[18] H. Meinhardt, *Morphogenesis of lines and nets*, Differentiation, **6** (1976), 117–123.

[19] J. D. Murray, "Mathematical Biology I and II," Interdisciplinary Applied Mathematics 17 and 18, Springer-Verlag, New York, 2002/03.

[20] H. Othmer, S. Dunbar and W. Alt, *Models of dispersal in biological systems*, J. Math. Biol., **26** (1988), 263–298.

[21] B. Perthame, "Transport Equations in Biology," Frontiers in Mathematics, Birkhäuser-Verlag, Basel, 2007.

[22] B. Pfistner, "Ein Eindimensionales Modell Zum Schwarmverhalten der Myxobakterien Unter Besonderer Berücksichtigung der Randzonenentwicklung," (German) [A one-dimensional model on the swarming behavior of Myxobacteria, with special consideration of the development of the boundary zone], Ph.D thesis, University of Bonn, 1992.

[23] I. Primi, A. Stevens and J. J. L. Velázquez, *Mass-selection in alignment models with non-deterministic effects*, Communication in PDE, **34** (2009), 419–456.

[24] M. Rotenberg, *Transport theory for growing cell populations*, J. Theor. Biology, **103** (1983), 181–199.

[25] J. Scheuer, "Pattern Formation in Reaction-Drift and Diffusion Systems," Diploma thesis, University of Heidelberg, 2009.

[26] H. R. Thieme, "Mathematics in Population Biology," Princeton Series in Theoretical and Computational Biology, Princeton University Press, Princeton, NJ, 2003.

[27] A. M. Turing, *The chemical basis of morphogenesis*, Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, **237** (1952), 37–72.

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