Localization of response functions of spiral waves in the FitzHugh-Nagumo system

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Running title: "Response functions of spiral waves"

Abstract

Dynamics of spiral waves in perturbed, *e.g.* slightly inhomogeneous or subject to a small periodic external force, two-dimensional autowave media can be described asymptotically in terms of Aristotelean dynamics, so that the velocities of the spiral wave drift in space and time are proportional to the forces caused by the perturbation. The forces are defined as a convolution of the perturbation with the spirals Response Functions, which are eigenfunctions of the adjoint linearised problem. In this paper we find numerically the Response Functions of a spiral wave solution in the classic excitable FitzHugh-Nagumo model, and show that they are effectively localised in the vicinity of the spiral core.

1 Introduction

Autowaves are nonlinear waves observed in spatially distributed media of physical, chemical, and biological nature, where wave propagation is supported by a source of energy stored in the medium. In a two-dimensional autowave medium there may exist autowave vortices appearing as rotating spiral waves and thus acting as sources of periodic waves. Their existence is not due to singularities in the medium but is determined only by development from initial conditions. In a slightly perturbed medium, *e.g.* spatially inhomogeneous or subject to time-dependent external forcing, a spiral wave drifts, *i.e.* its core location and frequency change with time (Biktashev 2005, Biktasheva 2000, Biktasheva, Elkin & Biktashev 1999, Fast & Pertsov 1990, Pertsov & Ermakova 1988).

While the hypothesis of re-entry of excitation underlying cardiac arrhythmias belongs to the beginning of the twentieth century, *e.g.* (Mines 1913), the first direct experimental observation of spiral waves was reported in 1960s in a chemical oscillatory medium, the Belousov-Zhabotinsky (BZ) reaction (Zhabotinsky & Zaikin 1971). That triggered a huge amount of interest and activity in the area. Soon after that spiral waves were observed in a rabbit ventricular tissue (Allessie, Bonk & Schopman 1973), and later in a variety of other spatially distributed active systems: in chick retina (Gorelova & Bures 1983), colonies of social amoebae (Alcantara & Monk 1974), cytoplasm of single oöcytes (Lechleiter, Girard, Peralta & Clapham 1991), in the reaction of catalytic oxidation of carbon oxide (Jakubith, Rotermund, Engel, von Oertzen & Ertl 1990), rusting of the steel surface in acid with the air (Agladze & Steinbock 2000), in liquid crystal (Frisch, Rica, Coullet & Gilli 1994) and laser (Yu, Lu & Harrison 1999) systems. On a larger scale, there are waves of infectious diseases travelling through biological populations (Carey, Giles & Mclean 1978, Murray, Stanley & Brown 1986), and spiral galaxies (Madore & Freedman 1987, Schulman & Seiden 1986). Yet for experimental studies of spiral waves dynamics the BZ reaction medium remains the most favourite.

A common feature of all these phenomena is that they can be mathematically approximated by "reaction-diffusion" partial differential equations,

$$\partial_t \mathbf{u} = \mathbf{f}(\mathbf{u}) + \mathbf{D}\nabla^2\mathbf{u}, \quad \mathbf{u}, \mathbf{f} \in \mathbb{R}^\ell,\ \mathbf{D} \in \mathbb{R}^{\ell\times\ell},\ \ell \geq 2, \tag{1}$$

where $\mathbf{u}(\vec{r}, t)$ is a column-vector of the reagent concentrations, $\mathbf{f}(\mathbf{u})$ of the reaction rates, $\mathbf{D}$ is the matrix of diffusion coefficients, and $\vec{r} \in \mathbb{R}^2$ is the vector of coordinates on the plane. Since these equations are essentially nonlinear, their spiral wave solutions in general case are studied numerically. Thus, given the complexity of the problem, the current understanding of spiral waves is mostly empirical and gives neither possibility for systematic quantitative predictions of the drift, nor general understanding on how to control the smooth dynamics of autowave vortices, which is important for many practical applications. Effective control of re-entry in excitable cardiac tissue will provide a solution to dangerous arrhythmias and fatal fibrillation.

As a model self-organizing structure, spiral wave demonstrates a remarkable stability, just changing its rotational frequency and core location, *i.e.* drifting, in response to small perturbations of the medium. As experiments with BZ reaction medium (Agladze 2000) and computer simulations showed spiral waves insensitivity to distant events, it was conjectured (Biktashev 1989) that the RFs must decay quickly with distance from the spiral wave core, *i.e.* spiral waves *look like* essentially non-localized regimes but *behave* as effectively localized particles (Biktasheva & Biktashev 2003). The asymptotical theory of the spiral wave drift, proposed in (Keener 1988, Biktashev & Holden 1995) and shortly described below, is based on the idea of summation of elementary responses of the spiral wave core position and rotation phase to elementary perturbations of different modalities and at different times and places. This is mathematically expressed in terms of the spiral wave *response functions* (RFs) equal to zero in the region where the spiral wave is insensitive to small perturbations.

The response functions have been explicitly found with good quantitative accuracy for spiral waves in oscillatory medium described by the Complex Ginzburg–Landau Equation (CGLE) (Biktasheva, Elkin & Biktashev 1998, Biktasheva & Biktashev 2001, Biktasheva & Biktashev 2003). It was shown that the response functions of vortices in the CGLE medium are essentially nonzero only in the vicinity of the core for all sets of model parameters stable spiral wave solution exists for (Biktasheva & Biktashev 2001, Biktasheva & Biktashev 2003), which explains the localised sensitivity of spiral waves to small perturbations. Most important is the RFs ability to make quantitative prediction of spiral wave drift velocity due to small perturbations of any nature.

Thus, a spiral wave organise the medium dividing it into two unequal parts, the core, events in which are translated throughout the medium, and the periphery, obeying the signals from the core. It creates a *macroscopic* wave-particle dualism as an emergent property of the nonlinear field, when the regime *appears* as a non-localized object filling up all available space, but *behaves* as a localized object, only sensitive to perturbations affecting its core.

Another class of media supporting spiral waves are excitable media. These are even of more interest than the oscillatory ones, due to their role in the cardiac, smooth muscle research and neuroscience. In order to check localisation properties of the response functions of vortices in excitable media, the RFs need to be found explicitly for a particular excitable model. Hamm (Hamm 1997) tried to find the response functions for the Barkley model of an excitable system. The obtained response functions were effectively localised in the vicinity of the spiral wave core, but the accuracy of the solution was not sufficient to allow it to be used for prediction of the velocity of the spiral wave drift. A better accuracy for the same model has been achieved later by Henry and Hakim (Henry & Hakim 2002), who used the response functions for the analysis of scroll wave dynamics.

In this paper we suggest a new algorithm of calculating response functions, and use it find the response functions for a spiral wave solution in the FitzHugh-Nagumo (FHN) model (FitzHugh 1961, Nagumo, Arimoto & Yoshizawa 1962) and show that the RFs are effectively localized in the vicinity of the spiral wave core. The model parameters were selected to produce an excitable medium with a rigidly rotating spiral wave. The method of computation is based on the idea of a moving frame of reference, whose movement is controlled by the spiral wave solution calculated in that frame (Biktashev, Holden & Nikolaev 1996).

The FitzHugh-Nagumo model is historically the first simplified model of biological excitation. It has been studied and used as a classic model for computer simulation of spiral wave dynamics for decades, for it captures the key phenomena of the excitable media while consisting of just two partial differential equations, which makes the FHN model easy to study both numerically and analytically,

$$\begin{aligned}\partial_t u_1 &= \epsilon^{-1}\left(u_1 - u_1^3/3 - u_2\right) + D_1 \nabla^2 u_1 \\ \partial_t u_2 &= \epsilon\left(u_1 + \beta - \gamma u_2\right)\end{aligned} \tag{2}$$

where β, γ, ϵ and D_1 are parameters.

In the FHN model the variable u_1 is the fast variable, corresponding to the voltage in biophysically realistic models of membrane action potential, and u_2 does not have any specific physiological interpretation, just plays the role of the slow "recovery" variable. The cubic nonlinearity of the system results in the simple N-shape nullcline on the phase portrait and explains the key aspects of excitability.

Existence of spiral wave solutions in the FHN model, their characteristics and behaviour depending on the model parameters have been extensively studied by many authors. The classic review on the subject is the Winfree article (Winfree 1991).

2 Asymptotic theory of spiral waves dynamics

2.1 Initial definitions

Consider a slightly perturbed "reaction-diffusion" system (1) in two spatial dimensions,

$$\partial_t \mathbf{u} = \mathbf{f}(\mathbf{u}) + \mathbf{D}\nabla^2\mathbf{u} + \varepsilon\mathbf{h}, \quad \mathbf{u}, \mathbf{f}, \mathbf{h} \in \mathbb{R}^\ell,\ \mathbf{D} \in \mathbb{R}^{\ell\times\ell},\ \ell \geq 2, \tag{3}$$

where $\varepsilon\mathbf{h}(\mathbf{u}, \vec{r}, t)$ is a small perturbation, and $\vec{r} \in \mathbb{R}^2$.

We assume that unperturbed system (1) has solutions in the form of steadily rotating spiral waves,

$$\mathbf{u} = \mathbf{U}(\vec{r}, t) = \tilde{\mathbf{U}}(\rho(\vec{r}), \vartheta(\vec{r}) + \omega t). \tag{4}$$

Here

$$\theta = \vartheta(\vec{r}) + \omega t$$

is a polar angle in the "corotating" frame of reference, which is rigidly rotating with the angular velocity ω, while $\rho(\vec{r})$ and $\vartheta(\vec{r})$ are the polar coordinates in the original (laboratory) frame of reference.

The unperturbed reaction-diffusion system (1), or (3) with $\varepsilon\mathbf{h} = 0$, has an obvious but important symmetry: it is invariant with respect to the Euclidean group of motions of the plane $\{\vec{r}\}$. Since solution (4) at any fixed t is not invariant against this group, the group "multiplies" this solution. That is,

$$\mathbf{U}'(\vec{r}, t) = \tilde{\mathbf{U}}(\rho(\vec{r} - \vec{R}), \vartheta(\vec{r} - \vec{R}) + \Theta), \tag{5}$$

where $\Theta = \omega t - \Phi$, is another solution for any constant displacement vector $\vec{R} = (X, Y)^\dagger$ and initial rotation phase Φ.

Thus, if the unperturbed system has one spiral wave solution, then it has a whole three-dimensional *manifold* of such solutions, that are relatively stable with respect to the shift along the manifold.

2.2 Finite-dimensional analogy

The asymptotic theory of drift of spiral waves (Biktashev & Holden 1995) was proposed based on the analogy with finite-dimension problem of perturbation of an invariant manifold (see Fig. 1). If a vector field $\mathbf{f}(\mathbf{u})$ in an n-dimensional phase space has an invariant m-dimensional manifold $\mathbf{U}(\mathbf{a})$, $m < n$, stable as a whole, then small perturbation of this vector field will, under certain conditions, preserve the invariant manifold, just slightly displacing it, $\mathbf{U} \mapsto \mathbf{U}'$. Another effect of the perturbation is that the vector field on the shifted manifold $\mathbf{A}'(\mathbf{a})$ will be slightly different from the original one, $\mathbf{A}(\mathbf{a})$. In practice, the existence of the original invariant manifold $\mathbf{U}(\mathbf{a})$ could be due to a symmetry group. In that case, the flow on that manifold could be in some sense degenerate, and then the perturbation will remove this degeneracy.

To compare the two vector fields, on the original manifold and on the perturbed, we need to relate their coordinate systems $\{\mathbf{a}\}$. A natural way is to require that the vector connecting two corresponding points $\mathbf{U}(\mathbf{a})$ and $\mathbf{U}'(\mathbf{a})$, would not have a component along the manifold, *i.e.* along any of the tangent vectors $\mathbf{V}_j(\mathbf{a}) = \partial\mathbf{U}/\partial a_j$. In other words, it should be orthogonal,

$$\langle \mathbf{W}_j(a), \mathbf{U}'(a) - \mathbf{U}(a) \rangle = 0, \quad j = 1 \ldots m, \tag{6}$$

to the projectors $\mathbf{W}_j(a)$ onto the tangent vectors $\mathbf{V}_j(a)$:

$$\langle \mathbf{W}_j(a), \mathbf{V}_k(a) \rangle = \delta_{j,k}. \tag{7}$$

These projectors are eigenvectors of the adjoint linearized matrix $(\partial\mathbf{f}/\partial\mathbf{u})^T(\mathbf{a})$. The two effects of the perturbation are produced by its two components, along and across the manifold, as determined by the projectors $\mathbf{W}_j$.

Thus, if the manifold comprises only non-moving points, the tangent component will determine the slow drift along the manifold.

If this finite-dimensional scheme can be applied to spiral waves, the role of the vector field is played by the reaction-diffusion system, so the phase space is a functional space. The invariant manifold is the three-dimensional manifold of spiral waves and is due to a symmetry group, the Euclidean group of the plane. The coordinates on the manifold are $\vec{R} \in \mathbb{R}^2$, the centre of rotation of the spiral wave, and Θ, its rotation angle. The flow on the manifold is degenerate, as it consists of relatively stable periodic orbits, which correspond to steady rotation of spiral waves around fixed centres:

$$\Theta = \omega t - \Phi, \quad \Phi = \text{const}; \; \vec{R} = \text{const}. \tag{8}$$

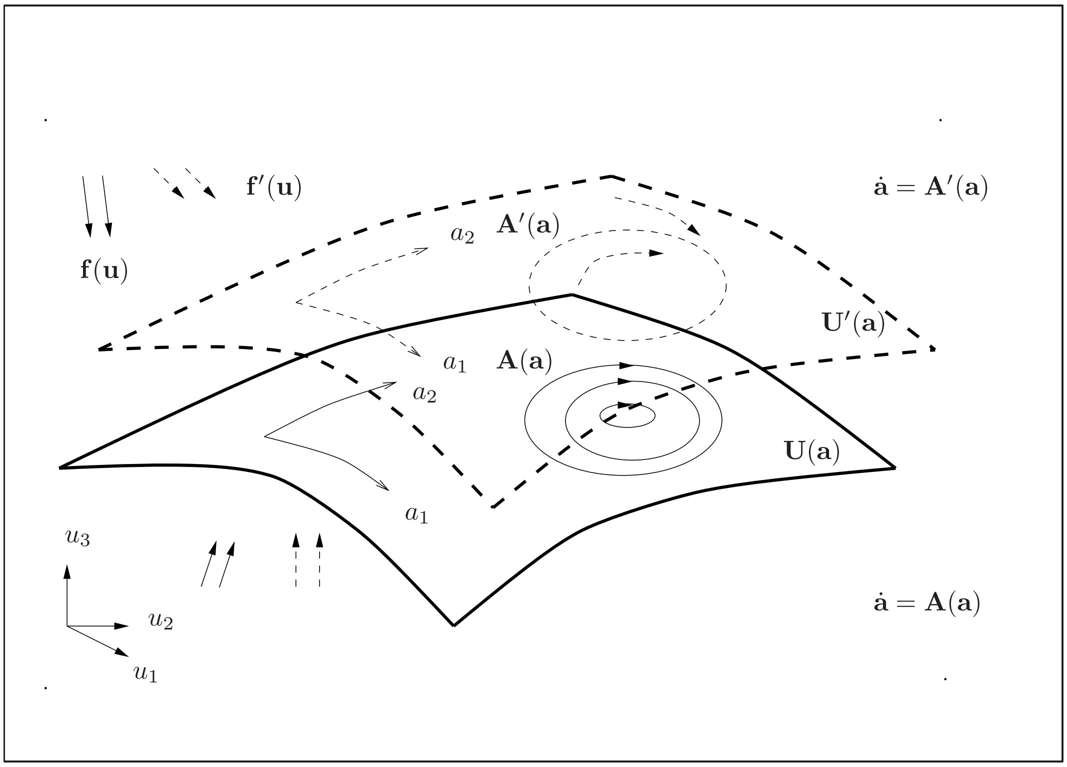

Figure 1: Perturbation of an invariant manifold. Vector field $\mathbf{f}(\mathbf{u})$ in phase space with coordinates $\mathbf{u}$ has an invariant manifold $\mathbf{U}$ with coordinates $\mathbf{a}$, and vector field $\mathbf{A}$ on the manifold. Perturbed vector field $\mathbf{f}'(\mathbf{u})$ has a slightly different invariant manifold, $\mathbf{U}'$, and a slightly different vector field $\mathbf{A}'$ on it. Original objects are shown by solid lines, and perturbed objects by dashed lines.

The perturbation removes this degeneracy, and we observe the drift of the spirals. By analogy with the finite-dimensional case, we expect that the flow on the manifold of spiral waves will be described by

$$\partial_t\Theta = \omega + \varepsilon H_0(\vec{R},\Theta), \quad \partial_t\vec{R} = \varepsilon\vec{H}_1(\vec{R},\Theta), \tag{9}$$

where H_0 and $\vec{H}_1$ are "projections" of the perturbation onto the tangent space of the manifold $\mathbf{U}(\mathbf{a})$. The right-hand sides of (9) depend on the phase Θ. On the time scale ε^{-1} this phase oscillates fast; averaging over these oscillations gives motion equations of the spiral waves,

$$\partial_t\overline{\Theta} = \omega + \varepsilon\overline{H_0}(\vec{R}) + O\left(\varepsilon^2\right), \quad \partial_t\overline{\vec{R}} = \varepsilon\overline{\vec{H}_1}(\vec{R}) + O\left(\varepsilon^2\right). \tag{10}$$

2.3 Response functions

Thus, the finite-dimensional analogy suggests that the dynamics of spiral waves (perhaps like that of many other dissipative structures) is described by "Aristotelean" mechanics, when the velocity of motion is proportional to the applied perturbation. The right-hand sides in the equations, the "forces", are projections of the perturbation onto the corresponding tangent space of the invariant manifold $\mathbf{U}(\mathbf{a})$. This tangent space is a linear space, the span of the Goldstone modes, corresponding to the translations along the symmetry group, at $\vec{R} = \mathbf{0}$ and $\Theta = 0$,

$$\begin{aligned}\mathbf{V}_0 &= -\omega^{-1}\partial_t\mathbf{U}(\vec{r},t)|_{t=0} = -\partial_\theta\tilde{\mathbf{U}}(\rho(\vec{r}),\theta(\vec{r})),\\ \mathbf{V}_{\pm1} &= -\frac{1}{2}e^{\mp i\omega t}\left(\partial_x \mp i\partial_y\right)\mathbf{U}(\vec{r},t)|_{t=0} = -\frac{1}{2}\left(\partial_{\tilde{x}} \mp i\partial_{\tilde{y}}\right)\tilde{\mathbf{U}}(\vec{r},t) = -\frac{1}{2}e^{\mp i\theta}\left(\partial_\rho \mp i\rho^{-1}\partial_\theta\right)\tilde{\mathbf{U}}(\rho(\vec{r}),\theta(\vec{r})).\end{aligned} \tag{11}$$

Here mode $\mathbf{V}_0$ corresponds to the shift in time (or to what is the same, rotation in space), and $\mathbf{V}_1$ corresponds to the shift in space. Tildes in (11) designate the corotating frame of reference, so $\tilde{x}$, $\tilde{y}$ are Cartesian coordinates there and $\tilde{\mathbf{U}}$ is the unperturbed spiral wave solution, which is stationary in that frame of reference. We omit the tildes henceforth for brevity.

The Goldstone modes are critical eigenfunctions

$$\tilde{\mathcal{L}}\mathbf{V}_n = i\omega n\mathbf{V}_n, \quad n = 0, \pm1 \tag{12}$$

of the linearized operator $\tilde{\mathcal{L}}$:

$$\tilde{\mathcal{L}} = \mathbf{D}\nabla^2 - \omega\partial_\theta + \left.\left(\frac{\partial\mathbf{f}}{\partial\mathbf{u}}\right)\right|_{\mathbf{u}=\mathbf{U}(\vec{r})}. \tag{13}$$

Here again the tilde at $\tilde{\mathcal{L}}$ reminds that the linearized operator is considered in the co-rotating frame of reference where it does not depend on time. The additive "$-\omega\partial_\theta$" appears here due to rotation with respect to the original system of coordinates.

Thus, for each particular point at the manifold, the projection operators map the functional space of the perturbations into the three-dimensional tangent space, and are thus just three functionals. Since all points of our manifold are equivalent to each other up to a Euclidean transformation of the plane, it is enough to know the projection functionals at one point, *i.e.* just for one location of the spiral wave. This symmetry consideration shows that if the functionals $\overline{H_n}$ are written as integrals, they should have the form:

$$\overline{H_n}(t) = e^{in\Phi}\oint\limits_{t-\pi/\omega}^{t+\pi/\omega}\frac{\omega\mathrm{d}\tau}{2\pi}\iint\limits_{\mathbb{R}^2}\mathrm{d}^2\vec{r}\,e^{-in\omega\tau}\left\langle\mathbf{W}_n\left(\rho(\vec{r}-\vec{R}),\vartheta(\vec{r}-\vec{R})+\omega\tau-\Phi\right),\mathbf{h}\right\rangle, \tag{14}$$

where

$$\begin{aligned}&\mathbf{h} = \mathbf{h}(\mathbf{U}(\vec{r},\tau),\vec{r},\tau),\\ &\vec{R} = \vec{R}(t),\\ &\Phi = \Phi(t),\\ &\overline{H_1} = (\overline{\vec{H}_1})_x + i(\overline{\vec{H}_1})_y.\end{aligned} \tag{15}$$

The kernels $\mathbf{W}_n$ of the integrals (14) are eigenfunctions

$$\tilde{\mathcal{L}}^{+}\mathbf{W}_n = -i\omega n\mathbf{W}_n, \quad n = 0, \pm 1. \tag{16}$$

of the adjoint linearized operator considered in the co-rotating frame of reference:

$$\tilde{\mathcal{L}}^{+} = \mathbf{D}\nabla^2 + \omega\partial_\theta + \left.\left(\frac{\partial \mathbf{f}}{\partial \mathbf{u}}\right)^{+}\right|_{\mathbf{u}=\mathbf{U}(\vec{r})}. \tag{17}$$

As in the finite dimensional example, we assume here that $\mathbf{W}$ are normalized in such a way that (7) is satisfied.

The functions $\mathbf{W}_n$ are called *the response functions* (RFs) of the spiral wave. Folloring the analogy with the Goldstone modes, $\mathbf{W}_0$ defines the shift in time (or the turning in space), and $\mathbf{W}_1$ defines the shift in space. So $\mathbf{W}_0$ is called the temporal or rotation RF, and $\mathbf{W}_1$ is called the spatial or shift RF.

3 Mathematical formulation of the problem for the FitzHugh-Nagumo model

The problems (1), (4) and (16)–(17) for the FitzHugh-Nagumo system (2) take the form

$$\begin{aligned}
&\epsilon^{-1}\left(U_1 - U_1^3/3 - U_2\right) + (D_1\nabla^2 - \omega\partial_\theta)U_1 = 0, \\
&\epsilon\left(U_1 + \beta - \gamma U_2\right) - \omega\partial_\theta)U_2 = 0,
\end{aligned} \tag{18}$$

$$\begin{aligned}
&\left(\epsilon^{-1}(1 - U_1^2) + \omega(in + \partial_\theta) + D_1\nabla^2\right)W_1^n + \epsilon W_2^n = 0, \\
&-\epsilon^{-1}W_1^n + \left(-\epsilon\gamma + \omega(in + \partial_\theta)\right)W_2^n = 0, \quad n = 0, 1
\end{aligned} \tag{19}$$

for the unperturbed solution U_j, its angular velocity ω and the RFs W_j^n, $n = 0, 1$, $j = 1, 2$, $W_{1,2}^0 \in \mathbb{R}$, $W_{1,2}^1 \in \mathbb{C}$. System (18)–(19) should be supplied with normalisation and boundary conditions, and discretized. For discretisation we used rectangular grids in Cartesian coordinates.

3.1 Spiral wave problem

Since the Response Functions are the solution of the adjoint linearized problem in the system of reference that is rotating with the angular velocity of the spiral itself, we need first to find the spiral wave solution in this system of reference, *i.e.* we need to find the spiral wave solution *together* with its rotation angular velocity. So we have a nonlinear eigenvalue together with a boundary value problem.

We solved this problem numerically on a square domain $(x, y) \in \mathcal{S} = [-L/2, L/2] \times [-L/2, L/2]$, for different L from 25 to 50. First, the spiral wave was initiated by solving a Cauchy problem for (2) for initial conditions $u(x, y, 0) = 0.7\,\mathrm{sign}(x)$, $v(x, y, 0) = 0.6\,\mathrm{sign}(y)$. When a stationary rotating spiral wave was established, typically within time interval $t \in [0, T]$, $T \sim 40$, the resulting distribution $u(x, y, T)$, $v(x, y, T)$ was used as an initial condition for the following system:

$$\begin{aligned}
\partial_t u_1 &= \epsilon^{-1}\left(u_1 - u_1^3/3 - u_2\right) + D_1\nabla^2 u_1 + \sum_{j=x,y,\theta} C_j\partial_j u_1, \\
\partial_t u_2 &= \epsilon\left(u_1 + \beta - \gamma u_2\right) + \sum_{j=x,y,\theta} C_j\partial_j u_2, \\
\dot{C}_j &= -q_j C_j - \frac{p_j}{A}\int\limits_{\mathcal{D}} \left(\partial_t u_1\partial_j u_1 + \partial_t u_2\partial_j u_2\right)\mathrm{d}x\mathrm{d}y, \quad j = x, y, \theta,
\end{aligned} \tag{20}$$

where $\partial_\theta = x\partial_y - y\partial_x$, $\mathcal{D} = \{(x, y) : x^2 + y^2 \le (L/2)^2\}$, $A = \pi(L/2)^2$, $q_\theta = 0$, and positive coefficients $p_{x,y,\theta}$ and $q_{x,y}$ have been selected by experimentation. Informally, the idea of this system, adopted with appropriate modification from (Biktashev et al. 1996), is that the first two equations are system (2) in a frame of reference moving with speeds $-C_{x,y,\theta}$ in the x, y and θ directions, and the integrals in the evolution equations for $C_{x,y,\theta}$ are "detectors of movement" in those directions. So the movement of the frame of reference is adjusted in such a way so as to make the solution in this frame of reference is stationary. On the formal level, it is straightforward to see that if solution of (20) converges to a stationary state, then $u_{1,2}$ will satisfy (18) with $\omega = -C_\theta$, neglecting the boundary conditions.

We considered the problem (20) for the following set of parameters: $D_1 = 1.0$, $\epsilon = 0.30$, $\beta = 0.75$, $\gamma = 0.50$, which correspond to a rigidly rotating spiral wave solution (Winfree 1991). Calculations were performed using the explicit Euler method in time, central differences in space, with fixed time step from $\Delta t = 3 \cdot 10^{-3}$ down to $\Delta t = 5 \cdot 10^{-4}$ and space step $\Delta x = 0.5$, with Neuman boundary conditions on a rectangular grid in Cartesian coordinates: $\partial_x u_1(\pm L/2, y) = \partial_y u_1(x, \pm L/2) = 0$. The frame of reference adjustment parameters were chosen $q_{x,y} = 1$, $p_{x,y} = 7$ and $p_\theta = 5$.

The result is a stable, stationary spiral (demonstrated on Fig. 2) in the system of reference, which rotates with the angular velocity $\omega \approx 0.32$ clockwise. Having this angular velocity and the spiral wave solution, it is possible to find the corresponding response functions.

3.2 The response functions problem

The response functions $\mathbf{W}$ were calculated simultaneously with finding the spiral wave solution for (20), by solving the adjoint linearized problems

$$\begin{aligned}
\partial_t w_1 &= \epsilon^{-1}(1-u_1^2)w_1 + \epsilon w_2 + D\nabla^2 w_1 - \sum_{j=x,y,\theta} C_j \partial_j w_1, \\
\partial_t w_2 &= -\epsilon^{-1} w_1 - \epsilon\gamma w_2 - \sum_{j=x,y,\theta} C_j \partial_j w_2.
\end{aligned} \tag{21}$$

As $(u_1, u_2, C_1, C_2, C_3)$, solution of (20), converges to $(U_1, U_2, 0, 0, -\omega)$, solution of (19), then $\mathbf{w} = (w_1, w_2)^T$, a typical solution of (21), is expected to converge to

$$\mathbf{w}(x,y,t) \approx c_0 \mathbf{W}_0(x,y) + \mathrm{Re}\left(c_1 \mathbf{W}_1(x,y) e^{-i\omega t}\right), \tag{22}$$

where $c_0 \in \mathbb{R}$ and $c_1 \in \mathbb{C}$, ideally, are constants depending on initial conditions, but in real calculations can slowly change in time due to numerical approximation. To obtain $\mathbf{W}_{0,1}$, we calculate three solutions $\mathbf{w}^{(m)}$, $m = 1, 2, 3$, to (21) with three linearly independent initial conditions. Assuming that, after a sufficiently long time, these satisfy (22), we can take their appropriate linear combinations to satisfy (7). So for a given triplet $\mathbf{w}^{(m)}$, $m = 1, 2, 3$, we are looking for constants $P_{j,m}$, $j = \theta, x, y$, $m = 1, 2, 3$, so that

$$\mathbf{W}_j = \sum_{m=1}^{3} P_{j,m} \mathbf{w}^{(m)}$$

would satisfy biorthogonality condition (7) with respect to the set $\mathbf{V}_k = \partial_k \mathbf{U}$, $k = \theta, x, y$. This requirement implies that

$$\sum_{m=1}^{3} P_{j,m} \langle \mathbf{w}^{(m)}, \mathbf{U}_k \rangle = \delta_{j,k},$$

i.e. $\mathbf{P} = (P_{j,m})$ is an inverse to the matrix $\mathbf{B} = (B_{m,k})$, where $B_{m,k} = \langle \mathbf{w}^{(m)}, \mathbf{U}_k \rangle$ are obtained by integrating the given solutions of (21) with the derivatives of the solution of the nonlinear problem. Having thus found $\mathbf{W}_{x,y,\theta}$ after integrating (21) for a time interval of certain τ, we used these $\mathbf{W}_{x,y,\theta}$ as three linearly independent initial conditions for (21) for a further time interval of length τ.

Equation (21) was integrated on the disk $(x, y) \in \mathcal{D} \subset \mathcal{S}$ with Dirichlet boundary conditions $w_1(x, y) = w_2(x, y) = 0$, $(x, y) \in \partial\mathcal{D}$, which were implemented by setting $w_{1,2}(x, y) = 0$ for

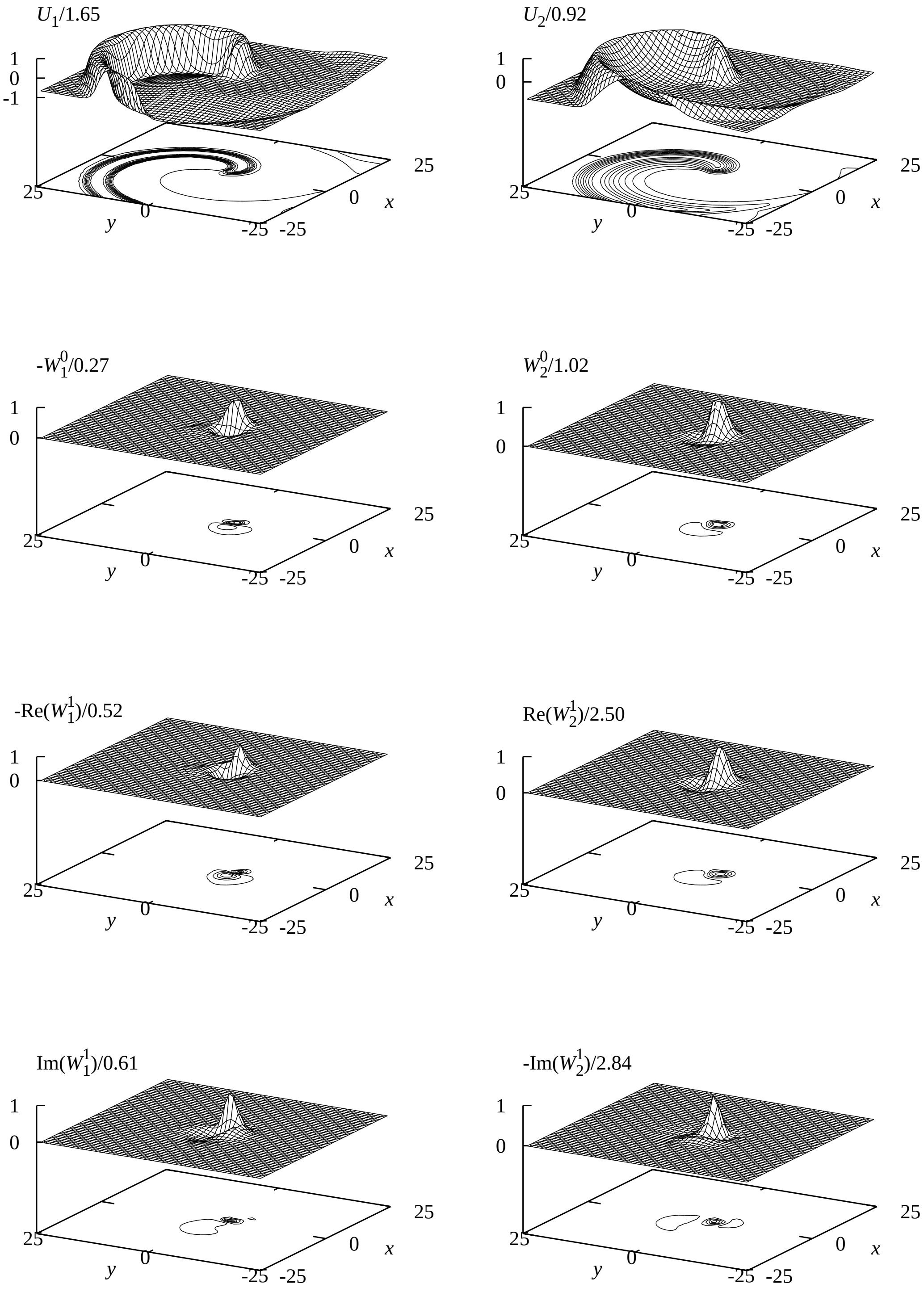

Figure 2: Spiral wave solution and the response functions. Parameters: $L = 50$, $\Delta x = 0.5$, $\Delta t = 5 \cdot 10^{-4}$, Neuman boundary conditions on $\partial\mathcal{S}$ for $\mathbf{U}$ and Dirichlet boundary conditions on $\partial\mathcal{D}$ for $\mathbf{W}$.

$(x, y) \in \mathcal{S} \setminus \mathcal{D}$. We tried $\tau = 1$ and $\tau = 10$ with identical results; the solution obtained by this procedure converged within time scale of $t \sim 20$. As $\mathbf{V}_k = \partial_k \mathbf{U}$ are related to the Goldstone modes $\mathbf{V}_{0,\pm1}$ by (11), this gives relationship between functions $\mathbf{W}_{x,y,\theta}$ found in this way, with RFs, in the form $\mathbf{W}_0 = -\mathbf{W}_\theta$ and $\mathbf{W}_1 = -(\mathbf{W}_x - i\mathbf{W}_y)$.

Figure 2 shows the components of the Response Functions obtained in this way. The most important result is that all components are localized in a close vicinity of the tip of the spiral. It can also be observed that the amplitude of the second components of the RFs is higher than that of the first, so controlling movement of the spiral wave via the second component, the inhibitor, if it is pratically feasible, could be more efficient than via the first component the activator.

The accuracy of the solution has been checked by varying the discretization steps Δt and Δx, the domain size L, boundary conditions (Neuman vs Dirichlet, $\partial\mathcal{D}$ vs $\partial\mathcal{S}$). Based on such checks, we estimate that the accuracy of the solutions is within a few percent. Further improvement of accuracy requires decrease of Δx while keeping L same or increasing, and due to stability limitations of the fully explicit Euler time stepping, such improvement is extremely costly if done within the same numeric scheme, and requires a more advanced scheme, *e.g.* fully implicit/pseudospectral in the θ direction.

4 Conclusion

Response functions are very important characteristics of the spiral wave, for they define the phenomenology of the spiral behaviour. Experiments and computer simulations, demonstrating the spirals insensitivity to distant events, implied that the RFs of vortices must decay quickly with distance from the core. Such decay will guarantee the convergence of the integrals (14) even for non-localized perturbations, for example caused by the simultaneous change of the properties of the whole medium. But the mathematical peculiarity of the idea presuming qualitatively different behaviour of eigenfunctions of the linear operator and its adjoint one resulted in a natural scepticism.

The results obtained in this paper confirm the existence of effectively localized response functions of a spiral wave solution in the classical excitable FitzHugh-Nagumo model, at least for the particular set of the model parameters corresponding to a rigidly rotating spiral wave.

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