NL3451 Vortex dynamics in excitable media

Statics Vortices in excitable media (see *Excitability*) are *spiral waves* (see) in two spatial dimensions and *scroll waves* in three spatial dimensions. They are described by *reaction diffusion systems* of equations,

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

where $\mathbf{u}(\vec{r},t) = (u_1, u_2, \dots)^T$ is a column-vector of the reagent concentrations, $\mathbf{f}(\mathbf{u})$ of the reaction rates, $\mathbf{D}$ is the matrix of diffusion coefficients, $\epsilon\mathbf{h}(\mathbf{u},\vec{r},t)$ is some small perturbation and $\vec{r} \in \mathbb{R}^2$ or $\mathbb{R}^3$ is the vector of coordinates on the plane or in space.

In the unbounded two-dimensional medium with $\epsilon\mathbf{h} = 0$, a spiral wave solution rotating with angular velocity ω has the form

$$\mathbf{u} = \mathbf{U}(\vec{r},t) = \mathbf{U}(\rho(\vec{r}), \vartheta(\vec{r}) + \omega t) \approx \mathbf{P}(\rho(\vec{r}) - \frac{\lambda}{2\pi}(\vartheta(\vec{r}) + \omega t))\Big|_{\rho\to+\infty}, \tag{2}$$

where $\rho(\vec{r})$ and $\vartheta(\vec{r})$ are the polar coordinates corresponding to the Cartesian coordinates $\vec{r}$. $\mathbf{P}(\xi;\omega,\lambda)$ is a periodic wave solution with frequency ω and spatial period λ, so the $\rho \to +\infty$ asymptotic means that isolines are approximately Archimedian spirals with pitch λ. Solutions (2) are typically possible for isolated, most often unique, values of ω and corresponding λ.

Most of the facts in this article apply not only to excitable systems, but also to self-oscillatory (see *Complex Ginzburg Landau equation*, *Oregonator*) media.

Note that system (1) with $\epsilon\mathbf{h} = 0$ is invariant with respect to the Euclidean group of motions of the plane $\{\vec{r}\}$. Solution (2) is a "relative equilibrium", *i.e.* the states of the wave at all moments of time are equivalent to each other up to a Euclidean motion, namely, a rotation around the origin. Due to the symmetry, if (2) is a solution, then

$$\tilde{\mathbf{U}} = \mathbf{U}(\rho(\vec{r} - \vec{R}_\odot), \vartheta(\vec{r} - \vec{R}_\odot) + \omega t - \Phi_\odot), \tag{3}$$

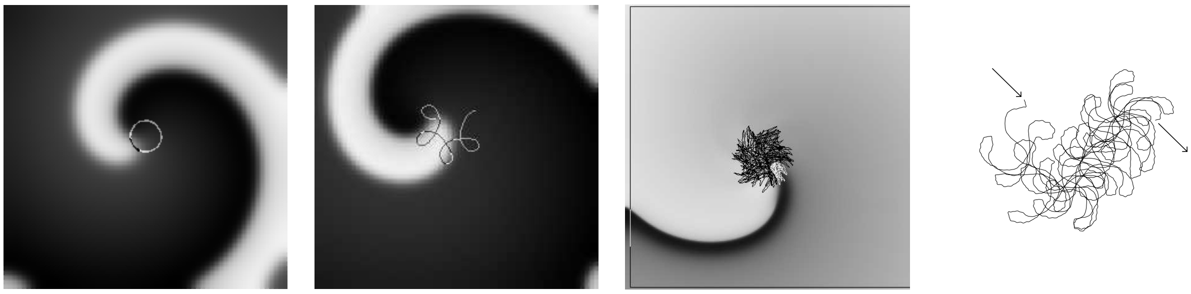
is another solution for any constant displacement vector $\vec{R}_\odot = (X_\odot, Y_\odot)^T$ and initial rotation phase $\Phi_\odot$. Thus we have a three-dimensional *manifold*, parametrised by coordinates $X_\odot, Y_\odot, \Phi_\odot$, of spiral wave solutions neutrally stable with respect to each other.

In this article, by "dynamics" of the vortices we understand any deviation of the solutions from the stationary rotation (2).

Meander is a non-stationary rotation of a spiral wave, accompanied by constant change of its shape. It is convenient to describe in terms of the spiral *tip*, which can be defined *e.g.* as an intersection of selected isolines of two components of the nonlinear field $\mathbf{u}$,

$$u_{j_1}(X_\bullet, Y_\bullet, t) = v_1, \quad u_{j_2}(X_\bullet, Y_\bullet, t) = v_2, \quad \Phi_\bullet = \arg(\partial_x + i\partial_y)u_{j_3}(X_\bullet, Y_\bullet, t), \tag{4}$$

$j_1 \neq j_2$, where $X_\bullet(t)$, $Y_\bullet(t)$ are the coordinates of the tip and $\Phi_\bullet(t)$ is its orientation angle. Typically, a spiral wave in a given system develops the same kind of meander



(a) (b) (c) (d)

Figure 1. Typical meander patterns. Shown are snapshots of the excitation field with pieces of preceding tip paths superimposed. (a) Stationary (rigid) rotation: equilibrium in the base system (5). (b) Classical biperiodic "flower" meander: limit cycle in the base system (5). (c) Quasi-periodic hypermeander: invariant torus in the base system (5). (d) Pseudo-random walk hypermeander: chaotic attractor in the base system (5) (only the tip path shown).

pattern $X_\bullet(t)$, $Y_\bullet(t)$ independent on the initial conditions. Change of parameters in the same system cause change of the meander pattern, and types of patterns can be qualitatively similar in very different excitable media models.

Possible types of meander can be classified using an orbit manifold decomposition of (1) by the Euclidean group. Evolution of the shape of the wave can be described in coordinates (ξ, η) in a moving frame of reference attached to the spiral tip,

$$\begin{aligned} &\partial_t \mathbf{u} = \mathbf{D}(\partial_\xi^2 + \partial_\eta^2)\mathbf{u} + \left[C_1(t)\partial_\xi + C_2(t)\partial_\eta + \omega(t)\left(\xi\partial_\eta - \eta\partial_\xi\right)\right]\mathbf{u} + \mathbf{f}(\mathbf{u}) \\ &u_{j_{1,2}}(0,0) = 0, \quad \partial_\eta u_{j_3} = 0, \end{aligned} \tag{5}$$

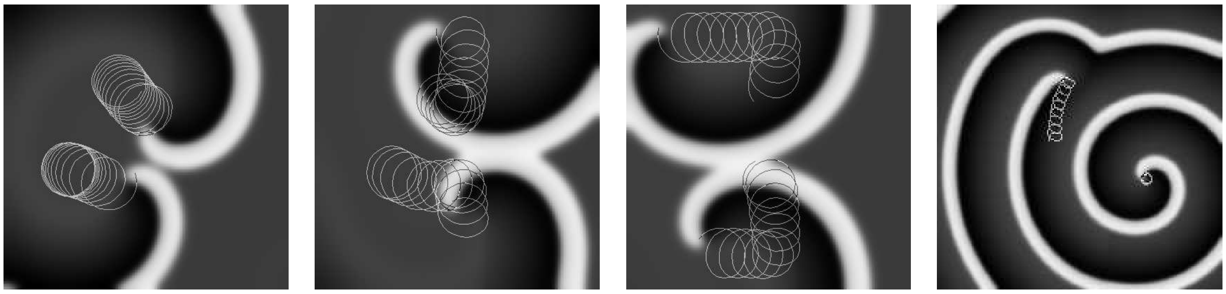
and the movement of the tip is described by ordinary differential equations

$$\frac{\mathrm{d}\Phi_\bullet}{\mathrm{d}t} = \omega(t), \qquad \frac{\mathrm{d}X_\bullet}{\mathrm{d}t} + i\frac{\mathrm{d}Y_\bullet}{\mathrm{d}t} = (C_1(t) + iC_2(t))e^{i\Phi_\bullet}. \tag{6}$$

Equations (5) define a dynamic system with the phase space $\{(\mathbf{u}(\xi,\eta), C_1, C_2, \omega)\}$, devoid of the Euclidean symmetry of the original system (1). Knowing the attractor in (5), one can deduce the properties of the meander patterns by integrating the ODE system (6) (Figure 1)

Forced drift Another kind of deviation from (2) is drift of spirals due to perturbations $\epsilon\mathbf{h} \neq 0$, "forces". As solutions of the family (3) are neutrally stable with respect to each other, a small perturbation of a spiral wave caused by an $\epsilon\mathbf{h}$ limited in time, will die out, but will typically result in a small change in the spiral wave coordinates $X_\odot$, $Y_\odot$ and $\Phi_\odot$.

If similar perturbations are applied repeatedly with a period equal to the period of the spiral, then small shifts of $X_\odot$ and $Y_\odot$ accumulate, which is the *resonant drift*. Another type of slow drift is *inhomogeneity-induced drift* occurring when $\epsilon\mathbf{h}$ depends explicitly on spatial coordinates, *i.e.* medium properties are slightly inhomogeneous (Figure 2(b)). In the first order of perturbation theory, this is equivalent to a time-dependent perturbation synchronised with the spiral rotation and is therefore always



(a) (b) (c) (d)

Figure 2. Different drifts of spiral waves. Shown are snapshots of the excitation field with pieces of preceding tip paths superimposed. The right half of the medium is slightly "stronger" than the left half; (a)(c) are consecutive stages of the same numeric experiment. (a) Two close oppositely charged spirals attract with each other and form a pair drifting in SE direction. (b) The spirals have reached the inhomogeneity and are being driven apart by it. (c) The spirals have reached the medium boundary and now drift along it. (d) In a bigger medium: the right spiral has subdued the left spiral into an induced drift.

resonant. A third type of drift occurs if the medium is bounded, and the boundary influence on the spiral wave is not negligible. Although a boundary is not a slight perturbation, if the boundary conditions are passive *e.g.* non-flux, then their effect on the spiral wave can be small and similar to that of small spatial inhomogeneity (Figure 2(c)). Other kinds of perturbations breaking the Euclidean symmetry of (1) can also cause drift.

Being a first-order effect, the slow drift of a spiral due to small forces of different types obeys a superposition principle. It leads to motion equations

$$\partial_t(X_\odot+iY_\odot) = C(X_\odot,Y_\odot)+v(X_\odot,Y_\odot)e^{i\Theta}, \qquad \partial_t\Theta = \Omega(t)-\omega(X_\odot,Y_\odot), \tag{7}$$

where $C(X_\odot,Y_\odot)$ is the velocity of the inhomogeneity and boundary induced drift, $v(X_\odot,Y_\odot)$ the velocity of the resonant drift, Θ is the phase difference between the spiral and the resonant forcing, $\Omega(t)$ is the perturbation frequency and $\omega(X_\odot,Y_\odot)$ is the own spiral angular frequency possibly depending on the current spiral location.

These are motion equation for rigidly rotating spirals, and $X_\odot$ and $Y_\odot$ are sliding period averages of $X_\bullet$, $Y_\bullet$. Dynamics of forced meandering spirals are more complicated because of possible resonances.

Spiral waves as particles Motion equation (7) are obtained by summation of the effects of elementary perturbations of different modalities localised in different sites and occurring at different moments of time, onto the spiral's location and phase. These elementary responses are described by *response functions*, which are critical eigenfunctions of the adjoint linearised operator. A remarkable property of the response function is their localisation in the vicinity of the spiral core (see Figure 3). The spiral will only drift if the perturbation is applied not too far from its core.

Thus a paradox: although a spiral wave appears as a significantly non-local process,

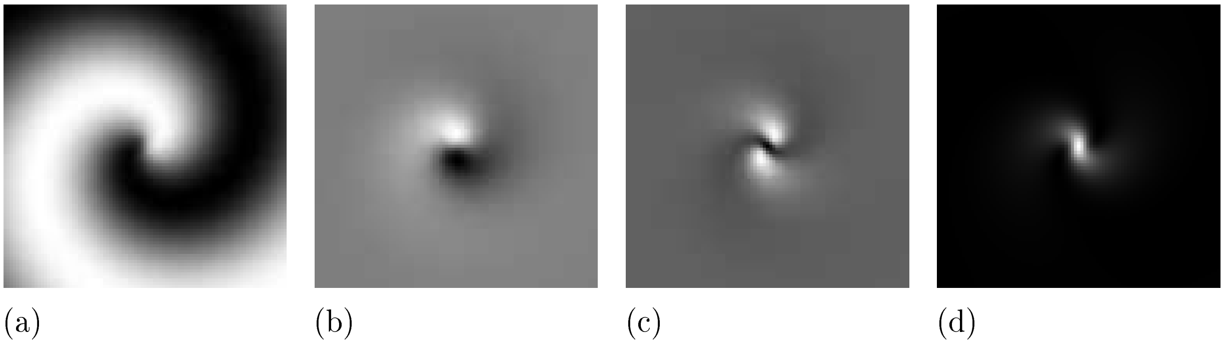


Figure 3. A spiral wave solution (a) and its temporal (b) and spatial (c,d) response functions, as density plots. Monotone gray periphery on (b–d) corresponds to zero. Thus the spiral wave is a non-local process, but its response functions are well localized.

involving in its rhythm all available excitable medium, it behaves as a localised, particle-like object in its response to perturbations.

A spatial response function, defining the proportionality between drift velocity and inhomogeneity magnitude, typically has a scalar (drift along the parameter gradient or towards the boundary) and pseudo-scalar (across the parameter gradient or along the boundary) components; the sign of the latter depends on the direction of the spiral rotation.

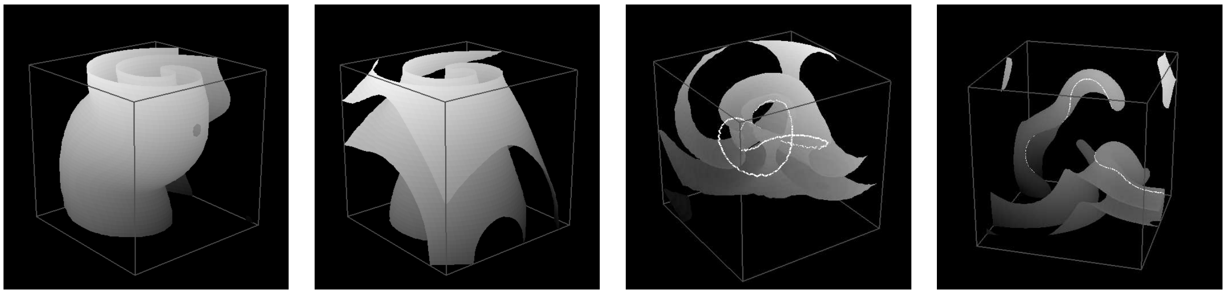
Bending and twisting of scroll waves As a scroll wave is a three-dimensional analogue of a spiral wave, all comments about spiral wave dynamics remain valid for the scrolls. However, there are new aspects due to the third dimension. The simplest 3D vortex is the straight scroll wave, a spiral wave continued unchanged in the third dimension. The spiral tip, a point in the plane, becomes the edge of the scroll, a line in space, and the spiral core, a circle in the plane, becomes the scroll filament, a tube. The term filament sometimes also denotes the centre line of the tube filament.

More nontrivial regimes are scrolls with bended filaments (Figure 4(a)), and with rotation phase varying the filament, *i.e.* twisted scrolls Figure 4(b)). Both bending and twist of scrolls are factors of their dynamics. A vortex ring will collapse or expand, and at the same time drift along its symmetry axis; and twisted vortex will usually spread the twist evenly along its filament, or if possible untwist.

The asymptotic motion equation for the scroll waves can be derived using response functions. If the twist is not too strong, then the dynamics of the scroll due to bending and due to twist are decoupled. The motion equation of the filament is

$$\partial_t \vec{R}_f = b_2 \partial_s^2 \vec{R}_f + c_3 \left[\partial_s \vec{R}_f \times \partial_s^2 \vec{R}_f \right], \tag{8}$$

where $\vec{R}_f = \vec{R}_f(p,t) \in \mathbb{R}^3$ is position of the filament as function of a length parameter p and time, and ∂_s is arclength differentiation, $\partial_s \equiv \left| \partial_p \vec{R}_f \right|^{-1} \partial_p$. At $b_2 = 0$, equation (8) is completely integrable, in particular, the total length of the filament is conserved. Otherwise, the total filament length decreases if $b_2 > 0$ and increases if $b_2 < 0$; in the latter case a straight filament is unstable.



(a) (b) (c) (d)

Figure 4. Scroll waves. (a) Scroll with a curved filament. (b) Twisted scroll with straight filament. (c) Scroll with a knotted filament. (d) "Turbulent regime": many scrolls developed from one via negative filament tension multiplication mechanism. On panels (c) and (d), part of the wavefronts is cut out, to make the filaments (white lines) visible.

If twist is high, it changes the filament tension, and may make it negative. This causes an instability of the straight filament shape, leading to "sproing", a sudden transition from a strongly twisted scroll with straight filament to a less twisted scroll with a helical filament.

Competition and interaction: Divide et impera Normally, two colliding excitation waves completely annihilate each other. Thus, if there are many periodic sources of waves, *e.g.* vortices, then the medium splits to domains, or regions of influence, each domain receiving waves from its source. The domains are separated by "shock structures" where the waves collide (see Figure 2(a–c)).

The domain boundaries work like non-flux boundaries. Thus, two spiral waves can be said to interact with each other, *i.e.* cause each other's drift and frequency shift, whereas each of them actually interacts with the boundary between their domains. Such interaction between spirals may lead to formation of linked pairs (see Figure 2(a)).

Different scroll filaments or different parts of the same filament also can interact with each other. If this interaction is repulsive, it may compensate positive tension normally causing closed filaments to contract and collapse; that may lead to stable "particle-like" 3D scrolls with compact filaments (see Figure 4(c)).

Induced drift If colliding waves annihilate 1:1, continuity of phase applies. If two vortices have different frequencies, *e.g.* because of a spatial inhomogeneity of the medium, then by continuity of phase, the domain boundary between them moves towards the slower vortex. When it reaches its core, the slower vortex looses its identity as such and turns into a dislocation in the wave field emitted by the faster vortex. This dislocation, appearing as a free end of an excitation wave, periodically re-joins from one wave to another with some overall drift, depending on the frequency and direction of the incident waves (see Figure 2(d)). If the incident wave packet ceases, the dislocation can develop back into a vortex.

As a dislocation is very different from a vortex, this *induced drift* is an example of hard, non-perturbative dynamics.

Hard dynamics: births, deaths and multiplication of vortices Another kind of hard dynamics is complete elimination of a vortex. This may happen if the wave propagation around the vortex becomes impossible, *e.g.* if the vortex has been driven too close to a medium boundary. Alternatively, two spiral waves with opposite topological charges may annihilate if driven too close to each other. For a scroll wave, annihilation may happen to a piece of its filament, which then appears as splitting of a scroll wave into two.

Birth of a vortex may happen as a result of a temporary local block of excitation propagation. Unless this happens near the medium boundary, this means birth of a pair of oppositely rotating spirals in the plane, or a scroll with a closed filament around the perimeter of the propagation block. The block may happen as a result of external forcing or special initial conditions, or develop as a result of an instability of an existing vortex. Such instability this can underlie a chain reaction of the vortex multiplication, which may lead to a "turbulence" of excitation vortices, a spatio-temporal chaotic state where generation of new vortices is balanced by their annihilation when they get close to each other due to overcrowding.

There have been identified quite a few mechanisms of such instabilities, include mechanisms working in two or three dimensions, such as Eckhaus instability/alternans, zigzag/lateral instability (see *Wave stability and instability*) or imposed mechanical movement of the medium, and those only possible in three dimensions, *e.g.* instability due to the negative "tension" b_2 of the vortex filament (see Figure 4(d)), or caused by spatially inhomogeneous anisotropy of the medium such as that observed heart ventricular muscle. Some of these types of instabilities may be responsible for the phenomenon of fibrillation of the heart (see *Cardiac arrhythmias*).

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See also Reaction diffusion systems; Spiral waves; Scroll waves.

Further Reading

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