

Elastic excitable medium

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A type of excitable medium—an elastic excitable medium—has been created by incorporating the Belousov-Zhabotinsky reaction into a polyacrylamide-silica gel. It permits one to address the problem of how the cardiac muscle contractions affect the dynamics of rotating spiral waves. Investigations of the effects of mechanical deformations on the excitation wave propagation exhibit a resonance dynamics of vortices. For equal frequencies of deformation and of vortex rotation, vortices drift. The drift velocity is about 3% of the excitation wave velocity, for a 50% elongation. The direction of the drift does not coincide with the stretching direction and can be varied by changing the phase shift between deformations and vortex rotation. Numerical calculations suggest that the effects of mechanical deformations on excitation wave propagation are independent of the exact nature of the excitable medium.

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In a skeletal or cardiac muscle, a mechanical contraction is initiated by an electrochemical wave propagating along the excitable membranes. The sequence of processes triggered by the excitation wave and resulting in muscle contraction is known as an electromechanical coupling. A mechano-electrical coupling has been found as well [1]: the contraction modifies the propagation of the excitation wave. An interaction between mechanical contractions and wave propagation is supposed to underlie some mechanisms of morphogenesis (pattern formation) in biological systems [2,3].

We have designed an excitable system which permits to study the effects of mechanical deformations on wave propagation. The Belousov-Zhabotinsky (BZ) reaction provides a paradigm for a well controlled excitable system [4]. The mechanically deformable substratum for this reaction has been obtained by creating an appropriate elastic gel. Hence the elastic excitable medium is made of the BZ reaction incorporated into a new gel: complex polyacrylamide (PA)–silica (Si) gel.

The gel combines useful properties of Si gel [5], which incorporates the catalyst (ferriin) but is fragile, and the PA gel [6,7], which is elastic but does not immobilize the catalyst. This gel is prepared as a PA gel [7] to which the catalyst and sodium silicate (without any polymerizing agent) are added. At 0 °C, 4 ml of acrylamide (Merck, 2M), 4 droplets of *N,N'*-methylene-bis-acrylamide (Merck, 2% wt/vol. in water), 4 droplets of ammonium persulfate (Merck, 0.88M), 4 droplets of trietanolamine (Merck, 2M) are mixed with 4 droplets of sodium silicate (Prolabo), and 15 droplets of ferriin (Sigma, 0.008M). The gel is immersed into the standard BZ solution without a catalyst: H₂SO₄ (0.3M), malonic acid (0.1M), NaBrO₃ (0.225M), KBr (0.039M) in water. The excitability of the medium is controlled by changing the con-

centrations of malonic acid (MA) and sulfuric acid (SA). The gel does not noticeably lose the catalyst during a 1.5 h experiment (at 20 °C).

The gel is fixed to a special device made with a standard plastic caliper. This allows for a reproducible stretching of 1.5 times the rest size along a fixed direction (*X* direction).

Our aim is to study the influence of mechanical contractions of an elastic excitable medium on the behavior of vortices, since it is similar to what might happen in cardiac muscle. Rotating vortices (spiral waves) underlie various phenomena in natural excitable media; for instance, they are involved in the control of morphogenesis in colonies of the social amoebae *Dictyostelium discoideum* (see [2]). In the heart, rotating vortices are a major cause of life-threatening rhythm disturbances such as tachycardia and fibrillation [8–11].

One of the qualitative changes in the behavior of vortices which might be expected under periodic contractions is the initiation of the vortex drift. Drift of vortices was observed under different influences: external excitation waves [12], periodic illumination [13,14], a parameter gradient [9,15], dc [16,17] or ac [18] electric field.

Let us describe a physical mechanism which might induce the drift of a vortex in an elastic medium. The motion of the spiral is studied through the motion of the point of maximum curvature of a given isoconcentration line. This point is called the tip. The unit vector pointing outwards and orthogonal to the tangent at the tip is called the direction of the tip. Since the spiral waves in the experiment appear as thin lines, the tip is simply the end point and the direction is just the (properly oriented) tangent to the curve at the end point.

Note that for large stepwise deformations, K ($K \gg 1$) of the gel, any displacement which occurred in the stretched gel will be diminished K times when the gel comes back to the unstretched state. Now, it is easy to find a condition for a vortex drift—we should stretch the gel when the vortex tip moves in one direction, and contract the gel when the tip moves in the opposite direction. As a result, total displacement of the vortex in one preferential direction will be observed.

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A rotating vortex is created in the experiment by breaking a wave. In a first experiment, the gel is stretched when the direction of the tip is parallel to the X direction (we will say that the tip is parallel to the X direction), and contracted when the tip is antiparallel to the X direction. Hence the frequency of the periodic stretching of the gel is equal to the frequency of the vortex rotation. Then the instantaneous center of rotation of the spiral drifts along a straight line (Fig. 1) with a drift velocity of 0.06 mm/min, about 3% of the wave velocity. In the next experiment, after 40 min of forcing with the same initial phase as in Fig. 1, the phase of the forcing is reversed, and the vortex starts drifting in the opposite direction (Fig. 2). Note that drifting does not only occur along the forcing direction, but also has a component perpendicular to it (similar to [19]).

In Fig. 3(a), four spirals with different phases are shown just before forcing starts. After 22 min of forcing at resonant frequency, they have drifted in different directions depending on the initial phases [Fig 3(b)].

We have also numerically investigated the effects of mechanical deformations on a standard model of an excitable medium (two variable Oregonator model [20,21]). The stretching of the medium is modeled by changing the size of the grid in the X direction. The explicit Euler method with no flux boundary conditions is used. The diffusion coefficient is taken as constant during deformations.

The dependence of the drift direction on the phase shift between the vortex rotation and forcing is shown in Fig. 4. All directions are accessible. The maximum drift velocity takes place for phase shifts of 0° and 180° .

A simple kinematical model provides an understanding of the main observed features. We just write that the tip is following its own motion in a reference frame which is moving because of the stretching. Since the X coordinate of any fixed point $x(0)$ of the medium is changing according to

$$x(t) = x(0)\xi(t), \quad (1)$$

where $\xi(t)$ describes the deformations of the medium, the entreatment velocity of the corresponding point is simply

$$V_e(x(0)) = x(0) \frac{d \ln \xi(t)}{dt}. \quad (2)$$

By writing the composition of velocities, one gets the kinematic equation for the motion of a vortex tip:

$$\frac{dx(t)}{dt} = V_x(t) + x(t) \frac{d \ln \xi(t)}{dt}, \quad \frac{dy(t)}{dt} = V_y(t), \quad (3)$$

where $V_x(t)$ and $V_y(t)$ are the components of the velocity of the unforced spiral tip. Since the spiral is normally rotating along a circle [21], $V_x(t)$ and $V_y(t)$ are usually purely sinusoidal, and at least periodic functions with pulsation ω . The solution of this equation is

$$x(t) = x(0) + \xi(t) \int_0^t \frac{V_x(\tau)}{\xi(\tau)} d\tau. \quad (4)$$

If $\xi(t)$ is a periodic function with pulsation ω_1 , one sees in Eq. (4) that drift occurs for $\omega_1 = \omega$ and, in general, for subharmonics of ω . Nevertheless, for special symmetries of



FIG. 1. Vortex behavior under periodic stretching of a gel with incorporated BZ reaction. (a) Initial state of the spiral wave in the unstretched gel. (b) Same spiral, after stretching of the gel [9 s after the frame (a)]. (c) Final state of the spiral after 33 min of periodic stretching of the gel at resonant frequency. The spiral has drifted over 2.8 mm (grid size is 4 mm, period of the spiral $T_\omega = 84$ s, $[SA] = 0.2M$, $[MA] = 0.05M$).

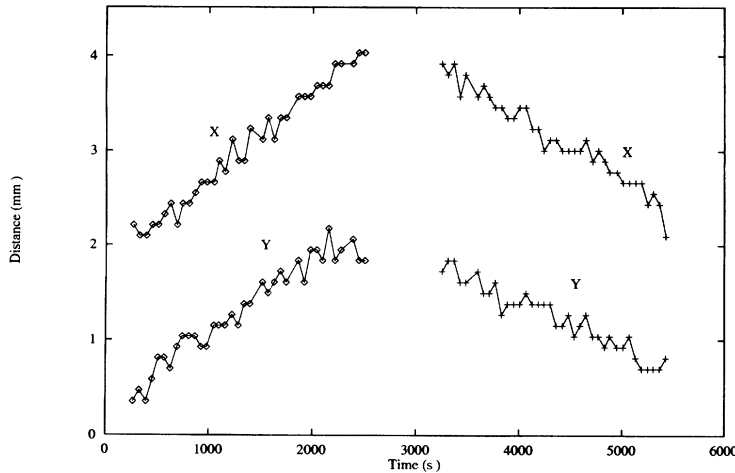


FIG. 2. *X* and *Y* positions of a vortex tip versus time for resonant forcing. At $t=2500$ s, the direction of the drift is reversed by increasing the phase of the forcing by 180° . (Period of the spiral $T_\oplus = 60$ s, $[SA]=0.2M$, $[MA]=0.1M$.)

the forcing with respect to the velocity, drift can be zero for subharmonics (this special case is the one that has actually been simulated). Equation (4) also shows that the spiral should undergo a random walk when forced with low frequency noise.

Following [22], one can write

$$\begin{aligned} V_x(t) &= V_n \sin \omega t + V_\tau \cos \omega t, \\ V_y(t) &= -V_n \cos \omega t + V_\tau \sin \omega t, \end{aligned} \tag{5}$$

where V_τ and V_n are the tangential and normal velocities of the vortex tip. For small periodic deformations $\xi(t) = 1 + k \sin \omega_1 t$, $k \ll 1$, Eq. (3) is easily integrated. When at resonant frequency, averaging over fast rotations yields to leading order in k ,

$$\left\langle \frac{dx(t)}{dt} \right\rangle = -k \frac{V_n}{2}, \quad \left\langle \frac{dy(t)}{dt} \right\rangle = 0. \tag{6}$$

This result demonstrates the influence of deformations of

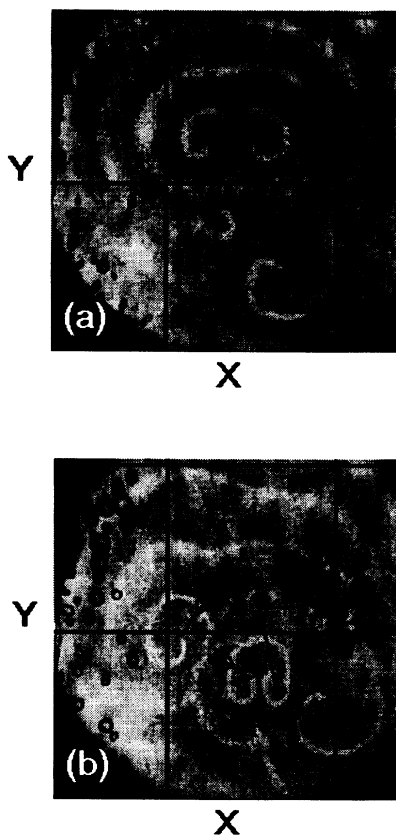


FIG. 3. Drift of several spirals in the same gel at resonant frequency. (a) Initial position. (b) Final position after 22 min of forcing. Since forcing was in phase with spiral *A*, spirals *B*, *C*, and *D* drifted differently (see arrows). (Period of the spiral $T_\oplus = 84$ s, $[SA]=0.2M$, $[MA]=0.05M$, grid size 10 mm.)

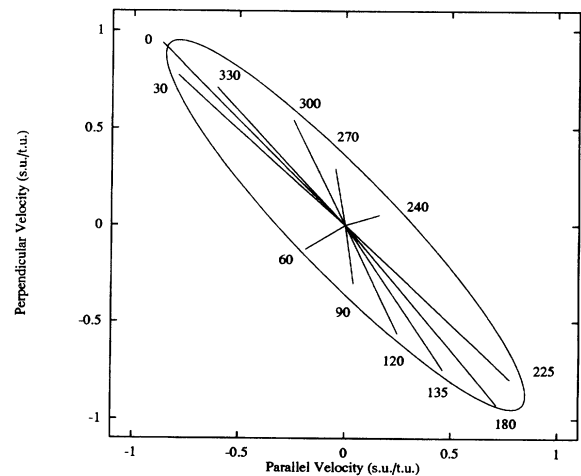


FIG. 4. Dependence of drift velocity on the phase shift (the units are in space units/time units, i.e., s.u./t.u.). Hodograph of drift velocities at resonant frequency. Modulus and direction of the drift velocity are plotted for different phase shifts between forcing and vortex rotation. (Numerical calculation with the Oregonator model, parameters $\epsilon = 0.05$, $q = 0.002$, $f = 1.4$, $D_u = 1$, $D_v = 0.6$, maximum elongation = 3.)

an elastic excitable medium on vortex dynamics. A nonzero phase can be added to the periodic deformations. Basic algebra then provides a cosine dependence of the drift on the phase shift between the spiral rotation and the periodic forcing. This agrees qualitatively with the numerical results shown in Fig. 4.

The idea of Professor P. Coulet that vortex drift may result from a generic symmetry breaking mechanism (and

not from specific ones for each particular case) has proven to be decisive for planning the work. We want also to thank M. Morabito and Dr. A. Pumir for help and useful discussions. Numerical calculations have been performed on the Cray YMP Computer at the Institut Méditerranéen de Technologie, Marseille. One of the authors (A.P.M.) wants to acknowledge Comisión Interministerial de Ciencia y Tecnología (Spain) for partial financial support (Project No. DGICYT-PB91-0660).

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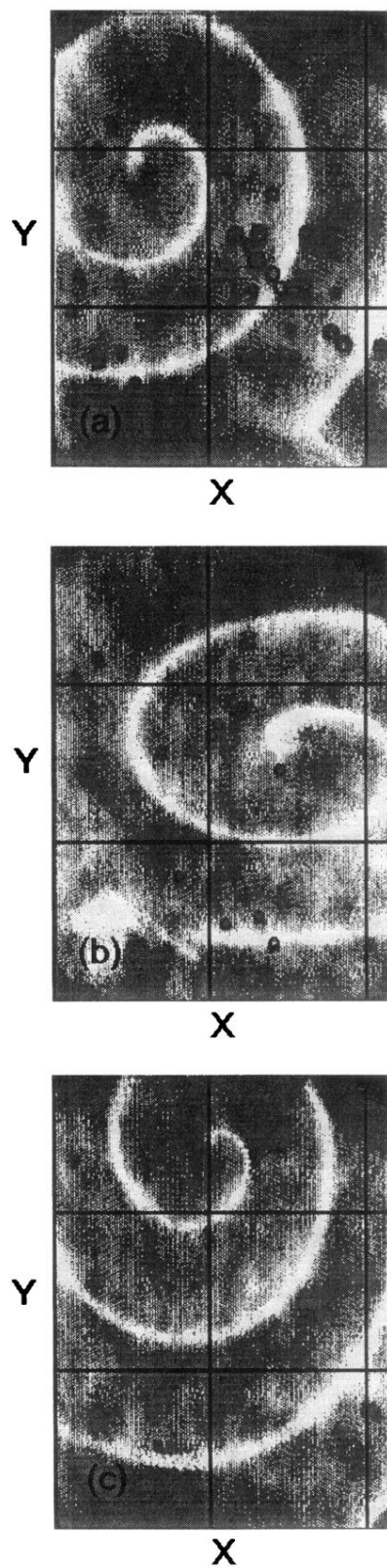


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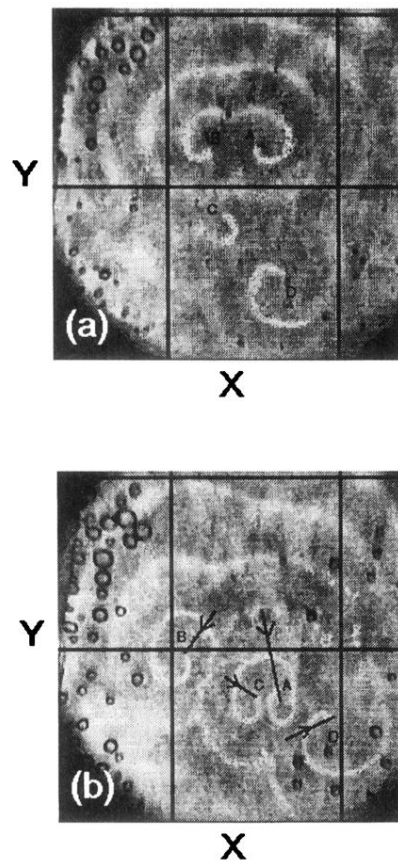


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