Spontaneous Circulation of Confined Active Suspensions

Francis G. Woodhouse and Raymond E. Goldstein

Department of Applied Mathematics and Theoretical Physics, Centre for Mathematical Sciences,

University of Cambridge, Wilberforce Road, Cambridge CB3 0WA, United Kingdom

(Dated: July 22, 2012)

Many active fluid systems encountered in biology are set in total geometric confinement. Cytoplasmic streaming in plant cells is a prominent and ubiquitous example, in which cargo-carrying molecular motors move along polymer flaments and generate coherent cell-scale flow. When filaments are not fixed to the cell periphery, a situation found both *in vivo* and *in vitro*, we observe that the basic dynamics of streaming are closely related to those of a dipolar microswimmer suspension. This paradigm is used to demonstrate that confinement brings about a qualitative change in behavior; a linear stability analysis and numerical studies show that there is an activity threshold for spontaneous auto-circulation. Analysis of the long-time behavior reveals a phenomenon akin to defect separation in nematic liquid crystals, and a high-activity bifurcation to an oscillatory regime.

PACS numbers: 87.16.Wd, 87.16.Ln, 47.63.-b, 47.54.-r

Cytoplasmic streaming is the deliberate, driven motion of the entire contents of large eukaryotic cells. It is effected by cargo-laden molecular motors walking along polymer filaments and entraining the surrounding fluid (Figure 1a); the combined action of many of these motors can generate flow speeds in excess of 100 μ m/s for certain freshwater algae. While inroads are being made into understanding its function [1, 2], surprisingly little is known about how it is initially established within cells.

In a remarkable, yet apparently little-known investigation into the development of streaming, Yotsuyanagi [3] in 1953 examined isolated droplets of cytoplasm forcibly extracted from algal cells. He observed a progression from isolated Brownian fluctuations to a coherent, global circulation of the entire droplet contents (Figure 1b). However, we need not limit ourselves to *ex vivo* experiments: Kamiya [4] describes a similar blooming of rotational cyclosis in the development of *Lilium* pollen cells, and Jarosch [5] quantitatively analyzed the same disorder-to-order transition occurring within *Allium* cells over the course of a few hours. Based on these observations, one is led to ask: is it possible that a simple selforganization process could lie at the heart of streaming?

When the filaments are not locked in position, as is likely in Yotsuyanagi's experiments, a cargo-carrying motor walking on a free filament constitutes a force dipole. Therefore, these cytoplasmic dynamics belong to the burgeoning field of *active fluids*. At its simplest, an active fluid is a continuum suspension of force dipoles interacting via short- and long-range forces, leading to a system like a liquid crystal, but with continuous injection of energy at the microscale. Such systems can exhibit complex patterns and flows [6], including asters and vortices [7– 9], laning [10] and density waves [9, 10]. While various complex short-range interactions can be included in these formulations, it is hydrodynamics that drives many of the pattern formation behaviors.

Despite the ubiquity of relevant situations, of which

streaming is a major example, the influence of total confinement is relatively little-studied. Recent work by Fürthauer *et al.* [11] used spontaneous flow of generic active polar fluids to construct theoretically a 'Taylor– Couette motor' that can be used to do work against two cylindrical boundaries. However, this is topologically distinct from a single confined chamber. Schaller *et al.* [12] underline the critical importance of long-range hydrodynamics in confined systems: swirling patterns were observed experimentally in a totally confined actin motility assay, but no such circulation was reproduced in simple actin-substrate cellular automaton computer simulations. They concluded that confined flows are responsible for the formation and stability of the global circulation.

Through theory and simulation, we demonstrate here that only two key ingredients are required to capture the spontaneous emergence of self-organized stable rotational flow in biological systems: activity and confinement. Our



FIG. 1. (color online). Cytoplasmic streaming *in vivo* and *ex vivo*. (a) A molecular motor attached to a vesicle (i) encounters a filament, (ii) binds and walks along it, entraining fluid, before (iii) unbinding stochastically. (b) A drop of cytoplasm extracted from a plant cell transitions from random Brownian fluctuations to ordered circulation [3].

model assumes that short, rigid filaments are suspended in a Newtonian, zero Reynolds number fluid. The filaments are assumed to exert extensile, or 'pusher', dipolar forces on the fluid; this can be viewed as the effect of processive molecular motors landing randomly along a filament and walking toward one end, implying an average motor location forward of the filament midpoint. Additionally, the suspension is taken to be dilute, so filaments interact via hydrodynamics only, and is confined within a no-slip sphere of diameter L.

Working in d dimensions we generalize the standard kinetic approach to these systems [13]. The spatial and angular distribution function $\Psi(\mathbf{x}, \mathbf{p}, t)$ of the filaments, where $|\mathbf{p}| = 1$, satisfies a Smoluchowski equation

$$\frac{\partial \Psi}{\partial t} = -\boldsymbol{\nabla}_{\mathbf{x}} \cdot (\dot{\mathbf{x}}\Psi) - \boldsymbol{\nabla}_{\mathbf{p}} \cdot (\dot{\mathbf{p}}\Psi) \tag{1}$$

where $\nabla_{\mathbf{x}} \equiv \partial/\partial \mathbf{x}$ and $\nabla_{\mathbf{p}} \equiv (\mathbf{I} - \mathbf{p}\mathbf{p}) \cdot \partial/\partial \mathbf{p}$. The spatial and rotational fluxes are

$$\begin{split} \dot{\mathbf{x}} &\equiv \mathbf{u} + V \mathbf{p} - \mathbf{D}^{(s)} \cdot \boldsymbol{\nabla}_{\mathbf{x}} \log \Psi, \\ \dot{\mathbf{p}} &\equiv (\boldsymbol{I} - \mathbf{p} \mathbf{p}) \cdot (\gamma \mathbf{E} + \mathbf{W}) \cdot \mathbf{p} - D^{(r)} \boldsymbol{\nabla}_{\mathbf{p}} \log \Psi, \end{split}$$

where V is a self-advection speed, $\gamma \in [-1, 1]$ is a shape parameter ($\gamma \rightarrow 1$ for a slender rod), $\mathbf{D}^{(s)}$ is a spatial diffusion tensor and $D^{(r)}$ is a rotational diffusion constant. The fluid has velocity field \mathbf{u} , rate-of-strain tensor $\mathbf{E} \equiv (\nabla \mathbf{u} + \nabla \mathbf{u}^{\mathsf{T}})/2$ and vorticity tensor $\mathbf{W} \equiv (\nabla \mathbf{u} - \nabla \mathbf{u}^{\mathsf{T}})/2$. The filament pusher stresslet of strength $\sigma > 0$ generates a stress tensor $\boldsymbol{\Sigma} \equiv -\sigma \int_{\mathbf{p}} d\mathbf{p} (\mathbf{p}\mathbf{p} - \mathbf{I}/d)\Psi$ that drives fluid flow by the Stokes equation $-\mu \nabla^2 \mathbf{u} + \nabla \Pi = \boldsymbol{\nabla} \cdot \boldsymbol{\Sigma}$ with viscosity μ and pressure Π , subject to incompressibility $\boldsymbol{\nabla} \cdot \mathbf{u} = 0$. Confinement induces the no-slip boundary condition $\mathbf{u} = 0$ on $|\mathbf{x}| = L/2$.

While simulations of the full system (1) are possible [13–15], here we develop evolution equations for the primary orientation moments [16–18]. Given the orientational average $\langle \phi \rangle \equiv \int_{\mathbf{p}} d\mathbf{p} \, \phi \Psi$, define the concentration $c \equiv \langle 1 \rangle$, polar moment $\mathbf{P} \equiv \langle \mathbf{p} \rangle$ and nematic moment $\mathbf{Q} \equiv \langle \mathbf{pp} - \mathbf{I}/d \rangle$. Equations of motion for these fields in terms of higher moments can then be derived by taking appropriate weighted integrals of Eq. (1) [19].

We pare down complications by specializing to two dimensions (d = 2), rodlike particles $(\gamma = 1)$ and isotropic diffusion $(\mathbf{D}^{(s)} = D^{(s)}\mathbf{I})$, and neglect self-advection $(V \equiv 0)$. This last assumption decouples the *c* dynamics into pure advection-diffusion and eliminates all polar interactions, so we take a constant concentration $c \equiv c_0$ and neglect **P**. However, the remaining **Q** dynamics still depends on the fourth moment contraction $\langle \mathbf{pppp} \rangle : \mathbf{E}$, and a closure is needed. Typically this is done by taking the distribution Ψ to be a functional purely of the first three moments, yielding a closure linear in **Q** [18]. In dense active systems this is permissible, owing to the presence of local interaction terms; here, however, it is the above fourth moment term which provides all stabilizing nonlinearities, so greater care must be taken. Instead we adapt a closure of Hinch and Leal [20] to d = 2, yielding

$$\begin{split} \langle \mathbf{pppp} \rangle : \mathbf{E} &\approx \frac{1}{4c} \left[4\mathbf{Q} \cdot \mathbf{E} \cdot \mathbf{Q} + 2c(\mathbf{E} \cdot \mathbf{Q} + \mathbf{Q} \cdot \mathbf{E}) \right. \\ &+ c^2 \mathbf{E} - 2I\mathbf{Q}^2 : \mathbf{E} \right]. \end{split}$$

After non-dimensionalizing by rescaling $\mathbf{x} \to L\mathbf{x}, t \to (c_0 L^2/\mu)t, \ \mathbf{u} \to (\mu/c_0 L)\mathbf{u}, \ \Pi \to (\mu^2/c_0 L^2)\Pi, \ \boldsymbol{\Sigma} \to (c_0 L^2/\mu^2)\boldsymbol{\Sigma}$ and $\mathbf{Q} \to c_0 \mathbf{Q}$, the final model reads

$$\frac{D\mathbf{Q}}{Dt} = d^{(s)}\nabla^2\mathbf{Q} - 4d^{(r)}\mathbf{Q} + \frac{1}{2}\mathbf{E} - 2\mathbf{Q}\cdot\mathbf{E}\cdot\mathbf{Q} \qquad (2)$$

where $D/Dt \equiv \partial/\partial t + \mathbf{u} \cdot \nabla$, with non-dimensional diffusion constants $d^{(s)} \equiv (c_0/\mu)D^{(s)}$ and $d^{(r)} \equiv (c_0L^2/\mu)D^{(r)}$. This is subject to the Stokes equation $-\nabla^2 \mathbf{u} + \nabla \Pi = -\sigma_0 \nabla \cdot \mathbf{Q}$ and incompressibility $\nabla \cdot \mathbf{u} = 0$ with non-dimensional dipole stress $\sigma_0 \equiv (c_0L/\mu)^2 \sigma$. The fluid boundary condition reads $\mathbf{u} = 0$ on $|\mathbf{x}| = 1/2$. Among the variety of admissible boundary conditions on \mathbf{Q} we focus here on the *natural* condition $\mathbf{N} \cdot \nabla \mathbf{Q} = 0$, where \mathbf{N} is the boundary normal vector. Qualitatively similar results are found with fixed boundary-parallel or boundary-perpendicular conditions [19].

The model (2) has the structure of a Landau theory for the order parameter **Q**. As **E** is linear in the velocity **u**, and **u** is (nonlocally) linear in σ_0 **Q** via the Stokes equation, the term $(1/2)\mathbf{E} \propto \sigma_0 \mathbf{Q}$. It follows in the usual manner that there is an effective linear term in **Q** that will become positive for sufficiently large activity σ_0 relative to $-4d^{(r)}$. If this is sufficient to overcome the diffusive stabilization $d^{(s)}$ then the amplitude of the ensuing instability will be limited by the nonlinear term $2\mathbf{Q} \cdot \mathbf{E} \cdot \mathbf{Q} \propto \mathbf{Q}^3$.

We first seek a steady non-flowing axisymmetric state \mathbf{Q}^{0} . In polar coordinates $\alpha = (r, \theta)$ the tensor Laplacian of \mathbf{Q} has primary components

$$(\nabla^2 \mathbf{Q})_{r\alpha} = \mathcal{L}Q_{r\alpha} \equiv \frac{1}{r} \frac{\partial}{\partial r} \left(r \frac{\partial Q_{r\alpha}}{\partial r} \right) - \frac{4}{r^2} Q_{r\alpha} ,$$

while the others follow from symmetry and the tracelessness of **Q**. Eq. (2) therefore implies Q_{rr}^0 and $Q_{r\theta}^0$ each satisfy a (modified) Bessel equation in $z \equiv 2\Delta r$, viz. $z^2 \partial_z^2 Q_{r\alpha}^0 + z \partial_z Q_{r\alpha}^0 - (z^2 + 4) Q_{r\alpha}^0 = 0$, where $\Delta^2 \equiv d^{(r)}/d^{(s)}$. Thus $Q_{r\alpha}^0 \propto I_2(2\Delta r)$; since I_2 is monotonic, the boundary conditions imply $\mathbf{Q}^0 = 0$ everywhere.

Now, perturb axisymmetrically: let $\mathbf{Q} = \epsilon \mathbf{R}$, $\epsilon \ll 1$, and write $\mathbf{u} = \epsilon v \hat{\boldsymbol{\theta}}$, $\mathbf{E} = \epsilon \mathbf{e}$ for the induced flow (which has no radial component by incompressibility). Seek an exponentially growing state such that $\partial_t \mathbf{R} = s \mathbf{R}$. Then to $O(\epsilon)$, the perturbation obeys $s \mathbf{R} = d^{(s)} \nabla^2 \mathbf{R} - 4d^{(r)} \mathbf{R} + \frac{1}{2} \mathbf{e}$. To determine \mathbf{e} we employ the technique of Kruse *et al.* [7] and write the Stokes equation as $\nabla \cdot (-\Pi \mathbf{I} + 2\mathbf{e} - \sigma_0 \mathbf{R}) \equiv \nabla \cdot \Sigma^{\text{tot}} = 0$. The *r*-component determines Π . The θ -component reads $\partial_r \Sigma^{\text{tot}}_{r\theta} + (2/r) \Sigma^{\text{tot}}_{r\theta} = 0$, so for $\Sigma^{\text{tot}}_{r\theta}$ analytic at r = 0 we find $\Sigma^{\text{tot}}_{r\theta} = 0$, i.e. $e_{r\theta} = (\sigma_0/2)R_{r\theta}$.



FIG. 2. (color online). Numerical results beyond the spontaneous circulation threshold. (a,b,c) Simulated schlieren textures of nematic order director **n** (i.e. density plot of $(n_x n_y)^2$). Lighter corresponds to diagonally-oriented filaments, darker to horizontal or vertical. (a) Steady circulation with a central spiral defect at low activity, (b) steady central defect separation into a pair of hyperbolic defects, (c) snapshot of oscillatory behavior with widely separated mobile defects. (d) Flow streamlines for low activity, showing circulation about the system center; darker streamlines indicate faster flow. (e) Enlargement of nematic director field structure in texture (b), showing two hyperbolic defects. (f) Flow streamlines for highactivity oscillation associated with texture (c) exhibiting offcenter flow circulation. In all cases, $d^{(r)} = d^{(s)} = 0.025$.

Finally, $e_{rr} = 0$ as there is no radial velocity component. The perturbation therefore satisfies

$$d^{(s)}\mathcal{L}R_{rr} = (4d^{(r)} + s)R_{rr}, \qquad (3)$$

$$d^{(s)}\mathcal{L}R_{r\theta} = \left(4d^{(r)} + s - \frac{\sigma_0}{4}\right)R_{r\theta},\tag{4}$$

which are still of Bessel form. When $s > -4d^{(r)}$, Eq. (3) has a solution in terms of I_2 , so boundary conditions imply $R_{rr} = 0$. Now, let $\lambda \equiv (4d^{(r)} + s - \sigma_0/4)/d^{(s)}$ and write Eq. (4) as $\mathcal{L}R_{r\theta} = \lambda R_{r\theta}$. For $\lambda > 0$ this again gives solutions in terms of I_2 and so $R_{r\theta} = 0$. However, for $\lambda < 0$ (i.e. σ_0 sufficiently large) the solution is instead $R_{r\theta} \propto J_2(\sqrt{-\lambda r})$. Applying the boundary con-

$$\sigma^* = \frac{16\mu}{c_0} \left(9.33 \frac{D^{(s)}}{L^2} + D^{(r)}\right),\tag{5}$$

a criterion we have verified numerically by full simulations of Eq. (2). To lend perspective, we consider typical values of the material properties. The stress amplitude can be expressed as $\sigma = f\ell$, where f is the (typically pN) force exerted by motors and ℓ is the (typically μ m) separation of the opposing forces of the stresslet. For micronsize rods we expect $D^{(r)} \sim 0.01 \text{ s}^{-1}$ and $D^{(s)} \sim 10^{-9} \text{ cm}^2/\text{s}$, so for system sizes $L \gtrsim 10 \ \mu\text{m}$ rotational diffusion dominates the parenthetical term in Eq. (2). Then for a fluid of the viscosity of water the instability will set in at concentrations greater than $\sim 10^8 \text{ cm}^{-3}$, corresponding to a volume fraction well below 10^{-3} .

In numerical studies of the fully nonlinear dynamics we vary the dipolar activity σ_0 while fixing the diffusion constants at $d^{(r)} = d^{(s)} = 0.025$, and use the eigendecomposition $\mathbf{Q} = S(\mathbf{nn} - \mathbf{I}/2)$, where the order parameter S and (headless) director \mathbf{n} are the degree of local alignment and the average alignment direction, respectively. For sufficiently weak activity above σ^* , a stable steady state emerges of circulation about the system center (Figure 2a&d). The spiral pattern of the nematic director field is reminiscent of the predictions of Kruse $et \ al. \ [7]$ for unconfined active systems [see also 8, 21]. As σ_0 is increased, stronger contributions emerge from higher radial modes in the spectrum of the order parameter. Indeed, expanding the order parameter $S(r, \theta)$ in a Fourier series as $S(r, \theta) = \sum_n S_n(r)e^{in\theta}$, the axisymmet-



FIG. 3. (color online). Details of the bifurcation to circulation. (a) Numerically-evaluated steady state amplitudes $|S_0^{(m)}|$ of Bessel series expansion for axisymmetric part of order parameter S at varying activity σ_0 , with $d^{(r)} = d^{(s)} =$ 0.025. (b-d) Profiles of S at indicated points (b-d) in (a).



FIG. 4. (color online). Secondary bifurcation to oscillatory dynamics. (a) Amplitude of oscillation of the velocity autocorrelation function $\Xi(\tau)$ as a function of σ_0 , with $d^{(r)} = d^{(s)} = 0.025$, showing a bifurcation from steady defect separation to oscillatory behavior at a critical value of σ_0 . (b) $\Xi(\tau)$ for $\sigma_0 = 32$ showing periodic oscillatory behavior. (c) Position of flow circulation center over time for $\sigma_0 = 32.75$ during one oscillation period.

ric stability analysis suggests an n = 0 mode expansion of the form $S_0(r) = \sum_{m=0}^{\infty} S_0^{(m)} J_2(2y_m r)$ where $J'_2(y_m) = 0$ and $y_m < y_{m+1}$. Mode amplitudes then read

$$S_0^{(m)} = \frac{1}{\mathcal{N}_m} \int_0^{2\pi} d\theta \int_0^{1/2} dr \, r J_2(2y_m r) S(r,\theta)$$

with normalization $\mathcal{N}_m \equiv (\pi/4)(1-4/y_m^2)[J_2(y_m)]^2$. Figure 3 shows the steady-state values of the first three mode amplitudes $|S_0^{(0)}|, |S_0^{(1)}|, |S_0^{(2)}|$ as functions of σ_0 . Observe the non-zero contributions from modes with m > 0 in the steady state despite only the m = 0 mode being initially excited when $\sigma_0/16 < y_1^2 d^{(s)} + d^{(r)}$.

At larger values of σ_0 , the steady state exhibits de*fect separation*: the central axisymmetric spiral defect in the nematic director field (with topological charge +1) splits into two closely spaced hyperbolic defects (each of charge +1/2). The system still possesses fluid circulation about the central axis, due to the symmetric positioning of the defects. Such a configuration is illustrated in Figure 2b&e. The emergence of the defect separation phenomenon is perhaps unsurprising if we make contact with classical liquid crystal theory; for approximately isolated defects, the free energy penalty per defect is proportional to the square of its topological charge [22], rendering two +1/2 defects favorable over a single +1 spiral. Indeed, de las Heras et al. [23] recently investigated the equivalent confined setup for a microscopic two-dimensional liquid crystal and always encountered defect separation.

As σ_0 is increased beyond a new critical value, the system bifurcates into a regime of *periodic oscillation*, where the time symmetry has been broken and a steady state is

now unstable. The +1/2 defect pair (Figure 2c) execute periodic 'orbits' around each other, with the flow circulation center offset from the origin (Figure 2f) and following an approximately circular trajectory (Figure 4c). These states can be analyzed by examining the velocity autocorrelation function [12]

$$\Xi(\tau) \equiv \left\langle \frac{\langle \mathbf{v}(\mathbf{x},t) \cdot \mathbf{v}(\mathbf{x},t-\tau) \rangle_{\mathbf{x}}}{\langle \mathbf{v}(\mathbf{x},t) \cdot \mathbf{v}(\mathbf{x},t) \rangle_{\mathbf{x}}} \right\rangle_{t}$$

where the temporal average is taken over late times when the oscillatory state is fully established. Extracting the amplitude A of oscillation of Ξ (Figure 4b) we numerically determine a bifurcation diagram as a function of σ_0 as in Figure 4a. There is a clear threshold for the onset of periodic oscillations.

Motivated by principles of cytoplasmic streaming, we have constructed a clean, simple model for a dilute suspension of extensile force-generating filaments in total geometric confinement, and have demonstrated that the inclusion of elementary hydrodynamics is entirely sufficient to yield spontaneous self-organization behavior, in spite of the absence of more complex local interaction terms. In an experimental realization, the prediction of a critical activity for transition from quiescence to circulation can be tested by varying the chamber size or the motor activity, perhaps through temperature or ATP concentration. Modern realizations of the experiment of Yotsuyanagi will likely provide a wealth of information on this type of bifurcation.

We thank S. Ganguly, A. Honerkamp-Smith, P. Khuc Trong and H. Wioland for helpful discussions. This work was supported by the EPSRC and European Research Council Advanced Investigator Grant 247333.

- J. Verchot-Lubicz and R.E. Goldstein, *Protoplasma* 240, 99 (2009).
- [2] R.E. Goldstein, I. Tuval and J.W. van de Meent, Proc. Natl. Acad. Sci. USA 105, 3663 (2008).
- [3] Y. Yotsuyanagi, Cytologia 18, 146 (1953); 18, 202 (1953).
- [4] N. Kamiya, Protoplasmic Streaming (Springer-Verlag, Berlin, 1959).
- [5] R. Jarosch, Protoplasma 47, 478 (1956).
- [6] R. Voituriez, J.F. Joanny, and J. Prost., *Europhys. Lett.* 70, 404 (2005).
- [7] K. Kruse, J.F. Joanny, F. Jülicher, J. Prost, and K. Sekimoto, *Phys. Rev. Lett.* **92**, 078101 (2004).
- [8] J. Elgeti, M.E. Cates and D. Marenduzzo, Soft Matter 7, 3177 (2011).
- [9] K. Kruse, J.F. Joanny, F. Jülicher, J. Prost and K. Sekimoto, *Eur. Phys. J. E* 16, 5 (2005).
- [10] L. Giomi and M.C. Marchetti, Soft Matter 8, 129 (2011).
- [11] S. Fürthauer, M. Neef, S.W. Grill, K. Kruse and F. Jülicher, New J. Phys. 14 023001 (2012).
- [12] V. Schaller, C.Weber, C. Semmrich, E. Frey, and A.R. Bausch, *Nature* 467, 73 (2010).

- [13] D. Saintillan and M.J. Shelley, *Phys. Fluids* 20, 123304 (2008); *Phys. Rev. Lett.* 100, 178103 (2008).
- [14] C. Helzel and F. Otto, J. Comput. Phys. 216, 52 (2006).
- [15] A.A. Pahlavan and D. Saintillan, Phys. Fluids 23, 011901 (2011).
- [16] M. Doi and S.F. Edwards, The Theory of Polymer Dynamics (Oxford University Press, USA,1988).
- [17] P.G. de Gennes and J. Prost, The Physics of Liquid Crystals (Clarendon Press, Oxford, 1995).
- [18] A. Baskaran and M.C. Marchetti, Phys. Rev. E 77,

011920 (2008).

- [19] F.G. Woodhouse and R.E. Goldstein, in preparation.
- [20] E.J. Hinch and L.G. Leal, J. Fluid Mech. 76, 187 (1976).
- [21] D. Marenduzzo and E. Orlandini, Soft Matter 6, 774 (2010).
- [22] T. Lubensky and J. Prost, J. Phys. II 2, 371 (1992).
- [23] D. de las Heras, E. Velasco and L. Mederos, *Phys. Rev.* E 79, 061703 (2009).