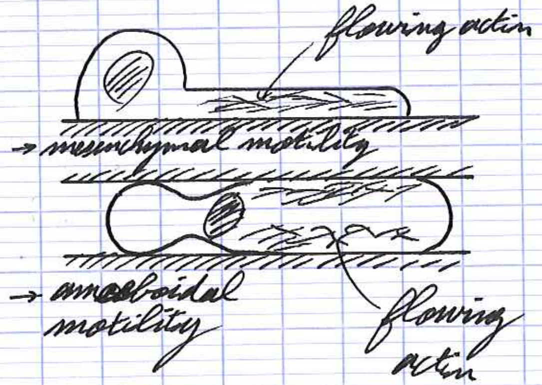
Spontaneous flow of an active fluid: a model for cellular motion

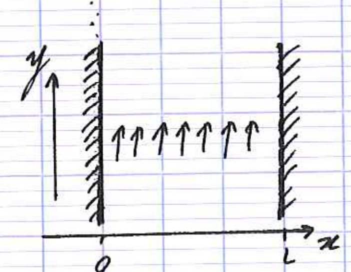
Actomyosin and other types of active fluids can flow in the absence of externally exerted stress in in vitro experiments. This is somewhat reminiscent of ~~cellular~~ cytoskeletal flows in moving cells that power their locomotion. Here we show in a simple setup that a layer of active fluid spontaneously develops motion of this type.



After Voituriez, Joanny & Prost, Europhys. Lett. 70, 404 (2005)

I) Setup of the problem ~~[illegible]~~

We consider a 2d channel with no-~~slip~~ stress boundary conditions filled with the active fluid. The anchoring of the filaments is // to the walls, and



we assess the stability of the homogeneous, motionless state with polarization in the y direction.
We assume invariance in the y-direction throughout.

The equations of the last chapter have 6 unknowns:

$$\partial_x v_x \,;\, \partial_y v_x \,;\, \partial_x v_y \,;\, \partial_y v_y \,;\, p_x \,;\, p_y$$

each of which is a function of space. y-invariance sets

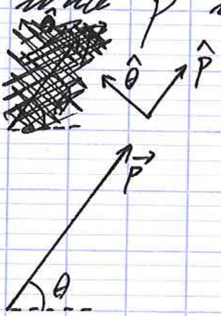
$$\partial_y v_x = \partial_y v_y = 0$$

We moreover assume in the following that our fluid is incompressible (i.e., $\mathcal{P}^{eq}$ is a Lagrange multiplier ensuring constant volume). Thus

$$\vec{\nabla}\cdot\vec{v} = 0$$
$$\Longleftrightarrow \quad \partial_x v_x + \partial_y v_y = 0$$
$$\Longrightarrow \quad \partial_x v_x = 0$$

Thus v_x is a constant, and since it vanishes at the walls $v_x = 0$.

We write $\vec{p}$ in polar coordinates:



$$\vec{p} = p\,\hat{p} = p\cos\theta\,\hat{x} + p\sin\theta\,\hat{y}$$

We also write h in this reference frame:

$$h = h_{\parallel}\,\hat{p} + h_{\perp}\,\hat{\theta}$$

$$\Longrightarrow \begin{cases} h_x = h_{\parallel}\cos\theta - h_{\perp}\sin\theta \\ h_y = h_{\parallel}\sin\theta + h_{\perp}\cos\theta \end{cases}$$

$$\begin{cases} h_{\parallel} = h_x\cos\theta + h_y\sin\theta \\ h_{\perp} = -h_x\sin\theta + h_y\cos\theta \end{cases}$$

And changes in $\vec{p}$ read
$$\delta\vec{p} = \delta p\cdot\hat{p} + p\cdot\delta\theta\cdot\hat{\theta}$$
$$= (\delta p\cos\theta - p\,\delta\theta\sin\theta)\,\hat{x} + (\delta p\sin\theta + p\,\delta\theta\cos\theta)\,\hat{y}$$

Or
$$\delta p = \delta p_x\cos\theta + \delta p_y\sin\theta$$
$$p\,\delta\theta = -\delta p_x\sin\theta + \delta p_y\cos\theta$$

In the end there are 3 unknowns:
- $\partial_x v_y(x)$
- $p(x)$
- $\theta(x)$

We look at the large length scale limit, where $L \gg$ all molecular scales (the "hydrodynamic limit").

II) Alignment fields

We have yet to relate our fields h_i^d to our unknowns.

- Let us first consider the fields deriving from the Frank free en.; we consider the [redacted] case $K_1 = K_3$ for simplicity:

[redacted]

$$\vec{\nabla}\cdot\vec{p} = \partial_\parallel p_\parallel + \partial_\perp p_\perp$$
$$\vec{\nabla}\wedge\vec{p} = \partial_\parallel p_\perp - \partial_\perp p_\parallel$$

So $\mathcal{F} = \frac{K}{2}\int d\vec{r}\left[(\partial_\parallel p_\parallel + \partial_\perp p_\perp)^2 + (\partial_\parallel p_\perp - \partial_\perp p_\parallel)^2\right]$

yields $h_\perp(\vec{r}) = -\frac{\delta \mathcal{F}}{\delta p_\perp(\vec{r})} = -\frac{K}{2}\int d\vec{r}'\{2\partial_\perp[\delta(\vec{r}-\vec{r}')](\partial_\parallel p_\parallel + \partial_\perp p_\perp) + 2\partial_\parallel[\delta(\vec{r}-\vec{r}')](\partial_\parallel p_\perp - \partial_\perp p_\parallel)\}$

Integrating by parts:

$$h_\perp(\vec{r}) = K\{\partial_\perp(\partial_\parallel p_\parallel + \partial_\perp p_\perp) + \partial_\parallel(\partial_\parallel p_\perp - \partial_\perp p_\parallel)\}$$
$$= K\Delta p_\perp = Kp\,\Delta\theta = Kp\,\partial_x^2\theta$$

Likewise $h_\parallel(\vec{r}) = K\,\partial_x^2 p$

- Now considering the dissipative forces: (here we let $p_0 = 1$)

$$h_\parallel^d = h_\parallel - h_\parallel^r = \underbrace{K\partial_x^2 p}_{\text{negligible in the hydrodynamic limit}} - k(p-1) \simeq -k(p-1)$$

$$h_\perp^d = h_\perp - \underbrace{h_\perp^{eq}}_{\substack{=0 \\ \text{(Goldstone mode)}}} = K\partial_x^2\theta$$

Weak restoring force for $L\to\infty$; thus [redacted] θ will relax much more slowly than p; these are the hydrodynamic time scales we are interested in.

III) Evolution equation

We use these results in the general form of the active fluid equations of the last chapter.

1°) Mechanical equilibrium

$$\partial_j \left(\sigma_{ij} \right) = 0$$

Thus for $i = y$:

$$\sigma_{yx} = \text{constant} = 0$$

Inserting into the first flux-force relation:

$$\eta\, \partial_x v_y = -\frac{\nu}{2}\left(p_y h_x^d + p_x h_y^d\right) + \zeta \Delta\mu\, p_x p_y - \frac{1}{2}\left(p_y h_x^d - p_x h_y^d\right)$$

$$= -\frac{\nu}{2}\Big(p \sin\theta \left(h_\parallel^d \cos\theta - h_\perp^d \sin\theta\right) + p\cos\theta \left(h_\parallel^d \sin\theta + h_\perp^d \cos\theta\right)\Big) + \zeta \Delta\mu\, p^2 \cos\theta \sin\theta + \frac{1}{2} \times 0$$

$$\eta\, \partial_x v_y = -\frac{\nu}{2}\, p + \frac{\zeta \Delta\mu}{2}\, p^2 \sin(2\theta)$$

$$\left(h_\parallel^d \sin 2\theta + h_\perp^d \cos 2\theta\right)$$

2°) Longitudinal polarization: non-hydrodynamic behavior

$$\partial_t p_\parallel = \cos\theta\, \partial_t p_x + \sin\theta\, \partial_t p_y$$

$$= \cos\theta \left[\frac{h_x^d}{\gamma} + \lambda p_x \Delta\mu - \frac{\nu}{2} p_y \partial_x v_y \right] + \sin\theta \left[\frac{h_y^d}{\gamma} + \lambda p_y \Delta\mu - \frac{\nu}{2} p_x \partial_x v_y \right]$$

$$= \frac{h_\parallel^d}{\gamma} + \lambda \Delta\mu\, p_\parallel - \frac{\nu}{2} \partial_x v_y \left(2p \cos\theta \sin\theta \right)$$

$$= \frac{h_\parallel^d}{\gamma} + \lambda \Delta\mu\, p_\parallel - \frac{\nu}{2} p (\partial_x v_y) \sin(2\theta)$$

For p close to one we thus have:

$$\partial_t (\delta p_\parallel) + \frac{k}{\gamma} \delta p = \underbrace{\lambda \Delta\mu - \frac{\nu}{2} p (\partial_x v_y) \sin(2\theta)}_{\text{small close to equilibrium}}$$

So this quickly (time $\propto \frac{\gamma}{k}$) relaxes to a value close to zero; We can thus consider that $p \simeq 1$ throughout as we consider the longer hydrodynamic time scales over which $\vec{p}$ rotates.
Besides, $h_{\parallel}^{d}$ quickly goes to

$$\frac{\partial_x v_y}{2} \nu \sin(2\theta) = \frac{h_{\parallel}^{d}}{\gamma} + \lambda \Delta\mu$$

3°) Transverse polarization dynamics

$$\partial_t p_{\perp} = p \partial_t \theta$$
$$= \frac{h_{\perp}^{d}}{\gamma} - \frac{\nu}{2} \partial_x v_y \left(-\sin\theta \, p_y + \cos\theta \, p_x\right)$$
$$= \frac{h_{\perp}^{d}}{\gamma} - \frac{\nu}{2} \partial_x v_y \, p \cos(2\theta)$$

IV) Flow profile

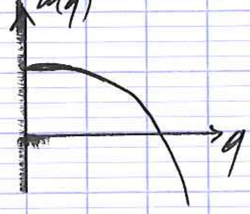
1°) Linear stability

Using the two equations of the previous subsection we express $h_{\parallel}^{d}$ and $\partial_x v_y$ and insert above. We end up with a dynamical equation of the form

$$\partial_t \theta = a(\theta) + b(\theta) \partial_x^2 \theta$$

$$\underset{\substack{\text{linear stability} \\ \text{analysis for } \varepsilon = (\theta - \frac{\pi}{2}) \text{ small}}}{\rightsquigarrow} \quad \partial_t \varepsilon = a'\left(\tfrac{\pi}{2}\right)\varepsilon - b\left(\tfrac{\pi}{2}\right) q^2 \varepsilon$$

which is unstable at short wavevectors if the slab is wide enough.



2°) Steady-state flow

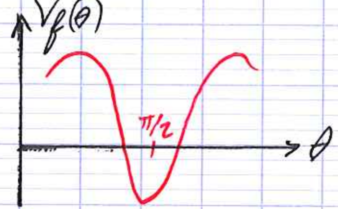
The steady-state equations take the form

$$\partial_x^2 \theta = \frac{\bar{\zeta}\Delta\mu \sin(2\theta)(\nu\cos 2\theta - 1)}{K\left(\frac{4\eta}{\gamma} + \nu^2 - 2\nu\cos 2\theta + 1\right)} = -V_f'(\theta)$$

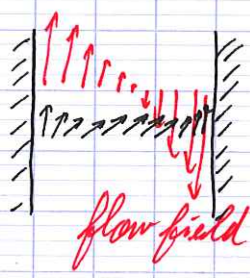
or

$$\frac{1}{2}(\partial_x\theta)^2 + V_f(\theta) = ct$$

with $V_f(\theta)$ of the form :



Thus the angle profile is analogous to the trajectory of a marble in a potential.



Similar to Fredericks transition.

~~The homogeneous polarization region in the center will get~~

V) Discussion

The homogeneous polarization region in the center will get further destabilized, ~~which~~ which will give rise to turbulent-looking flows in the active fluid.

Overall, active fluids are widely regarded as generically unstable, and will break up into self-sustained "turbulent" messes as in Zvonimir's experiments (show video).

Final remarks

- Living matter is very complex, but some of its aspects are amenable to physical analysis. When it is, we often discover interesting material properties due to the prevalence of disorder and it out-of-equilibrium character, which can give rise to exotic behaviors (spontaneous flow, alignment in 2d, flocking, giant number fluctuations...).

- Keep in mind that these are only toy models that help us think about these problems. We don't understand all that much about these processes. This makes the field messy, but also exciting to work in.

- Be wary of elaborate theoretical developments too far removed from experiments in this field. Talk to the biologists!