## Microorganism Billiards

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# Swimming trajectories near a wall



#### Accumulation (E. coli, spermatozoa)



[Rothschild (1963); Berke *et al.* (2008); Smith *et al.* (2009)]



[Lauga et al. (2006)]

#### Glancing (potential flow squirmers)

Volvox, paramecia





[Goldstein, Jung labs]



[Spagnolie & Lauga (2012); Crowdy & Or (2010); Li & Ardekani (2014)] play movie

## Chlamydomonas reinhardtii near a wall





CC-125 wild-type

θ,

CC-2289 lf3-2

CC-2347 shf1

[Kantsler et al. (2013)]

# Kantsler et al. (2013): scattering angles



Typical outgoing angle varies from  $12^{\circ}$  to  $20^{\circ}$ , with some spread.

## Modeling the swimmer-wall interaction





Simple model of wall interaction:

- swimmers move in straight line between collisions;
- when hitting they 'hug' the wall for a distance δ;
- the outgoing angle is  $\theta_c$ ;
- regular polygonal domains, with interior angle  $\theta_p = (1 - 2/N)\pi$ .
- The position along a side on the *n*th hit is  $x_n \in [0, 1]$ .



Interior angle:  $\theta_p = (1 - 2/N)\pi$ ;

First assume reflection angle  $\theta_c \in (0, \pi/N)$ , so that the swimmer always hits the next adjacent wall.

Take for now  $\delta = 0$ ; we find using simple geometry

$$x_{n+1} = f(x_n) = \frac{\beta}{\beta} \left(1 - x_n\right)$$

where

$$\beta = \sin(\theta_c) / \sin(2\pi/N - \theta_c) \le 1.$$

A simple linear map tells us where the swimmer hits the sides.

## Hitting the adjacent wall (cont'd)



Trivial to solve:

$$x_n = (-\beta)^n x_0 - \sum_{i=1}^n (-\beta)^i \\ = (-\beta)^n x_0 + \beta \frac{1 - (-\beta)^n}{1 + \beta}.$$

For  $\beta < 1$ , the dynamics lose memory of the initial position  $x_0$  exponentially fast in the number of impacts, and the swimmer settles in a stable periodic orbit with

$$x^* = \lim_{n \to \infty} x_n = \frac{\beta}{1+\beta} < \frac{1}{2}.$$

 $[\beta=1 \text{ leads to an }\infty \text{ of neutrally-stable periodic orbits.}]$ 

## Hitting the adjacent wall (cont'd)





Converges more slowly as  $\beta \uparrow 1$  (36°).



$$x_n = (-\beta)^n x_0 + (\beta + \delta) \frac{1 - (-\beta)^n}{1 + \beta}.$$

For  $\beta < 1 \text{, we get a corrected fixed point}$ 

$$x^* = (\delta + \beta)/(1 + \beta)$$

as  $n \to \infty$ .



## Non-adjacent walls

If the angle  $\theta_c > \pi/N$  then the swimmer can 'skip' the next adjacent wall:



We need to orient the next side properly with respect to the direction of the bounce. A given side may have different orientations for different hits.



## Hitting two walls of a hexagon

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Typically swimmers can hit more than one wall depending on  $x_n$ :



Get a one-dimensional piecewise-linear discontinuous map!



Here is the explicit map:

$$x_{n+1} = f(x_n) = \begin{cases} \beta \alpha^{-1} (\alpha - x_n), & x_n \le \alpha, \\ (1 - \alpha)^{-1} (1 - x_n), & x_n > \alpha, \end{cases}$$

where  $\alpha$  is the swimmer that hits the corner, and  $\beta$  is the image of 0 (previous slide). These can be worked out from simple geometry. Note that:

$$|f'(x)| < 1$$
 for  $x < \alpha$  (stable);  
 $|f'(x)| > 1$  for  $x > \alpha$  (unstable).

There is thus a competition between stable and unstable behaviour... or is there? Staring at the map, one can see the stable side always wins.

#### Hitting two walls of a hexagon: stable

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For some values we recover stable orbits, but for a smaller polygon:



Here we get an inscribed triangle.

## A square domain: simpler?

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Let's try something else, a simple square:



This time the map is continuous, owing to the reversal of one interval.



Here's the map for this case:

$$x_{n+1} = f(x_n) = \begin{cases} \beta \alpha^{-1} (\alpha - x_n) & x_n \le \alpha, \\ (1 - \alpha)^{-1} (1 - x_n) & x_n > \alpha, \end{cases}$$

This is a classic tent map.

For  $x < \alpha$ , we have |f'(x)| = 1 (neutrally stable);

For  $x > \alpha$ , we have |f'(x)| > 1 (unstable).

There is no stable region, and the single fixed point is unstable. Likely to get chaotic dynamics!

#### A square domain: invariant measures







For a one-dimensional map, the Lyapunov exponent is defined

$$\lambda = \lim_{n \to \infty} \frac{1}{n} \sum_{i=0}^{n-1} \log |f'(x_i)|$$

(There's only one exponent.) It describes the exponential rate of separation of neighbouring trajectories. It is a measure of chaos (> 0).

Note that  $\lambda$  is dimensionless: we can convert it to an inverse time to get the 'physical' exponent  $\Lambda$  by dividing by the mean time between hits,  $\overline{T}$ :

$$\Lambda = \lambda \, / \, \overline{T}, \qquad |\Lambda| \ge |\lambda| / \tau.$$

Here  $\tau$  is the maximum time between hits. The important thing is that  $\Lambda$  and  $\lambda$  have the same sign (both chaotic, or not).

Fix shape and vary angle, for N = 4, 5, 10, 20 sides:



Note that when the exponent is negative we can in principle get an analytic formula, since it simply corresponds to a stable periodic orbit.

#### The effect of noise



Of course, since these are biological systems we expect lots of noise and uncertainty. For instance, maybe the swimmer doesn't travel in a straight line, so we add a Gaussian noise term to the simplest map:

$$x_{n+1} = \beta \left( 1 - x_n \right) + \sigma Z_{n+1}$$

This can be solved exactly:

$$x_n = (-\beta)^n x_0 + \beta \, \frac{1 - (-\beta)^n}{1 + \beta} + \sigma \, \sqrt{\frac{1 - \beta^{2n}}{1 - \beta^2}} \, \tilde{Z}_n$$

Asymptotes to (for  $\beta < 1$ )

$$x_n \sim \frac{\beta}{1+\beta} + \frac{\sigma \tilde{Z}_n}{\sqrt{1-\beta^2}} \qquad n \to \infty$$

Thus the fixed point survives as long as  $\beta$  is not too close to 1.



#### Two different swimmers:



The orientations are chosen such that the fixed points of the two types of swimmers are at the exits.  $$_{\rm 20\,/\,28}$$ 

## Sorting with larger noise

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Now with more noise: the old design doesn't work so well.



Need to compensate for larger spread of the triangle swimmers (larger  $\beta$ ).

## Sorting with smaller angles

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The small angles in Kantsler et al. (2013) make it more difficult to sort:



Too much noise  $(\sigma)$  makes it impossible to sort.



Note that Kantsler *et al.* (2013) also proposed (and built) a sorting mechanism using scattering and rectification.



Theirs works by a cascading process. (Ours doesn't use the rectification mechanism.)

#### Lattice of obstacles: the exterior problem





#### The exterior problem: larger angle





#### The exterior problem: even larger angle







Some things that remain to be done:

- A full classification, connecting to the theory of discontinuous piecewise-linear maps. (Mostly for mathematicians...)
- Irregular shapes? Channels?
- Large angles not observed (chaos), but small angles good for sorting.
- Three-dimensional swimming? (More input from experiments.)
- Exterior problem: when do swimmers escape the lattice?

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