Bacterial population solitary waves can defeat rings of funnels

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Abstract
We have constructed a microfabricated circular corral for bacteria made of rings of concentric funnels which channel motile bacteria outwards via non-hydrodynamic interactions with the funnel walls. Initially bacteria do move rapidly outwards to the periphery of the corral. At the edge, nano-slits allow for the transport of nutrients into the device while keeping the bacteria from escaping. After a period of time in which the bacteria increase their cell density in this perimeter region, they are then able to defeat the physical constrains of the funnels by launching back-propagating collective waves. We present the basic data and some nonlinear modeling which can explain how bacterial population waves propagate through a physical funnel, and discuss possible biological implications.

1. Introduction

Self-propelled bacteria such as E. coli are often viewed as solitary organisms looking for food via the classic biased random-walk model so elegantly described by Berg [1]. The biased random walk that individual E. coli bacteria perform is due to two capabilities of E. coli: (1) they are self-propelled due to complex rotating flagella which drive the bacterium forwards by rotating counterclockwise for a mean time $\tau$ before reversing rotation sense for a short time, making the left-hand-loaded flagella bundles fly apart [2]; (2) bacteria sense chemicals and either move towards or away from the chemicals, a process called chemotaxis [3]. The bacterium can move up a concentration gradient $\nabla c(x)$ in order to move towards the source of the food gradient.

We know two fundamental aspects of bacterial sensing: (1) they must make measurements of concentrations at two different points. (2) The sensitivity of the response of the chemoreceptors cannot be constant, they must adapt to the local concentration of chemicals. If this did not happen, then the dynamic ranges of the chemoreceptors would be limited, but we know that bacteria can adapt their sensitivity to wide range of concentrations [4]. Individual bacteria thus have a very sophisticated chemotaxis signaling network that allows an isolated bacterium to find food in a food gradient.

However, it is possible to physically defeat this system, using microfabricated funnels [5, 6]. In previous work we have shown that microfabricated funnels (with asymmetric openings front and rear) can only concentrate swimming bacteria [5, 7]. These experiments showed that funnels can result in an inhomogeneous distribution of swimming bacteria. We showed that funnels in the presence of motile bacteria create a number density difference $\delta b = b_{\text{left}} - b_{\text{right}}$ across a row of funnels, where $b$ is the local density of self-propelled agents. Although this self-concentration by swimming agents might seem to resemble a Maxwell’s demon [8], the 2nd Law of Thermodynamics is safe because the chemical energy created by a population difference ultimately has an energy source, in this case the metabolism of the swimming bacteria. By making a series of funnel rows we have shown that a self-powered population ratchet can be made which can remove motile bacteria from a volume, rather like a multi-stage vacuum pump.
There is more to the story. Bacteria are capable of collective response to self-generated chemical signals, for example in the case of quorum sensing in certain bacteria [9, 10]. In a more general sense, bacterial signaling and response capabilities can even be viewed as forming a multicellular organism in which the collective aspect of response can confer significant fitness advantages [11]. The concept of quorum sensing can be expanded to include the entire domain of cell-to-cell communication response to cell density [12].

We have previously shown in a linear configuration of funnels that the population waves generated by a self-interacting collection of motile bacteria can indeed defeat the physical focusing effects of a funnel array. Here we explore the time dynamics of the process using circular rings of funnels, and the waves of bacteria which solve the funnel problem, and develop a general model for the phenomena.

2. Experimental methods

2.1. Device fabrication

Our device consisted of rings of funnels etched 10 μm deep into a silicon wafer. The structure masks were designed in L-Edit and made on a Heidelberg DWL66 laser writer. There were two layers, one contained funnel rings, while the other contained the nanoslits. A 100 nm diameter inch silicon wafer was first spin coated with photoresist AZ5214, then the nanoslits mask was exposed by mask aligner. After developing, the nanoslits were etched 100 nm in the silicon by a reactive ion etching process using a Samco 800 machine. The photoresist was removed by acetone bath. The processes were then repeated with the funnel array mask, with an etch depth of 10 μm for the funnels. A protective layer of photoresist was spun after the last etching step. The wafer was then diced and 2.5 cm chips were then cut out of diced wafer using a pulsed Nd:YAG laser (MER 40 Laser System). Ports for fluid injection were also cut into the chips using the same method. Finally, a 200 nm layer of SiO2 was grown into the surface of the silicon substrate using a 1000°C vacuum furnace at 1 h with 0.1 bar O2 pressure. This oxide layer is used to make the surface of the device hydrophilic.

Figure 1 shows the exposure mask used for fabricating the chips. The diameter of the etched internal disc of the device is 1.0 cm. The funnels were designed with a 60° opening angle, with depth from apex to opening of 150 μm and a 5 μm opening gap at the funnel vertex. Four rings of funnels were created. The outer-most ring of funnels is followed by a ring of nanoslits which couple the interior of the device with circulating media diffusively.

2.2. Bacterial strain

The strains used are wild-type E. coli strain K-12 carrying a gene expressing GFP fused to lacZ and under control of the Lac repressor (17). Expression of the fluorescent proteins was induced by the addition of IPTG to the media at a concentration of 200 μM.

We streaked ~80 °C stock E. coli on an LB agar plate and allowed the culture to grow overnight at 37 °C. We grew bacteria in M9-casamino acid broth supplemented with 10% glucose. A single colony was picked and inoculated into a tube containing either 2 ml of M9-casamino acid media or LB. The bacteria were then incubated at 30 °C and shaken at 170 RPM for ~6 h where the culture reaches an OD of ~0.6. Optical density measurements were carried out on a Biochrom WPA CO8000 cell density meter.

2.3. Bacterial funnel chip holder

A rectangular aluminum housing with a circular glass window was manufactured to act as a holder for the microfabricated chip. The aluminum has two ports through which air can flow into the device. A disk of poly(dimethylsiloxane) (PDMS) was cut to act as a seat for the chip. Holes were punched into the PDMS disk and syringe needles were placed inside. The chip then sits on the PDMS seat held in place by the protrusion of the syringe needles through the ports. A 35 mm diameter Lumox gas-permeable 20 μm thick membrane culture dish for suspensions (https://sasrsted.com/en/products/laboratory/cell-tissue-culture/lumox-technology/) was placed between the glass window and a rubber O-ring was then placed atop the Lumox to allow pressurization of the Lumox against the silicon chip. An aluminum ring was then screwed on top to seal the Lumox membrane and keep it air-tight from below. To restrict bubble formation in the chip the media used in the experiment were degassed and then added to syringes.

The chip was then placed etched face down onto the Lumox membrane and a 1 cm thick silicone plug pre-drilled for access to the back of the chip was placed against the chip back. The whole apparatus was then seated into the microscope stage. The syringes were then attached to a syringe pump and set at a flow rate of 0.02 ml h⁻¹. Syringe A aquarium air pump was used to pressurize space between the window and the Lumox, pushing the Lumox against the etched chip surface. Thus the positive pressure of the air pushes the thin Lumox membrane onto the silicon chip and seals it. We found a pressure of 0.1 bar gave a good seal, although the gas had to be humidified by bubbling through distilled water at 45 °C to prevent the chip from drying out.
2.4. Time-lapse fluorescence imaging

Epi-fluorescence experiments were carried out on a Nikon Eclipse Ti microscope with motorized XYZ Prior stage and motorized objective turret. The turret was fitted with 2×, 10× and 20× Nikon objectives. A Canon 5D digital single lens reflex camera was controlled by MicroManager (https://micro-manager.org). The epifluorescence excitation source was a 470 nm LED from Thorlabs (Model LEDD1A), and green emission of the GFP fluorescence from the bacteria was collected through 510 center wavelength filter with 20 nm bandwidth. The trigger input of the LED was connected to the flash-output of the Canon camera so that the LED was on only during the exposure time. Images of the chip were taken every 3 minutes.

Automated control of the motorized microscope was accomplished by a custom Beanshell script written for Micro-Manager’s built-in scripting API. A full-chip image of the fluorescent bacteria was taken through the 2× objective, followed by successive images at different positions within the chip using the 10× and 20× objectives. Image analysis was performed using FIJI (https://fiji.sc) on an Apple Pro computer connected to a 20 Tb RAID storage.

3. Results

20 μl of bacteria at a density of 0.6 OD (mid-log phase), or approximately $4 \times 10^8$ bacteria ml$^{-1} \times 0.02 \sim 8 \times 10^6$ bacteria were added to the chip center at $t = 0$. Note that the volume of the funnel array area is only about 3 μl, so that there is a large excess of bacteria outside the chip. However, fresh media is only brought in via the nanoslits at the periphery of the funnel array, so that a food gradient can quickly develop at high bacterial density in the chip.

3.1. Basic phenomenology of bacteria in the funnel array

Upon inoculation of mid-log phase bacteria in the center well, they immediately swim through the funnels (which direct them to the periphery) and rapidly populate the outer ring of nanoslits within 2 hours, where there is fresh media circulating at a rate of 10 μl h$^{-1}$. The bacteria that move to the periphery proceed to multiply for approximately 8 hours at the nanoslits, as seen in figure 2.
Typically, at approximately 400 minutes, the bacteria on the periphery synchronously launch a semi-circular density wave which propagates *inwards* against the funnel, thereby defeating the physical obstacle of the funnels. We say 'typically' because the timing of the initiation of the wave and also its position on the periphery is different from experiment to experiment (this experiment has been repeated 5 times). The synchronization of the wave is also variable from run to run. The wave is not completely symmetric around the periphery of the ring of nanoslits, but seems to be a sensitive function of local bacteria concentrations around the periphery. Figure 3 shows a typical wave whose focal center is not at the inoculation port but is offset approximately 200 μm from the center. In this example the wave begins on the left side of the device as seen in figure 3.

Once wave initiation has begun there are typically a succession of wave events separated by roughly 400 minutes out to about 1300 minutes. Again we say 'roughly' because from experiment to experiment the position or number of waves vary. Figure 4 shows a snapshot of an entire chip at 1281 minutes after inoculation where three waves can be seen: (1) an annular one at angular position about 09h00, (2) a large radial one at 06h00, and (3) the beginnings of the launch of a new one at approximately 05h30.

The dynamics of the waves (1) and (2) are interesting. Consider the events in the run shown in figure 4 at 10× magnification around 1281 minutes. Figure 5 shows at 10× magnification (optical resolution about 1 micron, sufficient to image individual bacteria) the events as the wave grazes a funnel wall at an angle of about 45° with respect to the normal to the funnel ring. The wave is able to penetrate the funnel array, but there is a delay between the arrival at a given funnel and the transmission through the funnel of about 1 minute (3 funnels / 3 minutes, our frame rate). We believe, and it is discussed below, that the reason for this delay is that there is a time needed for the bacteria moving with the wave to come up against the wrong side of the funnel and build to a critical bacterial density $B_0$ to move through a funnel in the reverse direction. A further example of this delay and possible buildup to a critical bacterial concentration $B_0$ to penetrate backwards against a funnel can be seen in figure 6. Here a solitary wave collides with direction almost perpendicular to the funnel tangent. A delay of about 6 minutes can be observed while the wave sharpens up

![Figure 2](image-url)
against the funnel wall, then a rapid penetration of the funnels is seen and the wave moves swiftly away, with a speed of approximately $300 \mu s^{-1}$.

Eventually after a series of wave events (typically between 3–5 solitary waves depending on the experiment) there are no further wave events. Figure 7 shows that after the wave action has collapsed the population of the bacteria clustering around the nanoslits slowly disperses showing no more pumping by the funnels, because the bacteria are no longer motile.

4. A wave equation for bacteria

The basic starting point for understanding collective bacteria dynamics is the Patlak–Keller–Segel equations [13]:

$$\partial_t b + \kappa \nabla (b \nabla c) - D_b \nabla^2 b = \alpha b,$$

(1)
The degrees of freedom in the system are the bacteria density field $\rho(x, t)$, the chemoattractant concentration field $c(x, t)$ and the food concentration $f(x, t)$. There are parameters controlling the dynamics—the diffusion coefficients of the bacteria $D_b$, the chemoattractants $D_c$ and the food $D_f$, the bacteria growth-rate $\alpha$, the chemoattractants production-rate via food resource $\beta$, and the bacteria’s food metabolism rate $\gamma$. In the usual experiment setting, the food concentration is fixed and not a dynamical variable. In that case the Patlak–Keller–Segel equations is then reduced from (3) to (2) equations, which simplifies the physics of the bacteria system greatly:

$$
\partial_t c - D_c \nabla^2 c = \beta b, \quad (2)
$$

$$
\partial_t f - D_f \nabla^2 f = -\gamma b. \quad (3)
$$

Figure 4. $\times 2$ fluorescence image of a run at 1281 minutes elapsed time. At least three separate different waves can be seen, as described in the text. The length bar is 1000 $\mu$m.

Figure 5. Three successive frame shots separated by 3 minutes. The length bar is 1000 $\mu$m.

Figure 6. Five successive frame shots separated by 3 minutes at position 2. The length bar is 170 $\mu$m.
Even with this simplification, due to the nonlinearity of the equations, the exact solution of the reduced Patlak–Keller–Segel is not known. In order to somewhat understand the behavior of the bacterial system, one has to look closely at some special limit where approximations can be used and the equations become easier to deal with.

To get a feeling for the role of the chemoattractant, consider in 1D a slowly spatially varying chemoattractant background of characteristic length scale $L$, which can be approximated locally by a constant gradient:

$$\nabla c = \tilde{a}.$$  \hspace{1cm} (6)

The equation for the bacteria density, which is driven by the chemoattractant concentration, is:

$$\partial_t b + \nu \nabla (bu) - D_b \nabla^2 b = \alpha b.$$  \hspace{1cm} (7)

The Patlak–Keller–Segel equations are nonlinear and do not afford exact solutions. Since we know the bacteria can form solitary waves we can make a propagating wave ansatz:

$$b \sim e^{i k \tilde{x} - \omega t}.$$  \hspace{1cm} (8)

This yields a dispersion relation $\omega(k)$ for the wave:

$$\text{Re}(\omega) = \nu \tilde{a} k,$$

$$\text{Im}(\omega) = \alpha - D_b k^2.$$  \hspace{1cm} (9)

(10)

The real part of the time-frequency determines the group velocity $\overline{V}$ of a wave-packet—a bacteria lump, which is just proportional to the chemoattractant gradient:

$$\overline{V} = \nabla \tilde{c}_w = \nu \tilde{a}.$$  \hspace{1cm} (11)

The imaginary part of the time-frequency tells whether a bacterial pulse of size $\lambda \sim |k|^{-1}$ is maintained or smeared out (the peak decreases when the diffusion effect wins against chemoattraction):

$$\text{Im}(\omega) > 0 \Rightarrow \lambda \gtrsim \frac{D_b}{\alpha} \quad \text{(maintaining lump)},$$

$$\text{Im}(\omega) < 0 \Rightarrow \lambda \lesssim \frac{D_b}{\alpha} \quad \text{(smearing–out lump)}.$$  \hspace{1cm} (12)

(13)

If the chemoattractant concentration is treated as a background with no back-reaction, the generation of solitary–like waves due to bacteria—chemoattractant coupling is missed.

We can see next why the waves are solitary waves. Consider the 1D system in the slow bacteria limit as the diffusion of chemoattractants is much faster than that of the bacteria, we make an assumption that:

$$|\partial_t c| \ll D_b |\nabla^2 c| = - D_b \nabla^2 c \approx \beta b.$$  \hspace{1cm} (14)

For further simplification, take the food concentration to also be homogeneous in space (which is surely wrong in our case) and let the bacteria reproduction rate be zero to avoid the complications of increasing total bacteria numbers

$$f(x) = f_0,$$  \hspace{1cm} (15)
\( \alpha = 0. \) (16)

Change of variables for later convenience:
\[ s = \frac{D_c}{\beta f_e} \partial_s c \Rightarrow b = -\partial_s s. \] (17)

The equation of motion for the bacterial density then satisfies:
\[ \partial_t s - D_b \partial_s^2 s + \frac{\kappa \beta f_e}{D_c} \partial_s (s \partial_s s) = 0. \] (18)

This partial differential equation has Galilean symmetry. If the stationary solution \( s(x) \) is known, one can boost it to a velocity \( v \) and get a propagating solution:
\[ s(x) \rightarrow s_v(x, t) = s(x - vt) + \frac{D_c}{\kappa \beta f_e} v. \] (19)

In the stationary case \( \partial_t b = 0 \), the equation can be solved by a spatial-instanton ansatz:
\[ s = -s_0 \tanh(k(x - x_c)) \Rightarrow s_0 = \frac{\kappa \beta f_e}{2D_b D_c} k. \] (20)

The corresponding bacterial density and chemoattractant concentration (up to a constant \( c_0 \)) is:
\[ b = \frac{\kappa \beta f_e}{2D_b D_c} k^2 \text{sech}^2(k(x - x_c)), \] (21)
\[ c = \frac{\kappa}{2D_b} \ln \cosh(k(x - x_c)) + c_0. \] (22)

This lump of bacteria density has width \( \lambda \) and amplitude \( B \):
\[ \lambda \sim |k|^{-1}, \] (23)
\[ B = \max(b) = \frac{\kappa \beta f_e}{2D_b D_c} k^2. \] (24)

Apply the Galilean boost transformation of velocity \( v \) to get the propagating solution:
\[ b_v = \frac{\kappa \beta f_e}{2D_b D_c} k^2 \text{sech}^2(k(x - vt - x_c)), \] (25)
\[ c_v = \frac{\kappa}{2D_b} \ln \cosh(k(x - vt - x_c)) + \frac{v}{\kappa} x + c_0. \] (26)

The bacteria density is now a solitary-like wave moving with propagating velocity \( v \), which is proportional to the overall gradient part of the chemoattractant concentration \( u x \):
\[ u = \frac{v}{\kappa}. \] (27)

Note there is no bacteria reproduction, the bacteria lump is maintained due to the bacteria—chemoattractants coupling. Our main point here is that the Patlak–Keller–Segel equations yield solitary-like wave solutions. The question becomes: what role do these waves play in enhancing bacterial fitness and conquering the physical constraints of the funnels and permitting bacterial communication?

4.1. Funnel bacterial mechanics

The hydrodynamic trapping of motile objects near surfaces is well known and is to be distinguished from the remarkable observations that \( E. \ coli \) also express a preference for turning to the right when interacting with a wall due to the helicity of the rotational motion of the flagella [14], although it should be possible to exploit this aspect also in concentration of motile bacteria. Also, unlike other papers showing rectified motion using the interaction of objects with kinesin coated surfaces [15], all that is required is self-propulsion and asymmetry in the surface topology. Even self-propelled rubber duckies in a bathtub will show the same trapping near a surface and will concentrate if a funnel wall is built across the tub (data not shown).

Bacteria track along a wall when they collide with a wall, moving along the tangent of velocity projected onto the wall. Thus, taking into account an exponential growth with a rate \( r \), a set of simple equations governs the dynamics of a 1-wall enclosure in terms of the number of bacteria \( N \):
\[ \frac{d N_L}{dt} = (r - c_{RL}) \cdot N_L + c_{RL} \cdot N_R, \] (28)
\[ \frac{dN_R}{dt} = +c_{LR} \cdot N_L + (1 - c_{RL}) \cdot N_R. \]  

Here \( N_L \) and \( N_R \) is the number of bacteria on the left side and right side of the enclosure, \( c_{LR} \) and \( c_{RL} \) is the fraction of the populations crossing from left to right or right to left respectively. With a uniform initial distribution of bacteria on the enclosure the solution to this coupled set of equations can be written as the time-dependent ratio \( A(t) \):

\[ A(t) = \frac{N_L}{N_R} = \frac{c_{RL} - \frac{a}{2} x + \frac{a}{2} x^2 + t}{c_{LR} + \frac{a}{2} x - \frac{a}{2} x^2 - t} \cdot e^{(c_{RL} - c_{LR}) \cdot t}. \]  

It follows that the equilibrium ratio is:

\[ A(t = \infty) = \frac{c_{RL}}{c_{LR}}. \]  

The fluxes of the bacteria \( c_{LR} \) and \( c_{RL} \) are difficult to calculate because of the complexity of the interactions of the bacteria with the walls and the impact of the mean time between tumbles \( \tau \) and the mean swimming speed of the bacteria. If the net distance traveled between tumbles \( \langle d \rangle \) is much less then the opening gap of the funnel the bacteria will always be in equilibrium and there can be no funnel effect. On the other hand, if the bacteria when they hit the funnel wall simply follow along the wall independent of all other parameters the fluxes should scale simply by the ratio of the total opening distance of the funnel to the opening distance of the gap.

Consider an effectively 1D environment with many funnel arrays at positions:

\[ j \in \mathbb{Z}, \quad r_j = \left( j + \frac{1}{2} \right) a. \]  

If the distance between funnels of the very same row are small, then one can approximate that in any region \( R_j \) (between funnel arrays \( j - 1 \) and \( j \)) the bacteria density is uniformly \( b_j \):

\[ R_j = [r_{j-1}, r_j], \quad b_j \approx b(x = ja). \]  

Equilibrium condition results to the recurrence ratio:

\[ \forall j \quad b_j = 0 \Rightarrow b_j = \frac{b_{j+1}}{b_{j+1}} = \frac{c_{RL}}{c_{LR}}. \]  

In the continuum limit, approximations can be applied:

\[ b_j = b(x), \]  

\[ b_{j+1} \approx b(x) + a \partial_x b(x). \]  

Change of variables for notational convenience:

\[ \nu = \frac{c_{RL} - 1}{a}, \quad \partial_x b = \nu b. \]  

The solution is an exponentially increasing bacterial density in the LR direction if \( \nu > 0 \), that is the funnels pump bacteria:

\[ b(x) \sim e^{\nu x}. \]  

### 4.2. Bacteria solitary-like waves through funnel arrays

Finally we address how the solitary waves can defeat the pumping action of the bacteria. The 1D system with funnel arrays in the slow bacteria limit (with similar assumptions as in the previous sections) also has a solitary-like wave solution for the bacterial density:

\[ b_\nu \sim \frac{\kappa D_b}{2D_b D_r} k^2 \text{sech}^2(k(x - vt - x_c)), \]  

\[ c_\nu = \frac{\kappa}{2D_b} \ln \cosh(k(x - vt - x_c)) + \left( \frac{\nu}{\kappa} - \frac{\kappa \nu}{D_b} \right) x + c_0. \]  

Let us look at the behavior of the chemoattractants concentration at infinities:

\[ \nu_\infty = \frac{\kappa^2 \nu}{D_b}, \]
Although not rigorous at the moment, for the demonstration of matching boundary conditions to find the amplitude-speed relation, assume that the propagating solitary waves of interests satisfy:

\[ c(+\infty) \to 0.x \quad \text{or} \quad c(-\infty) \to 0.x. \]  

(46)

The velocity \( v \) dependence on the bacteria solitary wave amplitude \( B \) can then be read-off easily:

\[ B = \max (b) = \frac{\kappa |\beta_0| k^2}{2D_bD_c}, \quad v = v_s \pm \frac{\kappa^2 |k|}{2D_b}. \]  

(47)

(48)

To beat the funnel arrays, one needs a critical solitary wave amplitude \( B_c \):

\[ \nu_c = 0 = v_s - \frac{\kappa^2 |k|}{2D_b} \quad \Rightarrow \quad |k| = 2\nu, \]  

(49)

\[ B_c = \frac{2\kappa |\beta_0|\nu^2}{D_bD_c}. \]  

(50)

Physically speaking, when the difference of bacteria density between the two sides of a funnel array is roughly \( \sim B_c \), the solitary wave can be launched against the funnels. This toy-analysis, although incorrect, still give some ideas for the mechanism behind how the bacteria population wave can beat the funnel arrays. We assume that this is the basis behind the pausing of the bacteria at the wrong-end of the funnels, as the free wave encounters the reverse funnel it builds up a local concentration until the critical solitary wave amplitude is reached.

Finally, we note that the simplest way to modify the Patlak–Keller–Segel equations for bacteria encountering funnels is to add an appropriate parity-violation term:

\[ \partial_t b - D_b \partial_x^2 b + \kappa \partial_x (b \partial_x c) = -D_b \nu \partial_x b. \]  

(51)

The above equation can be rewritten in a more familiar form as:

\[ V(x) = -c(x) - \frac{D_b \nu}{\kappa} x, \]  

(52)

\[ \partial_t b - D_b \partial_x^2 b + \kappa \partial_x (b \partial_x V) = 0. \]  

(53)

This is the Fokker–Planck equation for particles in a spatial potential \( V(x) \). This implies that more complicated topologies than are discussed here can be mapped over to an effective spatial potential surface over which bacterial solitary waves can spread.

5. Discussion

It has been famously said that ‘nothing makes sense in biology except in the light of evolution’ [16], which we interpret to mean that natural selection chooses phenotypes which increase fitness within the ecology in which the organism is embedded. The presence of these solitary-like waves which somehow are able to defeat the physical pumping of the funnels in a dramatic way poses a puzzle: what can it mean, or, rather, how does this increase the fitness of the bacteria in our device.

The most surprising aspect to the experiment is the launching of a collective wave which rapidly circles the device and radiates inwards against the pumping action of the funnel. We assume that there is a reason why the bacteria create this wave over and above the mathematics, which is puzzling because the fresh media is at the periphery, not the center.

A weakness of the analysis is that it is effectively a mean-field analysis in that the motions of the individual bacteria are not known. These motions can be measured by switching to higher microscope objectives and real-time tracking of individual bacteria during a wave passage. Unfortunately, answering these questions will require more microscopic measurements of the detailed dynamics of the bacteria then is possible in this brief paper.

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