

# TWO-DIMENSIONAL CONTINUOUS MODEL FOR BACTERIAL FLOWS THROUGH MICROFLUIDIC CHANNELS

MODELO BIDIMENSIONAL CONTINUO PARA FLUJOS BACTERIANOS EN CANALES MICROFLUÍDICOS

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(Recibido 15/1/2013; Aceptado 15/3/2013)

Dispersion and migration of bacteria under flow in confined structures is related to a large spectrum of practical interests, and lacks a fully satisfactory understanding. We introduce a simple bidimensional continuous model trying to describe the main characteristics of the movement of *E. coli* along a microchannel. Their convective transport, lateral wall absorption/desorption processes and migration along lateral walls are taken into account. The model reproduces the anomalous dispersion of bacteria when passing through a constriction.

Los fenómenos de migración de bacterias en flujos en geometrías confinadas se encuentran involucrados en una gran variedad de aplicaciones prácticas, pero sobre ellas no se ha establecido un entendimiento satisfactorio. Nosotros presentamos un modelo bidimensional simple para describir los rasgos fundamentales del movimiento de bacterias *E. coli* en microcanales. Tenemos en cuenta el transporte convectivo de estas, los procesos de adherencia y desprendimiento de las paredes laterales, así como la migración a lo largo de las mismas. El modelo reproduce la dispersión anómala de las bacterias al atravesar secciones estrechas, observada experimentalmente.

**PACS:** Swimming of bacteria, 47.63.Gd; Biological fluid dynamics, 43.63.-b, 87.85.gf; Convection, 47.55.P-.

## INTRODUCTION

We still lack a basic knowledge on the microscopic mechanisms controlling bacterial transport under flow conditions. A complete understanding of the mechanisms behind bacterial behavior in confined media such as porous or fractured materials would allow to theoretically assess the problems of decontamination or pollution of ground water supplies, biocontamination, contaminations of biological micro-vessels or nosocomial infections through the use of catheters or other medical devices.

Along those lines, the fundamental question of hydrodynamic dispersion of bacteria suspended in a fluid, remains an issue that has not received yet a fully satisfactory treatment, due to the autonomous character of the bacterial motion, and their basically different behavior in open spaces and confined geometries [2-5].

Here we explain some of the characteristic features of the bacterial motion, by means of a bidimensional model that comprises the main features of the movement of *Escherichia coli* along a microchannel. We offer an explanation of recent experimental results obtained by Altshuler *et al.* in

[1] where a bacterial densification past a funnel is found in microflows.

## BACKGROUND

The *E. coli* bacterium is a 2  $\mu\text{m}$  body-length swimmer that has two to six 10  $\mu\text{m}$  length flagella, i.e. long thin helical filaments, each driven at its base by a reversible rotary motor. When rotating synchronized and counterclockwise, flagella form a bundle that propels the cell forward for a while, this is named "a run". During a run, the flagellar rotation is counterbalanced by cell clockwise body rotation [6]. The propulsive force of flagella competes with the drag viscous force, keeping the bacterium moving at an almost constant speed until it "tumbles" [7].

During a tumble, one or more filaments change their rotation direction for a short time, enough to make the bundle fly apart and change the bacterium's swimming direction. Then, flagella resynchronize and another run begins [8]. In this way, bacteria execute random walks, while alternating sequences of runs for long times (around 1 second [7]), and tumbles for relatively short time intervals during bacterium reorientations.

Another remarkable feature of the behavior of these cells is their

interaction with the near walls. When swimming in confined environments, *E. coli* are attracted by surfaces, showing a strong increase of the cell concentration at the boundaries [2][3]. While swimming very close to the boundary surface, the rotating cell body and flagellar filament each experience a net lateral drag force near the glass surface and bacteria describe curved trajectories [4].

Recently, it has been experimentally reported the densification of bacteria concentration in an aqueous solution that passes through a constriction in a microchannel [1]. Bacteria concentrate, -in a counter-intuitive way- once they have crossed the narrower part of the microchannel's cross section (Fig. 1). This concentration enhancement persists over long distances from the double-funnel. The symmetry breaking increases with the flux, up to a threshold value of stream velocity. Then, for larger fluxes this concentration difference decreases to zero, and no longer exists.

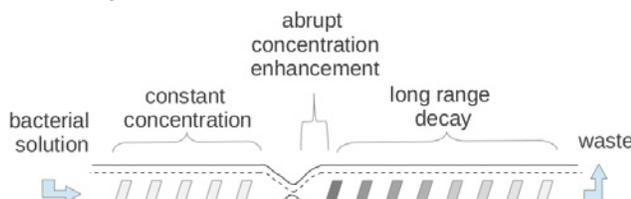


Figure 1. Cartoon representing the phenomenon reported in [1]. Bacteria concentration (represented by gray rectangles) increases when passing the double-funnel, and takes a long distance to return to its previous state.

Along the microchannel, bacteria reach the lateral walls, move parallel to them in a preferentially upstream way, and eventually desorb to the center of the channel. This phenomenon was previously reported in [5]. In [1] the net bacterial flux from the lateral walls was measured along the channel. The profile shows an abrupt positive peak in the funnel section, and a persistent negative value where the concentration enhancement takes place past the funnel, i.e., bacteria desorb to the center in the funnel and mostly attach to the walls past the narrow region. Out of this zone, the lateral adsorption-desorption process equilibrates.

The problem is then mapped onto a one-dimensional advection-diffusion equation taken at steady state, where the absorption-desorption exchange with the lateral walls is taken into account in a sink-source term experimentally measured. The result fits well with the experimental curve of concentration. However, a theoretical approach to this lateral interchange and its further implications is still lacking.

Our model tries to capture the relation between bacteria in the center part of the channel and those swimming along the lateral walls.

## THE MODEL

The cornerstone of the mechanisms producing the concentration profiles observed in *E. coli* is the capacity of

bacteria of swimming near the lateral walls in a mostly counter-stream way. We take into account the convective bacteria movement in the center part of the channel, their attachment to and runs along the lateral walls, and finally their desorption to the central part of the microchannel, where the cycle begins again.

When studying bacteria's dynamics, we shall assume that all bacteria moving in the center part swim next to the microchannel's bottom or top [3] (Fig. 2), and that the ones traveling near the lateral walls swim in a one-dimensional way along them. Their concentrations will be the surface concentration  $n(x)$  for the bacteria of the center part, and the linear concentration  $m(x)$  for the ones swimming near the two lateral walls together. Their velocity in the quiet liquid will be  $v$ , and we shall denote  $V(x)$  the mean fluid velocity in the thin stripes where bacteria move next to the top and bottom of the microchannel. The microfluidic device itself is  $2y(x)$  wide, and its depth is  $H = \text{const}$ .

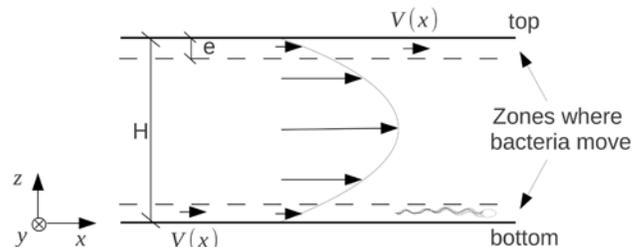


Figure 2. Cartoon representing a lateral view of the microchannel. Bacteria concentrate in thin gaps of depth  $e$  next to the top and bottom of the microchannel. The mean fluid velocity in these narrow regions -not in the whole channel- is  $V(x)$ .

Since we are considering bidimensional bacterial movements, our velocity  $V(x)$  can be taken as the average in stripes of thickness  $e$  next to the bottom and top boundaries, where bacteria are supposed to swim preferentially. Here  $e$  is the mean diameter of a bacterium's body. Considering that along the  $z$  direction the velocity has a parabolic profile, and that a flux  $Q$  is being injected, we can say that

$$V(x) = \frac{Qe(3H - 2e)}{2y(x)H^3}. \quad (1)$$

The problem of diffusion of particles in a liquid that flows can be described through an advection-diffusion equation. Since our channel is narrow and shallow, we will only consider diffusion along the microchannels' axial direction, i.e., the  $x$  axis. Bacteria arriving to the lateral walls, which abandon the main stream, will be counted as a sink term, and those that desorb from the wall and enter the central part will be considered in a source term.

To count the number of bacteria arriving to the lateral walls per unit time and length, let us suppose that in absence of flux the four directions are equiprobable. In this way, half the total of bacteria swim transversal to the fluid direction, and so the bacteria flux abandoning the central part will be  $\frac{vm(x)}{2}$ . For bacteria that swim along the lateral walls, the desorption flux will be  $P_{dm}(x)m(x)$ , where  $P_{dm}(x)$  is the probability per unit

time for a lateral bacterium to abandon the surface.

Let us write the equation for the concentration of bacteria that swim in the center part of the microchannel, at the steady state. A more detailed deduction of it, derived from the equation of conservation of the chemical species, is shown in the Appendix.

$$-D \frac{d^2 n(x)}{dx^2} + \frac{d}{dx} [V(x)n(x)] = -\frac{vn(x)}{4y(x)} + \frac{P_{dm}(x)m(x)}{2y(x)}. \quad (2)$$

This is an equation for the conservation of the number of bacteria. The first term in the left takes account for the diffusion, and the second one is the responsible for the bacteria transport due to the liquid motion.

A typical bacterium in a fluid at rest swims in a given direction or in a smooth curve for a time  $\tau_{run}$ , then tumbles and redefines sharply its direction in a short time, and then swims again for approximately the same time of run. This cannot be said for a bacterium swimming along the edge where two perpendicular walls intersect. In that case, not every tumble is able to change the bacterium's trajectory, but only the "effective" tumbles do. Since experiments suggest that there is an hydrodynamic force attracting bacteria to the edge in this situation, we propose that there exists a characteristic time for its spontaneous desorption  $\tau_{wall}$ , that is larger than  $\tau_{run}$ . Their ratio  $\tau_{run}/\tau_{wall}$  will be the probability  $p_e$  for a given tumble to be able to separate the bacterium from the wall. In this way, the probability for a given bacterium to spontaneously abandon the lateral wall in the interval  $dt$  is

$$\frac{dt}{\tau_{wall}} = p_e \frac{dt}{\tau_{run}} \quad p_e \leq 1. \quad (3)$$

The dimensionless number  $\tau_{run}/\tau_{wall}$  will be the first free parameter in our model.

In our system, bacteria can also be extracted by the effect of the shear stress of the fluid stream, which varies with the position along the microchannel. Let us suppose that lateral bacteria abandon the walls due to effective tumbles or due to the effect of the stream, and that these two mechanisms are independent and do not occur at the same time. Assuming that the probability for a bacterium to be extracted by the flow is proportional to the fluid velocity at the given position, the probability per unit time of a bacterium swimming along the lateral wall to be desorbed into the mainstream, will be

$$P_{dm}(x) = \frac{p_e}{\tau_{run}} + \frac{V(x)}{l_c}, \quad (4)$$

where  $l_c$  is a characteristic length to be determined –the second free parameter of our model.

Until now, we have only considered the dependence of the fluid velocity with the coordinate  $x$ , and not its dependence with the transversal coordinate  $y$ . We have said that the fluid velocity  $V(x)$  is 0 just by the lateral walls, and constant for every other position in  $y$  for all coordinates along the microchannel. Even when this is a good approximation near the center of the

channel, it cannot be said for the velocity near the lateral walls, where the fluid velocity takes continuous values between 0 and  $V(x)$  within a short length in the  $y$  direction. This velocity gradient in the  $y$  direction extends for lengths comparable with bacterial sizes. This, in addition to the effects of bacterial rotation, causes their deviation when crossing through those regions. The bacteria that go from the center to the lateral walls seem to "flip" and swim against the stream along the lateral walls, unless they enter the gradient region with less than a certain angle  $\gamma$  ( $\gamma \leq \pi/2$ ), pointing to the stream direction. Then, the fraction of lateral bacteria that swim in the direction of the fluid will be  $\gamma/\pi$ , and the rest  $(\pi - \gamma)/\pi$  will swim backwards. This parameter  $\gamma$  depends on  $v$  and  $V(x)$ , but we will consider it as a constant in the first approximation. So the minimal absorption angle,  $\gamma' = \gamma/\pi$ , will be the third free parameter of our model.

Besides the main flux transporting bacteria along the microchannel, next to the lateral walls there exists a current of bacteria going to the direction of the fluid, and another current that swims counter-stream. If we assume that the velocity of the main stream does not affect the bacteria velocities in any direction, we can write two different equations for the concentrations of bacteria that move forward ( $m_f$ ) and backwards ( $m_b$ ), both take the form of advection equations with velocities in opposite directions with the same magnitude  $v$ . In the stationary state:

$$v \frac{dm_f(x)}{dx} = \gamma' \frac{vn(x)}{2} - P_{dm} m_f(x) \quad (5)$$

$$-v \frac{dm_b(x)}{dx} = [1 - \gamma'] \frac{vn(x)}{2} - P_{dm} m_b(x). \quad (6)$$

To write the equation for bacteria moving forwards, we have assumed that a fraction  $\gamma'$  of all the arriving bacteria incorporate to the  $m_f$  current. The other  $(1 - \gamma')$  are supposed to increase the backwards concentration  $m_b$  in the source term in equation (6). The desorption probability per unit time for the two species  $m_f$  and  $m_b$  are taken as identical, since recent unpublished experimental data does not show an important difference.

We will assume that the concentration of bacteria moving forwards next to the lateral walls represents a fraction  $\gamma'$  of the total lateral concentration ( $m$ ). Thus, equations (5) and (6) result in

$$-v[1 - 2\gamma'] \frac{dm(x)}{dx} = \frac{vn(x)}{2} - P_{dm} m(x). \quad (7)$$

So far, we have found the system of coupled differential equations (2) and (7). For the values  $V(x) = 3.5 \mu\text{m/s}$  and  $D = 130 \mu\text{m}^2/\text{s}$  reported in [1], and considering that a typical length in which the concentration varies significantly is approximately 2.5 mm, we can calculate the Peclet number, defined as  $Pe = \frac{V(x)l_c}{D}$ . This gives the ratio between advection and diffusion, and for the given values,  $Pe \approx 80 \gg 1$ . Consequently, we can neglect the diffusion term in (2) and then write:

$$\frac{dm(x)}{dx} = \frac{2P_{dm}(x)m(x) - vn(x)}{2v[1 - 2\gamma']} \quad (8)$$

$$\frac{dn(x)}{dx} = \frac{P_{dm}(x)m(x)}{2V(x)y(x)} - \left( \frac{v}{4V(x)y(x)} + \frac{1}{V(x)} \frac{dV(x)}{dx} \right) n(x), \quad (9)$$

or in matrix form:

$$\begin{pmatrix} m'(x) \\ n'(x) \end{pmatrix} = \begin{pmatrix} a(x) & -b \\ c(x) & -d(x) \end{pmatrix} \begin{pmatrix} m(x) \\ n(x) \end{pmatrix}, \quad (10)$$

where

$$a(x) = \frac{P_{dm}(x)}{v[1-2\gamma']} \quad b = \frac{1}{2[1-2\gamma']} \quad (11)$$

$$c(x) = \frac{P_{dm}(x)}{2V(x)y(x)} \quad (12)$$

$$d(x) = \frac{v}{4V(x)y(x)} + \frac{1}{V(x)} \frac{dV(x)}{dx}. \quad (13)$$

Very far from boundaries and inhomogeneities of the microchannel, in a straight section, the dependence of the coefficients  $a$ ,  $c$  and  $d$  on the coordinate  $x$  will vanish. In those equilibrium positions  $x_e$ , the spatial derivatives are  $m'(x_e) = n'(x_e) = 0$ , and the concentrations are related according to

$$m_e = \frac{v}{2P_{dm}(x_e)} n_e, \quad (14)$$

where  $m_e = m(x_e)$  and  $n_e = n(x_e)$ .

Let us analyze the central matrix in equation (10) in these conditions, i.e., the Jacobian matrix of the system. Its determinant is  $\Delta = 0$ , which means that there are no isolated fixed points in our system, i.e., infinite values of  $n(x_e)$  are possible and all of them will give its respective values of  $m(x_e)$  according to equation (14). The equilibrium concentrations for a given experiment will depend on the boundary conditions on the microchannels' ends. This relation between the linear and surface density makes sense while the concentrations are not large enough for the inter-bacterial interactions to be relevant.

If the trace  $T_r$  of the matrix is negative, the fixed points will be stable, otherwise, the concentrations will grow without limits. Of course, the unlimited growth does not have a physical meaning, since the physical space has a limited capacity, and for high concentrations bacteria sizes must be taken into account. The condition of a negative trace becomes then:

$$P_{dm}(x_e) < \frac{v^2[1-2\gamma']}{4V(x)y(x)}. \quad (15)$$

When condition (15) is satisfied, any deviation from the equilibrium concentrations  $m_e$  and  $n_e$  is reduced to zero. In the opposite case, the model is no longer valid.

## RESULTS

*Bacteria conservation: net upstream motion?* In the stationary state, neither accumulation nor depopulation of bacteria occurs in any part of the microchannel. The net bacteria current through the cross-section must be constant for

every position  $x$  along it. If this were not true, concentrations would change in time and we were not in presence of a true stationary state.

We shall define  $I$  as the net bacteria current in the longitudinal direction of the microchannel,

$$I = -2y(x)D \frac{dn(x)}{dx} + 2V(x)y(x)n(x) - [1-2\gamma']vm(x). \quad (16)$$

This is also true in the straight and far equilibrium regions, where the spatial derivatives  $m'(x_e) = n'(x_e) = 0$ ,  $\frac{dV(x)}{dx} = 0$  and relation (14) holds. In those points

$$I = \frac{2V(x)y(x)n_e}{P_{dm}(x_e)} \left( P_{dm}(x_e) - \frac{[1-2\gamma']v^2}{4V(x)y(x)} \right). \quad (17)$$

In this equation, parenthesis in the right hand side is negative in the range of parameters where the fixed points are stable and relation (15) holds. This means that the net bacteria current is negative, i.e., it is opposite to the direction of the fluid velocity. In other words: the number of bacteria per unit time traveling along the lateral walls is bigger than that corresponding to bacteria swimming far from the lateral walls, in the direction of the liquid flow.

It can be seen from equation (17) that if  $y$  is decreased at a constant fluid velocity,  $I$  will become more negative, since a larger percent of bacteria will reach the lateral walls and then will travel backwards. In the same way, a wider microchannel will allow a larger number of bacteria to move a longer time with the main stream, without attaching to the lateral walls. For very large  $y$ , the influence of the lateral walls will vanish, and bacteria will move with a drift velocity equal to the fluid velocity.

It is worth saying that the case  $I < 0$  cannot be trivially expected in an actual microfluidic cell. Notice that this channel is shallow, but not strictly 2D: unavoidably, there is always a fraction of bacteria describing three-dimensional trajectories.

*Comparison with experiments.* To compare the model with the experimental data reported in [1], we have numerically solved equations (8) and (9) in a microchannel with a funnel-like constriction in its middle, similar to the one in [1] (Fig. 3). Its left lateral wall is given by the equation

$$y(x) = \begin{cases} 100 & \text{if } x < -100 \\ 60 - 40 \cos\left(\frac{x\pi}{100}\right) & \text{if } -100 \leq x \leq 100. \\ 100 & \text{if } x > 100 \end{cases} \quad (18)$$

The right wall is symmetric to the left one, and the channel is  $H = 18 \mu\text{m}$  deep.

The experimental data reported in [1] is a curve for the bulk bacteria concentration along the longitudinal axis of the microchannel, for a given fluid velocity. We shall assume that instead of a bulk distribution there is a 2D distribution located

at the top and bottom surfaces, that we match to  $n(x)$ .

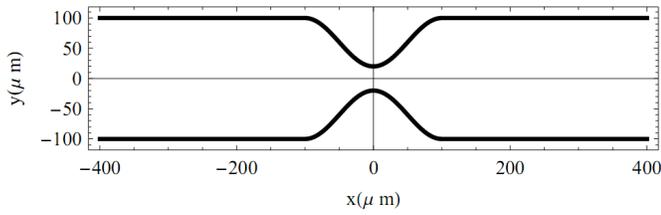


Figure 3: Top view of the modeled microchannel.

This experimental data was superposed to the numerical solution of our two-dimensional model in Fig. 4. The left boundary condition we chose (corresponding to the suspension inlet in the experiment) was a constant concentration similar to the experimental one ( $n$ ). In the right part of the microchannel we did not assume any particular boundary condition, as if the microchannel was long enough for the right outlet not to influence the dynamics.

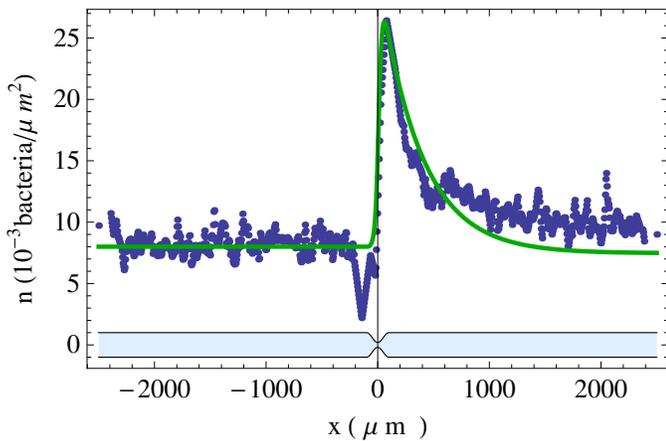


Figure 4. Superposition of the numerical solution of the differential equations (8) and (9) (continuous line), with the experimental concentration far from lateral walls (points). The used parameters were  $Q = 80000 \mu\text{m}^3/\text{s}$ ;  $H = 18 \mu\text{m}$ ;  $v = 20 \mu\text{m}/\text{s}$ ;  $e = 1 \mu\text{m}$ ;  $p_e = 1/13$ ;  $l_c = 63 \mu\text{m}$  and  $\gamma' = 0.2$ . The equations were solved using, as boundary conditions in the left end, the measured equilibrium concentration for  $n_e$  and the value  $m_e$  calculated according to (14).

The used parameter  $Q$  guarantees a fluid velocity, in the narrow stripes where bacteria swim next to the bottom and top of the microchannel, similar to the bacteria's advection velocity in [1]. The value of the parameter  $\gamma'$  was estimated from recent non-published experiments. Our two free parameters,  $p_e$  and  $l_c$  were chosen to fit the experimental curve.

The experimental result shows a constant concentration in the left straight part of the microchannel (Fig. 4). Then an abrupt increase of bacteria concentration takes place in the narrow zone, and a slow return to the equilibrium takes place to its right. We stress the fact that this return to the equilibrium is "faster" than experiment, but still long-ranged (it takes over 1 mm to stabilize). Notice the existence of a negative peak in the experimental concentration just before the constriction. This decrease is not reproduced by our model, probably because of the lack of the diffusive term.

We have also calculated  $n(x)$  for different velocities of the suspension (Fig. 5). Within the flux range under study, the difference in concentrations between left and right of the funnel increases with  $Q$ , in agreement with the experimental results reported in [1].

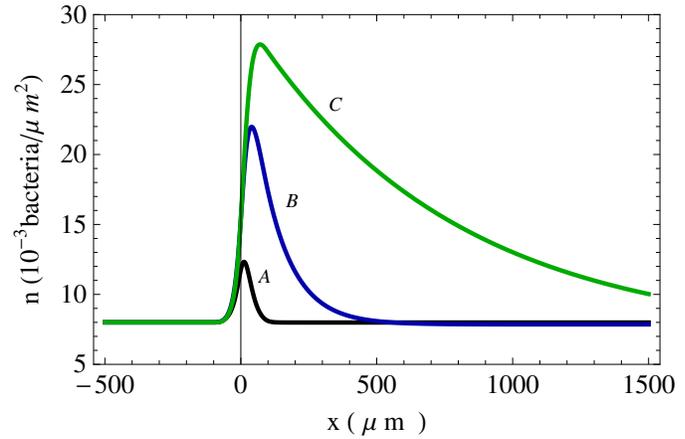


Figure 5. Results of the model using the same parameters  $H$ ;  $v$ ;  $e$ ;  $p_e$  and  $l_c$  of Figure 4, but at different fluxes. For the three different curves: A ( $Q = 10^4 \mu\text{m}^3/\text{s}$ ,  $\gamma' = 0.45$ ), B ( $Q = 5 \times 10^4 \mu\text{m}^3/\text{s}$ ,  $\gamma' = 0.29$ ) and C ( $Q = 5 \times 10^4 \mu\text{m}^3/\text{s}$ ,  $\gamma' = 0.18$ ). The symmetry breaking increases with the flux  $Q$ .

When the velocity of the fluid is increased so that relation (15) is violated, the model is no longer valid. We expect in real experiments a concentration saturation when the lateral walls reach their "maximal capacity". Our theoretical model does not contain this restriction yet, but we are looking forward to improving it.

## CONCLUSIONS

We have modeled the steady state flow of a bacterial suspension along a 2D microfluidic channel with a constriction, where the concentration of bacteria is kept constant at the left end of the channel. Bacteria can be absorbed by or desorbed from the lateral walls.

The model contains three "free" parameters:  $p_e$ ,  $l_c$  and  $\gamma'$ , and it successfully reproduces the main qualitative experimental features of the bacteria concentration in a microchannel with a double-funnel constriction, like the concentration enhancement past the constriction, and the increase of the symmetry breaking when the flux is increased at low fluxes. At higher fluxes, the model is not valid.

The model also predicts that the net flow of bacteria along the channel (i.e., including flows far and near the lateral walls) can be negative -i.e. against the imposed suspension flow. Experimentally, we believe that this may be observed in quasi-2D channels, for very low fluid velocities.

## ACKNOWLEDGEMENTS

E. A. thanks ESPCI for Joliot-Curie and total invited chairs. We acknowledge scientific support by Roberto Mulet.

APPENDIX: DERIVATION OF THE EQUATION FOR BACTERIA TRANSPORT IN THE CENTER OF THE CHANNEL

Let us start from the equation of continuity for a mixture [9]:

$$\frac{dn(x, y)}{dt} + (\vec{V}(x, y) \cdot \nabla) n(x, y) = D \nabla^2 n(x, y) + S(x, y) \quad (19)$$

The term  $S(x, y)$  is the *sink/source* term, taking into account the bacteria absorbing to, and desorbing from the lateral walls. In the steady state, the temporal derivative vanishes.

For the advective term we have:

$$(\vec{V}(x, y) \cdot \nabla) n(x, y) = V_x \frac{\partial n(x, y)}{\partial x} + V_y \frac{\partial n(x, y)}{\partial y}. \quad (20)$$

If we take the mean over the width of the channel, using the condition of no-slip in the lateral walls, we have, for the second term of the right hand side of equation (20)

$$\begin{aligned} \frac{1}{2y(x)} \int_{-y(x)}^{y(x)} V_y(x, y') \frac{\partial n(x, y')}{\partial y} dy' = \\ - \frac{1}{2y(x)} \int_{-y(x)}^{y(x)} \frac{\partial V_y(x, y')}{\partial y} n(x, y') dy'. \end{aligned} \quad (21)$$

From the incompressibility of the liquid, we have

$$\nabla \cdot \vec{V} = \frac{\partial V_x}{\partial x} + \frac{\partial V_y}{\partial y} = 0 \quad \text{and} \quad \frac{\partial V_x}{\partial x} = - \frac{\partial V_y}{\partial y}, \quad (22)$$

then, equation (21) becomes

$$\left\langle V_y(x, y) \frac{\partial n(x, y)}{\partial y} \right\rangle_y = \left\langle \frac{\partial V_x(x, y)}{\partial x} n(x, y) \right\rangle_y, \quad (23)$$

where  $\langle \dots \rangle_y$  stands for the mean in the  $y$  direction.

After the mean over the width of the microchannel, in the steady state, equation (19) becomes

$$\begin{aligned} - \left\langle D \frac{\partial^2 n(x, y)}{\partial x^2} \right\rangle_y + \left\langle V_x(x, y) \frac{\partial n(x, y)}{\partial x} \right\rangle_y + \\ + \left\langle \frac{\partial V_x(x, y)}{\partial x} n(x, y) \right\rangle_y = \langle S(x, y) \rangle_y. \end{aligned} \quad (24)$$

where we have put the term of the second derivative in  $y$  into the *sink/source* term.

We will approximate the mean of the product  $\left\langle V_x(x, y) \frac{\partial n(x, y)}{\partial x} \right\rangle_y$  by the product of means  $\langle V_x(x, y) \rangle_y \left\langle \frac{\partial n(x, y)}{\partial x} \right\rangle_y$ , using as an argument, the uniformity in the velocity profile along the  $y$  direction, since our microchannel is 10 times wider than deep.

The last term in the left hand side of equation (24) vanishes in the straight parts of microchannels. In the zone of the constriction of the microchannel of [1], where this term is non-zero, the bacteria concentration  $n(x, y)$  is almost constant along the  $y$  direction, *i.e.* independent of  $y$ . Then, we will approximate  $\left\langle \frac{\partial V_x(x, y)}{\partial x} n(x, y) \right\rangle_y$  by the product  $\left\langle \frac{\partial V_x(x, y)}{\partial x} \right\rangle_y \langle n(x, y) \rangle_y$ .

Now, we identify the mean of the component of the fluid velocity  $\langle V_x(x, y) \rangle_y = V(x)$ , expressed in equation (1). In this way, we obtain after the suppression of  $y$  in the notation:

$$-D \frac{d^2 n(x)}{dx^2} + \frac{d}{dx} [V(x)n(x)] = S(x). \quad (25)$$

The mean over the width of the channel of the *sink/source* term ( $S(x)$ ) is modeled then in equation (2).

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- [1] E. Altshuler, G. Miño, C. Pérez-Penichet, L. del Río, A. Lindner, A. Rousselet and E. Clément, *Soft Matter* **9**, 1864 (2013).
  - [2] J. P. Hernandez-Ortiz, C. G. Stoltz and M. D. Graham, *Phys. Rev. Lett.* **95**, 204501 (2005).
  - [3] A. P. Berke, L. Turner, H. C. Berg and E. Lauga, *Phys. Rev. Lett.* **101**, 038102 (2008).
  - [4] P. D. Frymier, R. M. Ford, H. C. Berg and P. T. Cummings, *Proc. Natl. Acad. Sci. USA* **92**, 6195 (1995).
  - [5] J. Hill, O. Kalkanci, J. L. McMurry and H. Koser, *Phys. Rev. Lett.* **98**, 068101 (2007).
  - [6] H. C. Berg, *Phys. Today* **53**, 24 (2000).
  - [7] H. C. Berg, *E. coli in Motion* (Springer, New York, 2004).
  - [8] N. C. Darnton, L. Turner, S. Rojevsky and H. C. Berg, *Journal of Bacteriology* **189**, 1756 (2007).
  - [9] R. B. Bird, W. E. Stuart and E. N. Lightfoot, *Transport Phenomena* (John Wiley and Sons, Inc, 2002).