One notable feature of bacterial motion is their ability to swim upstream along corners and crevices, by leveraging hydrodynamic interactions. This motion through anatomic ducts or medical devices might be at the origin of serious infections. However, it remains unclear how bacteria can maintain persistent upstream motion while exhibiting run-and-tumble dynamics. Here, we demonstrate that *Escherichia coli* can travel upstream in microfluidic devices over distances of 15 mm in times as short as 15 min. Using a stochastic model relating the run times to the time that bacteria spend on surfaces, we quantitatively reproduce the evolution of the contamination profiles when considering a broad distribution of run times. The experimental data cannot be reproduced using the usually accepted exponential distribution of run times. Our study demonstrates that the run-and-tumble statistics determine macroscopic bacterial transport properties. This effect, which we name “super-contamination,” could explain the fast onset of some life-threatening medical emergencies.

**RESULTS**

**Experiments**

The experimental setup, as sketched in Fig. 1A, consists of a few-millimeter-long polydimethylsiloxane (PDMS) rectangular channel of width $w = 40 \mu m$, height $h = 11 \mu m$, and length $L = 15 \mm$, glued
A microfluidic device is used to demonstrate bacterial movement. The device contains cylindrical reservoirs of 1-mm diameter, connected to tubing that allows fluids to circulate using a gravity flow.

At the beginning of the experiment, the outlet reservoir is filled with *E. coli* bacteria (strain RP437 expressing green fluorescent protein). For every experiment, the average bacterial velocity in the reservoir $V_{fr}$ is measured by injecting a sufficiently high flow rate of the fluid without bacteria through the inlet, bacteria are kept in the outlet reservoir, not yet invading the channel. See Materials and Methods for details on the procedure. Then, at $t = 0$, a controlled flow of the bacteria-free liquid is established from the inlet to the outlet, and the system is video recorded. Bacteria start swimming upstream along the channel. The flow rate in the channel is determined by tracking passive latex beads suspended in the perfusion fluid. The maximum flow velocity measured in the center of the channel is represented as $V_{f}(0 \leq V_{f} \leq 80 \mu m/s)$. Since our experimental conditions avoid the presence of chemical gradients, our experiment is different from those of (26) and (27).

To visualize individual bacteria over the macroscopic extent of the channel, which is several millimeters long starting from the outlet reservoir, we translate the channel at a constant velocity $V_{x} = 150 \mu m/s$ along the $-x$ direction, while a video is taken through an inverted microscope fixed on the laboratory reference frame (Fig. 1A). The channel is scanned several times during a single experiment at a fixed flow rate. Movie S1 shows a sequence of three scans starting at different times during the same experiment.

Figure 1 (B to D) shows a combination of images taken during scans starting at different time points. The total time interval associated with one image spans from the beginning of the scan to the moment of visualization of the farthest bacteria from the reservoir, which we call “pioneers.” There, we visualize all the bacteria along the channel length, independently of their vertical position. The multiple side-by-side images in Fig. 1 (C and D) are actually end-to-end in the physical system. Note that this channel reconstruction does not constitute a snapshot, since different segments display the conditions at different instants. However, the pictures demonstrate the arrival of bacteria as far as 13 mm from the bacterial reservoir in 13.5 min. This constitutes direct evidence for the ability of bacteria to swim upstream over macroscopic distances in a short time interval.

In Fig. 2A, we display details of the trajectories of some bacteria near the outlet (the bacterial reservoir). Figure 2B is a zoom illustrating how the flow (approximately five at the center of the channel) induces the bacteria to concentrate near the entrance of the channel. This is associated with bacteria attaching and detaching from the walls of the reservoir and moving progressively toward the channel, a phenomenon previously reported using a funnel geometry (14). This densification at the outlet creates favorable conditions to prime an efficient contamination process in the channel, as it will induce higher chances for the bacteria to get inside the microchannel via upstream swimming close to surfaces but mostly along the channel edges. This last phenomenon is illustrated by the vertical trajectories in the picture. The red arrows indicate a typical contaminating trajectory: After swimming upstream along the left wall of the channel, the bacterium is detached from it, and then, it is advected downstream and reattaches to the right wall of the channel, continuing its upstream motion. After many events like this, our persistent swimmer eventually reaches the opposite extreme of the channel. That event is illustrated in Fig. 2C, where the bacterial trajectory is pointed out by red arrows, while the orange arrows...
remain the same or if there is a group of pioneers alternating the possible to detect whether the pioneering bacteria hence identified

\[ b \text{, as a function of the flow rate.} \]

At zero flow, the velocity is highest, as expected. However, although we have large data scattering for the finite flow range explored, we cannot see any systematic variation with \( V_f \). We think that it may be related to the large variation of bacterial velocities between experiments.

In the experiment where \( V_f = 65 \mu \text{m/s} \) (average shear rate, 11.0 s\(^{-1}\)) bacteria advance upstream at the large velocity \( V_{\text{cont}} = 39 \mu \text{m/s} \) (2.3 mm/min). In the case \( V_f = 80 \mu \text{m/s} \) (nearly four times the average bacterial velocity; average shear rate, 13.6 s\(^{-1}\)), the pioneer bacterial front advances at nearly \( V_{\text{cont}} = 15 \mu \text{m/s} \) (0.9 mm/min).

It is worth noting that the advance of the pioneer contaminants should ultimately depend on the dispersion of the velocity distribution of the bacteria. The pioneers are likely to be the fastest and more persistent among the population, whereas the upstream contamination is a phenomenon involving the whole bacterial population.

To gain insight into the phenomenon, we analyze the concentration profiles that can be reconstructed from scans (see Materials and Methods for details). Figure 4 (A and B) illustrates these profiles for two different experimental conditions.

**Modeling upstream super-contamination**

Now, we analyze the microscopic mechanisms responsible for the upstream super-contamination. At low flow, the process takes place due to the upstream swimming of bacteria along edges and surfaces and only along the edges for higher fluid velocities (16). When bacteria leave the wall interceptions or the surfaces, they are transported downstream. These advected bacteria eventually reattach on the surfaces and again start their upstream migration as in Fig. 2 (13, 14, 16). This upstream-downstream dynamics is shown in movie S2 and Fig. 5A, which displays the trajectories of some bacteria taken from the video.

We propose to model the upstream transport process using a simple one-dimensional (1D) biased random walk. A given bacterium performs an upstream displacement \( l \), until it detaches from the wall. Then, it will be transported downstream a fixed distance \( d \), until it reattaches to the surface, starting its upstream swimming again. Figure 5B shows a diagram synthesizing these ideas. Our key hypothesis is that the passage from upstream to downstream motion is controlled by the occurrence of tumbling events, where bacteria cease swimming and debundle their flagella. Since the attraction at surfaces and borders is a generic result of hydrodynamic interactions between pusher-swimmers and solid boundaries (8), it is not present when bacteria stop swimming. Therefore, a tumbling bacterium would likely lose the attraction forces to the surface and then be carried downstream by the flow. Under flow, the detachment probability was found to increase leading to a shear-mediated erosion as observed in (16). However, the characteristic shear rates for erosion from surfaces and edges are rather high (140 and 250 s\(^{-1}\), respectively) (16). It is then reasonable to consider that at the low shear rates of our experiments, desorption is essentially caused by tumbling events. In this picture, the distance \( l \) is a random variable; hence, the contamination process should depend critically on the detailed statistics of the run-and-tumble events.

In the pioneering work of Korobkova et al. (18), the motor switching statistics were measured for individual bacteria. The duration of the counterclockwise state of the motors (which is related to the run mode of bacteria) was found to be widely distributed, as opposed to a simple exponential process often put forward to describe bacterial motility (17). To decipher the role of the run-time distribution on the contamination process, we present in our analysis two parallel approaches, one using a broad distribution illustrated by a power law \( \Psi_{PL} \), from the single flagellum statistics (18), and a
second using an exponential distribution $\psi(t)$ of run times (17). To model the broad distribution, we use the probability distribution of run times $\psi(t) = \gamma/[\gamma t_0 (1 + t/t_0)^{\gamma - 1}]$, with $t_{\text{run}} = t_0 (\gamma - 1)$. The parameters used are $t_0 = 1$ s and $\gamma = 1.2$ ($\tau_{\text{run}} = 5$ s) corresponding to the measurements performed on individual flagellar rotations (18). The corresponding distribution in the exponential case is $\psi(t) = \gamma e^{-\gamma t}$, with $\tau_{\text{run}} = 1$ s, a classical value describing the run-and-tumble process for wild-type $E.\ coli$. To render the efficiency of the tumble process to produce desorption, it is possible to define a parameter $p_e$ equal to the probability of a tumble to be effective, i.e., to remove the bacteria from the surface. This would lead to $\langle l \rangle = V_b \tau_{\text{run}}/p_e$.

We now define a dimensionless parameter quantifying the contamination, $\alpha = d\langle l \rangle/p_e d/(V_b \tau_{\text{run}})$. When $\alpha \ll 1$, the persistent upstream motion dominates and upstream contamination takes place. On the other hand, when $\alpha \sim 1$, the contamination will be slow since bacteria will be transported downstream almost as much as they can swim upstream between successive detachments. For $\alpha > 1$, no contamination occurs.

It should be underlined that for times larger than $\tau_{\text{run}}$, running a simulation with some values of $d$ and $p_e$ is equivalent to considering that all tumble events are effective (i.e., $p_e = 1$) but the downstream traveled distance would then be reduced to the value $p_e d$. Therefore, for simplicity, in the simulations, we use $p_e = 1$, and the stochastic biased random walk model is only controlled by a single dimensionless parameter $\alpha$. The average run time $\tau_{\text{run}}$ and the bacteria velocity $V_b$ fix the time and length units when comparing simulations and experiments. Other parameters can be absorbed into $\alpha$. (Note that although all the physical magnitudes and expressions have been defined in the text, table S1 shows a compilation of the definitions used).

The distribution of $d$ is difficult to evaluate quantitatively because, for many bacteria, most subsequent detachment or reattachment events do not lie within the visualization window. However, for the flow of Fig. 5A, we could identify some events and evaluate $d$ to be of the order of tens of micrometers. Once the value of $\tau_{\text{run}}$ is chosen from the first moment of the chosen run-time distribution, the experiment can be fitted by two free parameters: $V_b$ and $\alpha$.

We simulate the trajectories of individual bacteria undergoing upstream and downstream flow transport, according to the hypotheses of the model. Detachments from the walls are obtained via a Monte Carlo dynamics following different statistics for the run times. To illustrate the strong qualitative differences between the contamination processes for the classical exponential process and the power-law distribution, we present in Fig. 5 (C and D) simulated contamination curves. To produce those plots, many bacterial trajectories were generated using a constant flow rate boundary condition at the outlet,
i.e., bacteria entering in the channel at a constant rate. From the accumulation of all the tracks, one determines the simulated spatial concentration profiles at different instants. In these curves, we normalized the time scale by the mean run time $\tau_{\text{run}}$ and the spatial scale by $V_b \tau_{\text{run}}$. The results can now be compared, which turns out to be different for the two distributions. In the exponential case (Fig. 5C), one observes steep fronts moving upstream. In the power-law case (Fig. 5D), the concentration profiles have very long tails composed of a few very persistent upstream swimmers.

To perform a full comparison with the previous set of experiments, another crucial feature must be taken into account. Notably, the bacteria concentration displays a steady increase in the reservoir [see Fig. 4 (A and B) and the snapshots of Fig. 4C for the set of scans reported in Fig. 4B]. Bacteria come swimming upstream through the outlet tube, where the dimensions are big compared to the microfluidic channel. Once in the outlet reservoir, only a small fraction of bacteria swim upstream in the thin microchannel, and the concentration in the reservoir builds up. This effect imposes nonsteady boundary conditions at the outlet, which should be explicitly taken into account in the quantitative evaluation of the model. To address this issue, we count the total number of bacteria inside the channel for every scan $N_b(t)$ (shown in the plot of Fig. 4C). The flux of bacteria into the channel is simply $dN_b/dt$, which is fitted by a quadratic function and used as a nonsteady boundary condition in the simulations.

For every run of the simulations, using parameters $(V_b, \alpha)$, we define a quality factor $F(V_b, \alpha)$. $F(V_b, \alpha)$ is computed as the mean squared difference between the experimental and the simulation profiles, considering all the available concentration curves at different times. The details are in the Supplementary Materials. To find the optimal parameters for a given experiment, we generate a set of numerical curves in the $(V_b, \alpha)$ space. The optimal parameters yield the minimal value of $F$. To compare the relevance of the two different models of run-time distribution, $\psi_{\text{run}}$ and $\psi_{\text{run}}$, one needs to compare their respective quality factor plots $F_{\text{P}}(V_b, \alpha)$ and $F_{\text{E}}(V_b, \alpha)$.

In Fig. 4 (A and B), we display two contamination profiles obtained for bacteria of similar activity (mean velocity in the reservoir $V_b = 22 \mu m/s$) but for two different flow rates. The simulations Fig. 4A correspond to an upstream bacterial velocity chosen to match the velocity measured in the reservoir ($V_b = V_{br} = 22 \mu m/s$). The free parameter $\alpha = 0.5$ provides the best fit. Qualitatively, the agreement is very good, as it simultaneously fits the concentrations at different times. In Fig. 4B, we show the simulations using the optimal pair of parameters $V_b = 19.5 \mu m/s$ and $\alpha = 0.5$, with a very good agreement between experiment and simulation. In both cases (Fig. 4, A and B), the optimal values of upstream velocity are very close to the bacterial velocity measured in the reservoir. We show details of the optimization maps in the Supplementary Materials, for both the power law and the exponential model. In all experiments, the exponential distribution of run times $\psi(E)$ fails to reproduce the spatiotemporal profiles.

For consistency, we now question the results of the contamination process in absence of flow. The contamination profiles remains essentially localized near the outlet (see Fig. 6). The observed stationary profile stems from the balance between the invasion from the outlet and the decay of bacteria in the channel by diffusion and drift.
reservoir and the probability to leave the channel after a while by one of the two opposite reservoirs. As soon as the flow is turned on, the situation changes markedly: Bacteria reorient toward the upstream inlet, leading to the super-contamination process. At zero flow, the first moment of the distribution characterizes a typical penetration length over a distance $\Lambda \approx 5 \text{ mm}$ after few minutes (Fig. 6, inset). We simulated a 1D random walk with a probability to change the swimming directions simply triggered by the broad distribution $\psi_{\text{P}}(t)$. For a constant contamination flux of bacteria at the outlet, using a swimming velocity $V_b = 20 \text{ mm/s}$ and a channel of dimension $L = 15 \text{ mm}$, we obtain a distribution reaching a stationary profile, once again, in quantitative agreement with the experimental measurements (see Fig. 6).

**DISCUSSION**

We showed in a simple microfluidic experiment that bacteria can rapidly contaminate initially clean environments by propagating upstream in a narrow channel, over long distances and for a substantial range of flow rates. We found bacteria pioneering the contamination that are capable of swimming upstream at average constant velocity over distances in excess of 1 cm. Furthermore, the contamination process shows long-tailed profiles populated by bacteria persistently moving upstream, which constitutes the signature of super-contamination.

Solving numerically a simple 1D model of biased random walk, we quantitatively related the spatiotemporal contamination profiles to the underlying presence of a broad run-time distribution stemming from the clockwise/counterclockwise statistics of the bacterial motor rotation. On the other hand, the simple exponential distribution for run times that would be associated with a Poisson distribution of run times is not able to reproduce the contamination profiles. To our knowledge, we make a quantitative relation between single-cell experiments on bacterial motors and the outcome of a macroscopic transport process. This puts forward that singular features of the run-and-tumble statistics, born in the stochasticity in the chemo-tactic circuitry, have a definite influence on macroscopic transport, in agreement with recent observations from 3D Lagrangian tracking (20, 21).

In practice, our measurements suggest that swimming bacteria can overcome distances comparable to the sizes of animal organs (tens of centimeters) in some tens of minutes or a few hours under conditions of high confinement. In the human urinary tract, for example, ureters are tubes with muscular walls that undergo successive waves of active muscular contraction to move liquid from the kidney to the bladder. When totally contracted, it collapses to a slit-shaped, very confined cross section, possibly favorable to upstream bacterial migration. When fully distended, we estimate shear rates of around 10 to 60 s$^{-1}$ (28). At these low shear rates, bacteria undergo little erosion from surfaces and edges (16). Contamination fronts advancing at 15 to 25 $\mu$m/s could overcome the length of the ureters ($200 \sim 300 \text{ mm}$) and travel from the bladder to the kidneys in 3 to 7 hours, possibly starting a renal infection.

The super-contamination could be relevant in other scenarios: Histological studies of the bovine cervical mucosa showed longitudinal grooves of cervical folds, which maintained continuity throughout the cervix (29). These geometrical conditions potentially facilitate the fast upstream migration of bacteria with a subsequent infection. Acute cholangitis, another medical emergency, is usually caused by bacteria ascending from the duodenum through the bile duct and infecting it (30), especially when it is partially obstructed and therefore provides a very confined environment ideal for upstream contamination.

**MATERIALS AND METHODS**

**Bacterial strains and culture**

We use wild-type RP437 *E. coli* bacteria. The cells are cultured overnight at 30°C in M9 minimal medium supplemented with casamino acids (1 mg/ml) and glucose (4 mg/ml). Next, bacteria are washed twice by centrifugation (2300g for 5 min), and the cells are resuspended into a motility medium containing 10 mM potassium phosphate (pH 7.0), 0.1 mM K-EDTA, 34 mM K-acetate, 20 mM sodium lactate, and 0.005% polyvinylpyrrolidone (PVP-40). In this medium, bacteria remain motile but do not divide.

**Microfluidic device and procedure**

The experimental cell is a microfluidic channel (rectangular cross section; width $w = 40 \text{ mm}$, height $b = 11 \text{ mm}$, and length $L = 15 \text{ mm}$) ended with two large cylindrical reservoirs. The microfluidic cell is made in PDMS using a conventional soft photolithography technique and assembled onto glass plates previously coated with a thin layer of PDMS. Stainless steel tubes of 1-mm diameter were inserted at each end of the channel in the cylindrical reservoirs, connected to large liquid containers through plastic flexible tubes. After a full filling of the microfluidic system with the stock solution without bacteria, the metallic connector from the outlet was replaced by a similar one connected to a big container containing the same liquid as the inlet, as well as bacteria. As a result, we start the experiment with a bacterial suspension located at the left end of the channel (see the panel corresponding to $t = 0$ in Fig. 1), while the rest of its length was filled with a bacteria-free medium. The microfluidic channel is placed on an inverted microscope (Zeiss Observer Z1) equipped with an x30 mechanically controllable stage from Applied Scientific Instrumentation (ASI), a digital camera (ANDOR iXon 897 electron multiplying charge-coupled device (512 pixels by 512 pixels) at a frequency of $f = 30$ fps (frames/s)) with a ×40 magnification objective.

Flow is established by imposing a small height difference between the two large containers on both sides of the channel, which allows us to work at very small flow rates. We visualize all the bacteria along the microchannel height by epifluorescence. As time passes by, bacteria migrate upstream along the channel. A single realization of the contamination experiment consists in performing periodic scans along the whole channel length. The microscope stage is displaced along the channel axis at a scanning velocity of $V_s = 150 \mu m/s$ while recording a video. Bacterial positions are then determined, and by image postprocessing, we relate the number of bacteria in each frame to its distance $x$ from the reservoir.

Between subsequent scans, a video is taken at a fixed position using direct light illumination, thus enabling the visualization of latex bead tracers. The velocity profile was determined for each applied pressure difference, through the beads velocities in the flow.

**Construction of the bacterial concentration profiles along the channels**

To obtain the contamination profiles from the scans, we count the number of bacteria in each frame. Since the distance between two consecutive pictures, $\Delta x = V_s/f = 150 \mu m/s$ per 30 fps = $5 \mu m$, is

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smaller than the piece of the channel imaged in one frame ($L_x = 160$), some bacteria are imaged several times. To obtain a concentration profile, we normalize the total number of bacteria detected by the average number of times that a bacterium was recorded: $L_x / A_x$. As the profiles do not come from snapshots but from scans, they are naturally stretched, showing tails longer than what they really are. We correct for the stretching as follows: Consider a bacterium in naturally stretched, showing tails longer than what they really are.

The profiles do not come from snapshots but from scans, they are therefore the scanning velocity ($V_s$).

We correct for the stretching as follows: Consider a bacterium in naturally stretched, showing tails longer than what they really are. The new scanning velocity ($V_s$) is the scanning velocity ($V_s = V_s'$), which shows that the deformation is linear with the distance to the reservoir. In our experiments the coefficient is in the range of $0.02 < \frac{\Delta x}{x_m} < 0.2$. With this principle, we rescaled the $x$ axis to reduce the profile stretching. The new $x$ values are $x = x_m - \Delta x = x_m(1 - \frac{\Delta x}{V_s})$, where $x_m$ is the measured coordinate from the scan.

**SUPPLEMENTARY MATERIALS**

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/6/11/eaay0155/DC1

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E. coli "super-contaminates" narrow ducts fostered by broad run-time distribution
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