Supporting Appendix

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Steady-State Bacterial Distribution. Here we derive Eq. **10**, the steady-state distribution of bacteria in terms of the expected tumbling probabilities of bacteria coming from the right and left.

In the steady state, the net flux of bacteria through a point between x and dx must be zero. Bacterial concentration at point x is represented by $b^{\pm}(x)$, where the $\pm$ indicates the direction of movement. Setting the net flux to zero yields

$$b^+(x-dx)(1-\frac{1}{2}\overline{P}^+(x)\frac{dx}{v})+b^-(x-dx)\frac{1}{2}\overline{P}^-(x)\frac{dx}{v}= \qquad [\mathbf{A.1}]$$
$$b^-(x+dx)(1-\frac{1}{2}\overline{P}^-(x)\frac{dx}{v})+b^+(x+dx)\frac{1}{2}\overline{P}^+(x)\frac{dx}{v}\ .$$

The left-hand side counts bacteria moving up the gradient past x; the right-hand side counts bacteria moving down the gradient past x. The probability of actually reversing directions is half the probability of tumbling. The first term on each side represents bacteria continuing on their present course; the second represents bacteria passing through the point after an instantaneous reorientation. Retaining only zeroth order terms gives $b^+(x) = b^-(x)$, so one can replace each by $b(x)/2$. Expanding $b(x)$ about x and retaining only terms up to first order in dx yields a differential equation governing the steady-state distribution of bacteria:

$$\frac{\nabla b(x)}{b(x)} = \frac{\overline{P}^-(x)-\overline{P}^+(x)}{2v}\ . \qquad [\mathbf{A.2}]$$

This is integrated to find Eq. **10**. The zero flux condition holds at all points in the system. The equation is modified at system boundaries, depending on conditions there, but the first-order differential equation (Eq. **A.2**) describes the bacterial distribution far from the boundaries.

Optimizing the Steady-State Distribution. Here we calculate $\overline{P}^-(x) - \overline{P}^+(x)$ in the steady state and find a response function that optimizes the bacterial distribution, $b(x)$.

We are interested in

$$\overline{P}^-(x)-\overline{P}^+(x) = \frac{1}{\tau}\int_{-\infty}^{0} dt' R(-t')\left[\overline{c}^+(t')-\overline{c}^-(t')\right]\ , \qquad [\mathbf{A.3}]$$

where superscripts indicate that the averages are taken over all paths ending at the position x moving either up $(+)$ or down $(-)$ the gradient at x. We take the gradient to be positive, so that upward-moving bacteria are rightward-moving bacteria.

To calculate this quantity, we must insert averages over possible paths. Assuming that the most recent tumble occurred at time t_0, the one before that at time t_1, and so on, we will average over the values of $t_0, t_1, \ldots$ and over the directions of the runs during each of the intervals. Essentially, because $\bar{c}^{\pm}$ is multiplied by $R(t)$ in the integral, this calculation can neglect first-order effects of $R(t)$ on $\bar{c}^{\pm}$: Runs become simply exponential in length, and there is an equal probability that a bacterium came from left or right before its last tumble.

We first average over the directions of the runs. In the steady state, for a tumble at t_i, the probability $Q^+(t_i)$ that the bacterium was moving up the gradient before the tumble will be proportional to the population of bacteria found to the left of $x(t_i)$. That is,

$$Q^+(t_i) = \frac{b(x(t_i) - v(t_i - t_{i+1}))}{b(x(t_i) - v(t_i - t_{i+1})) + b(x(t_i) + v(t_i - t_{i+1}))} \ . \qquad [\mathbf{A.4}]$$

Now assume that $b(x)$ varies slowly over one run and expand $b(x)$ to first order in $t_i - t_{i+1}$. Then

$$Q^+(t_i) \simeq \frac{b(x(t_i)) - \nabla b v(t_i - t_{i+1})}{2b(x(t_i))} = \frac{1}{2}\left(1 - v\frac{\nabla b}{b}(t_i - t_{i+1})\right) . \qquad [\mathbf{A.5}]$$

Inserting just the averages over the directions of motion in the various intervals and leaving the t_i fixed for the moment, we can expand Eq. **A.3** as

$$\begin{aligned} &\textstyle\int_{-\infty}^{0} dt' R(-t')\bar{c}^{\pm}(t') \rightarrow \qquad [\mathbf{A.6}] \\ &\textstyle\int_{t_0}^{0} dt' R(-t')c^{\pm}(t') \\ &+ \textstyle\int_{t_1}^{t_0} dt' R(-t') \left[Q^+(t_0)c^{(\pm+)}(t') + Q^-(t_0)c^{(\pm-)}(t')\right] \\ &+ \textstyle\int_{t_2}^{t_1} dt' R(-t') \big[Q^+(t_0)Q^+(t_1)c^{(\pm++)}(t') + Q^+(t_0)Q^-(t_1)c^{(\pm+-)}(t') \\ &+ Q^-(t_0)Q^+(t_1)c^{(\pm-+)}(t') + Q^-(t_0)Q^-(t_1)c^{(\pm--)}(t')\big] + \ldots \ . \end{aligned}$$

Here, $c^{++-}(t)$, for instance, denotes the concentration seen by a bacterium that has moved in the + direction after t_0, moved in the + direction in the interval $[t_1, t_0]$, and in the − direction in the interval $[t_2, t_1]$. From Eq. **A.2**, $\nabla b/b = (\overline{P}^- - \overline{P}^+)/v$, which is a sum of terms proportional to integrals of the form $\int R(t - t')c(t')dt'$, so we may set $Q^{\pm}(t_i) = 1/2$ to keep only terms to first order in $\int R(t - t')c(t')dt'$.

Now we look at the averages in square brackets in Eq. **A.6**. In the first such average, we expand $c(t)$ about t_0 to find that

$$\begin{aligned} &Q^+(t_0)c^{(\pm+)}(t') + Q^-(t_0)c^{(\pm-)}(t') \qquad [\mathbf{A.7}] \\ &= 1/2(c^{\pm}(t_0) + v(t' - t_0)\nabla c + c^{\pm}(t_0) - v(t' - t_0)\nabla c) \\ &= c^{\pm}(t_0) \ . \end{aligned}$$

The second square bracket in Eq. **A.6** reduces to $(c^{(\pm+)}(t_1) + c^{(\pm-)}(t_1))/2$, and the rest of the square brackets will reduce similarly.

Inserting the averages over the tumbling times $t_0, t_1, \ldots$, Eq. **A.3** expands to

$$\begin{aligned}
&\int_{-\infty}^{0} dt' R(-t') \overline{c}^{\pm}(t') \rightarrow \qquad [\mathbf{A.8}] \\
&\int_{-\infty}^{0} dt_0 D(t_0|0) \int_{t_0}^{0} dt' R(-t') c^{\pm}(t') \\
&+ \int_{-\infty}^{0} dt_0 D(t_0|0) \int_{-\infty}^{t_0} dt_1 D(t_1|t_0) \int_{t_1}^{t_0} dt' R(-t') c^{\pm}(t_0) \\
&+ \int_{-\infty}^{0} dt_0 D(t_0|0) \int_{-\infty}^{t_0} dt_1 D(t_1|t_0) \int_{-\infty}^{t_1} dt_2 D(t_2|t_1) \\
&\times \int_{t_2}^{t_1} dt' R(-t') \frac{(c^{(\pm+)}(t_1) + c^{(\pm-)}(t_1))}{2} + \ldots \ ,
\end{aligned}$$

where $D(\theta_2|\theta_1)$ is the probability that the bacterium tumbled at θ_2 given that it tumbled later at θ_1, where $\theta_2 < \theta_1$ so that we are reconstructing the tumbles backwards in time.

It remains to write out the factors $D(t_{i+1}|t_i)$ explicitly in terms of $R(t)$. The model we are using implies that

$$D(t_{i+1}|t_i) = \frac{\exp\left\{ -\int\limits_{t_{i+1}}^{t_i} dt' P[x(t''); t'] \right\}}{\int\limits_{-\infty}^{t_i} dt_{i+1} \exp\left\{ -\int\limits_{t_{i+1}}^{t_i} dt' P[x(t''); t'] \right\}} \ , \qquad [\mathbf{A.9}]$$

where the expression is normalized to integrate to 1. Keeping only terms up to first order in $R(t)$ allows us to set $D(t_{i+1}|t_i) = 1/\tau \exp\{(t_{i+1} - t_i)/\tau\}$. Then $\overline{P}^{-}(x) - \overline{P}^{+}(x)$ becomes

$$\begin{aligned}
&\overline{P}^{-}(x) - \overline{P}^{+}(x) = \qquad [\mathbf{A.10}] \\
&\int_{-\infty}^{0} \tfrac{dt_0}{\tau} e^{t_0/\tau} \int_{t_0}^{0} \tfrac{dt'}{\tau} R(-t') \left[c^{+}(t') - c^{-}(t') \right] \\
&+ \int_{-\infty}^{0} \tfrac{dt_0}{\tau} \int_{-\infty}^{t_0} \tfrac{dt_1}{\tau} e^{t_1/\tau} \int_{t_1}^{t_0} \tfrac{dt'}{\tau} R(-t') \left[c^{+}(t_0) - c^{-}(t_0) \right] \\
&+ \int_{-\infty}^{0} \tfrac{dt_0}{\tau} \int_{-\infty}^{t_0} \tfrac{dt_1}{\tau} \int_{-\infty}^{t_1} \tfrac{dt_2}{\tau} e^{t_2/\tau} \\
&\times \int_{t_2}^{t_1} \tfrac{dt'}{\tau} R(-t') \frac{\left[c^{(++)}(t_1) + c^{(+-)}(t_1) - c^{(-+)}(t_1) - c^{(--)}(t_1) \right]}{2} + \ldots \ .
\end{aligned}$$

First, consider the quantities in square brackets. The first one can be approximated by $c^{+}(t') - c^{-}(t') = 2vt'\nabla c$. The second one can also be approximated the same way, but t_0 replaces t'. Whether the third one can be made proportional to the gradient of the concentration depends on how quickly the gradient varies in space. Several of the terms in Eq. **A.10** might be approximated in terms of ∇c; it is a question of what sorts of gradients a bacterium typically encounters.

Consider a generic chemical landscape that is approximately flat on a large length scale L. On length scales smaller than L the concentration may vary significantly. In such a landscape, quantities like those in square brackets in Eq. **A.10**, representing measurements made in the distant past ($|t'| \gg \frac{L^2}{v^2\tau}$), will

have a tendency to sum to zero. In particular, if $L \sim 2v\tau$, the quantity in the third square bracket in Eq. **A.10** will be close to zero because, on average,

$$c^{(++)}(t_1) + c^{(+-)}(t_1) \sim c^{(-+)}(t_1) + c^{(--)}(t_1) \ . \qquad [\mathbf{A.11}]$$

Terms coming from the past where $|t'| \gg \frac{L^2}{v^2\tau}$ cease to contribute to $\overline{P}^-(x) - \overline{P}^+(x)$. Where we cut off the series in Eq. **A.10** is a biological question. We expect bacterial strategy to make minimal assumptions about the extent of the gradient, and therefore we will cut off the series after only a few terms. We drop all terms that refer to times earlier than t_1. The resulting expression for $\overline{P}^-(x) - \overline{P}^+(x)$ has two terms proportional to ∇c. The terms proportional to ∇c are precisely the ones that allow us to optimize the steady-state distribution in a concentration independent way.

We find that

$$\begin{aligned} \overline{P}^-(x) - \overline{P}^+(x) = \tfrac{2v\nabla c}{\tau^2}\big[\textstyle\int_{-\infty}^{0} dt_0 e^{t_0/\tau} \int_{t_0}^{0} dt' R(-t')t' \qquad [\mathbf{A.12}] \\ + \textstyle\int_{-\infty}^{0} dt_0 \int_{-\infty}^{t_0} dt_1 e^{t_1/\tau} \int_{t_1}^{t_0} \frac{dt'}{\tau} R(-t')t_0 \big] \ . \end{aligned}$$

Letting $R(t) = \int_0^\infty ds R(s)\delta(t-s)$, we find the simple result that $\overline{P}^-(x) - \overline{P}^+(x)$ can be written as the overlap in Eq. **11**.

Keeping more terms in Eq. **A.10** corresponds to assuming that the bacteria propagate on gradients with variations of longer length scale. Such an assumption produces a kernel of $e^{-t/\tau}$ multiplied by an expansion of $(1 - e^{t/\tau})$ in t/τ. Retaining an infinite number of terms leads to a kernel proportional to $e^{-t/\tau} - 1$. As long as a finite number of terms are retained, the qualitative features of the performance kernel don't change: It starts at zero, peaks negatively, and returns to zero for large t. If the number of retained terms remains small (< 5, for example), the quantitative features are not much affected either.

Fig. 5 illustrates this discussion. It shows the results of simulations of the model that demonstrate the contribution to $\mathcal{S}$ from each portion of the response function. The response functions are chosen as in Fig. 3 to weight only $c(t - \theta)$ in determining the turning probability. Bacteria navigating concentration gradients of various length scales are considered. On the timescales shown, the white points in the figure represent bacteria in an effectively infinite linear gradient. Bacteria heading down such a gradient at x on average have a higher c history for all previous times than ones heading up the gradient at x. Therefore, measurements made any time in the past, including long ago, affect $\mathcal{S}$ by the same amount. On the other hand, when the gradient is not infinite, as in any real case, ∇c will change on some length scale. Measurements of $c(t)$ made with a delay large compared to the time to traverse this length scale will average out in the sum over histories. Such measurements therefore cease to affect $\mathcal{S}$. As the grey points in the figure show, on a relatively short length scale, measurements of concentration made $20\tilde{\tau}$ in the past no longer contribute to $\mathcal{S}$. In the time of $20\tilde{\tau}$, the bacterium is likely to have bounced against a wall (or moved over a peak, if one views the reflecting box as an infinite triangle

wave), so such measurements no longer reflect the bacterium's current gradient. With still shorter gradients, such effects become more pronounced. The black points in the figure are on a length scale that roughly matches our theory, in which we restricted bacteria to looking at only the previous two runs. The simulation conditions mean that bacteria cannot use measurements made long ago, whereas our theory posits that bacteria should make minimal assumptions about gradient length. Both lead to similar kernels showing the influence of $R(\theta)$ on $\mathcal{S}$.