

Optimal Distributions of Receptors on Arbitrarily Shaped Cell Surfaces

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Efficient absorption of molecules through receptors on cell surfaces is crucial for various biological processes. While ubiquitous patterns of receptor distributions, including polar localization in rod-shaped cells, have been widely observed, the underlying evolutionary advantage of these patterns is unclear. In this Letter, we investigate how the spatial distribution of receptors on the cell surface affects the total flux entering the cell. We develop a numerical method that allows for the calculation of fluxes through all receptors using linear equations. Our calculations show that the flux through each receptor is spatially dependent for uniformly distributed receptors: the fluxes are highest near the poles in rod-shaped cells and near the invagination in defective spherical cells. Surprisingly, we show that the optimal receptor distribution on an arbitrarily shaped cell, which maximizes the total flux, is precisely the charge density distribution on an ideal conductor of the same shape, in agreement with numerical simulations. Our Letter unveils the evolutionary origin of receptor localizations.

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Many intracellular processes rely on the arrival of essential molecules at the cell surface, where the cells absorb the molecules via specific membrane receptors [1,2]. For example, cellular metabolism requires the cell to uptake carbohydrates efficiently [3,4], e.g., through the phosphotransferase system (PTS) in bacteria [5–7]. For rod-shaped bacteria, e.g., *Escherichia coli*, experiments found that many types of receptors (or transporters) are localized at the cell poles, e.g., the osmosensory transporter ProP [8], the lactose transporter LacY [9], the PTS proteins EI and HPr [10], and the chemotaxis receptors [11–15]. Interestingly, in defective spherical *E. coli* cells with an invagination, the PTS proteins are instead localized at the edge of the invagination [16]. Mechanically, polar constituents, such as anionic lipids [8,17] and curvature sensor proteins [18,19], may serve as geometric cues for polar localization. In this Letter, we seek to understand the localizations of receptors from an evolutionary perspective: what kinds of spatial distribution of receptors maximize the total molecule flux entering the cell given a fixed number of receptors and a constant environment? We propose that

achieving the maximum flux may be the evolutionary driving force for certain distributions of receptors ubiquitous in biology.

The upper bound of flux is achieved when the entire cell surface is a perfect absorbing boundary so that any molecule hitting the surface is absorbed. For a spherical cell, the upper bound of molecule flux $J_{\max} = 4\pi DRc_{\infty}$, where D is the diffusion constant of the molecule of interest, R is the cell radius, and c_{∞} is the molecule concentration far from the cell. Phillips *et al.* modeled a spherical cell surface as a homogeneous, nonabsorbing boundary [20]. The total flux $J = Nk_{\text{on}}c(a)$, where N is the number of the receptor, k_{on} is the absorption rate of each receptor, and $c(a)$ is the molecule concentration on the cell surface, which is determined self-consistently. They showed that the molecule flux entering the cell is a Hill function of the receptor number, $J = J_{\max}(Nk_{\text{on}}/4\pi DR)/[1 + (Nk_{\text{on}}/4\pi DR)]$, consistent with the experimental measurements of the adsorption rate of bacteriophage λ on the number of λ receptors in *Escherichia coli* [21]. By taking $k_{\text{on}} \approx 10 \mu\text{M}^{-1} \text{s}^{-1}$, they showed that the receptors only need to cover about 0.1% of the cell surface to achieve a flux 50% of the upper bound. Therefore, cells can achieve high absorption efficiency by allocating only a small fraction of their surface area to one receptor type, allowing them to express multiple receptor types simultaneously.

The previous analyses by Phillips *et al.* were inspiring. Nevertheless, critical questions remain. First, the actual boundary condition on the cell surface is complex since receptors only cover a finite fraction. Most importantly, the

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effects of nonspherical cell shape on the molecule flux are far from clear. For an arbitrarily shaped cell, what is the optimal distribution of receptors maximizing the flux entering the cell? In this Letter, we answer these questions by studying an arbitrarily shaped cell with its surface decorated by multiple receptors. Each receptor is modeled as a circular patch with an absorbing boundary condition. Berg and Purcell have studied a particular case of uniformly distributed receptors on a spherical cell [22]. Theoretically, we solve the time-independent diffusion equation and convert the problem of solving Laplace's equation with complex boundary conditions to a linear algebra problem involving the flux of each receptor, applicable to arbitrarily shaped cells.

For spherical cells, we recover Berg and Purcell's classical results [22], which strongly support the validity of our method; in particular, we relate the absorption rate k_{on} introduced by Phillips *et al.* to the receptor size, $k_{\text{on}} = 4Dr$, where r is the receptor radius, and explicitly demonstrate that only a tiny fraction of area is needed to achieve a molecule flux close to the upper bound.

For an arbitrarily shaped cell with uniformly distributed receptors, the fluxes of receptors depend on their locations. For a rod-shaped cell, the fluxes of receptors at the poles are higher than those on the side. For a spherical cell with a bud, the fluxes are the highest at the bud tip. Surprisingly, for a spherical cell with an invagination, the fluxes at the edge of the invagination are the highest on the cell surface, rationalizing the localization of the PTS proteins observed in defective spherical *E. coli* [16].

For an arbitrarily shaped cell with nonuniformly distributed receptors, we prove that the optimal distribution of receptors that maximizes the total flux is precisely the charge density distribution on an ideal conductor of the same shape. We test our predictions by simulating an evolutionary process in which we let the locations of receptors evolve to maximize the total flux. As predicted, the receptor distribution converges to the charge density distribution on an ideal conductor. Our theories provide a physical foundation for the evolution of receptor localizations, e.g., rationalizing the ubiquitous polar locations of receptors in rod-shaped cells.

Computing fluxes for an arbitrarily shaped cell—We study an arbitrarily shaped cell with N circular receptors decorating its surface Γ . The concentration field satisfies Laplace's equation $\nabla^2 c(\mathbf{x}) = 0$. The boundary condition of the concentration field is that $c(\mathbf{x}) = 0$ for $\mathbf{x} \in S_i$, where $i = 1, 2, \dots, N$ and S_i is the region occupied by receptor i . For $\mathbf{x}$ outside any receptors, $[\partial c(\mathbf{x})/\partial \mathbf{n}_x] = 0$. Here, $\mathbf{n}_x$ is the unit vector perpendicular to the surface at $\mathbf{x}$ pointing to the cell interior. The flux through a receptor is $J_i = -D \int_{x \in S_i} [\partial c(\mathbf{x})/\partial \mathbf{n}_x] dS_x$, where the integral is over the receptor i region on the cell surface. Because the radius of typical receptors $r \sim 1$ nm, the average distance between nearby receptors $l \sim 10$ nm [23], and the typical size of

a bacterial cell $R \sim 1000$ nm [24], we use the condition $r \ll l \ll R$ in the following, a good approximation for most biological scenarios of our interest.

We use the boundary integral equation for Laplace's equation in three dimensions [25–28] and modify it to the case where the concentration at infinity is c_∞ ,

$$2\pi[c_\infty - c(\mathbf{x})] = - \int_{y \in \Gamma} \frac{1}{|\mathbf{x} - \mathbf{y}|} \frac{\partial c(\mathbf{y})}{\partial \mathbf{n}_y} dS_y - \int_{y \in \Gamma} [c_\infty - c(\mathbf{y})] \frac{\partial}{\partial \mathbf{n}_y} \frac{1}{|\mathbf{x} - \mathbf{y}|} dS_y. \quad (1)$$

Here, $(\partial/\partial \mathbf{n}_y)(1/|\mathbf{x} - \mathbf{y}|) = \{[(\mathbf{x} - \mathbf{y}) \cdot \mathbf{n}_y]/|\mathbf{x} - \mathbf{y}|^3\}$. We next sample M auxiliary points $\mathbf{x}_j$ ($j = 1, 2, \dots, M$) uniformly on the cell surface that are not close to any receptors, which means that $|\mathbf{x}_j - \mathbf{y}_i| \gg r$ for all i, j . Here $\mathbf{y}_i$ is the position of the center of receptor i . This is always doable under our assumptions. We define $C_j = c_\infty - c(\mathbf{x}_j)$. Making use of the length-scale separation, we convert the boundary integral equation to a set of linear equations from which we can compute the fluxes through all receptors (End Matter),

$$\frac{\pi}{2rD} J_i + \frac{1}{D} \sum_{k=1, k \neq i}^N \frac{1}{|\mathbf{y}_i - \mathbf{y}_k|} J_k - \frac{S}{M} \sum_{l=1}^M C_l \frac{\partial}{\partial \mathbf{n}_{x_l}} \frac{1}{|\mathbf{y}_i - \mathbf{x}_l|} = 2\pi c_\infty, \quad i = 1, 2, \dots, N \quad (2)$$

$$\frac{1}{D} \sum_{k=1}^N \frac{1}{|\mathbf{x}_j - \mathbf{y}_k|} J_k - 2\pi C_j - \frac{S}{M} \sum_{l=1, l \neq j}^M C_l \frac{\partial}{\partial \mathbf{n}_{x_l}} \frac{1}{|\mathbf{x}_j - \mathbf{x}_l|} = 0, \quad j = 1, 2, \dots, M. \quad (3)$$

The spherical cell—We first study a spherical cell with its receptors uniformly distributed on its surface. In this case, the flux through each receptor must be equal, and the concentration field at locations not close to any receptors must be uniform, that is, $J_1 = J_2 = \dots = J$, $C_1 = C_2 = \dots = C$. These simplifications allow us to calculate the summations in Eqs. (2) and (3) analytically and get the total flux as

$$J_{\text{tot}} = J_{\text{max}} \frac{\frac{Nr}{\pi R}}{1 + \frac{Nr}{\pi R}}, \quad (4)$$

where $J_{\text{max}} = 4\pi DRc_\infty$, the total flux when the entire cell surface is absorbing boundary [see the derivations in Supplemental Material (SM) [29]]. Our results perfectly recover Berg and Purcell's classical results for spherical cells [22], supporting the validity of our method. By comparing Eq. (4) with the results of Phillips *et al.*, we find the microscopic expression of the effective absorption rate $k_{\text{on}} = 4Dr$. Interestingly, the flux only depends on the total perimeter of all receptors. Our results explicitly demonstrate that as long as $R/r \gg 1$, the receptors only need to cover a

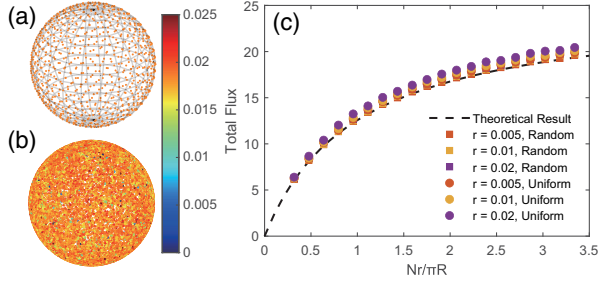


FIG. 1. (a) We uniformly sample $N = 800$ receptors with radius $r = 0.01$ on a spherical cell with radius $R = 2$. (b) The accumulated fluxes of 20 independent samplings where the receptors are randomly sampled with random locations and a uniform density. (c) We change the number of receptors N for a given r , and the calculated total fluxes agree well with the theoretical predictions for both uniformly and randomly distributed receptors. In this Letter, the color of each receptor represents the flux through it.

small fraction of surface area, which is $\phi = Nr^2/4R^2$, for the total flux to be comparable to the upper bound.

We verify Eq. (4) by sampling N receptors uniformly on a spherical cell using the Fibonacci lattice method [30] [Fig. 1(a)]. Details of numerical calculations are included in SM. In this Letter, we uniformly sample $M = N$ auxiliary points unless otherwise specified, and the total flux is essentially constant, with a deviation of less than 1% once M is comparable to or larger than N (SM Fig. S1). As expected, the fluxes are the same across different receptors. The numerical total fluxes agree well with the theoretical predictions, and the total flux only depends on $Nr/\pi R$ [Fig. 1(c)]. To test the robustness of our methods, we randomly sample N receptors with random locations and a uniform density: the average number per unit area is constant. To show the spatial dependence of fluxes, we plot the accumulated fluxes of multiple independent samplings [Fig. 1(b)], which are also uniform. The total fluxes also agree well with the theoretical predictions in this random case [Fig. 1(c)].

Arbitrarily shaped cells with uniformly distributed receptors—We next study the cases of nonspherical cells with uniformly distributed receptors using a modified Fibonacci lattice method (SM). For rod-shaped cells, e.g., *E. coli*, we find that the fluxes are higher in the receptors near the poles than those on the side, and as the cell length increases, the difference becomes more significant (Fig. 2). These observations are consistent with the ubiquitous polar localization of receptors in rod-shaped cells. Later, we show that if we allow receptors to move on the cell surface to maximize the total flux, they are indeed enriched at the cell poles.

For curved rod-shaped cells, such as *Caulobacter crescentus*, we find that the fluxes on the negative curvature side are lower than those on the other side [SM Figs. S2(a) and S2(b)]. We also study spherical cells with an invagination [Fig. 3(a)] and a bud [Fig. 3(b)]. Interestingly, for the

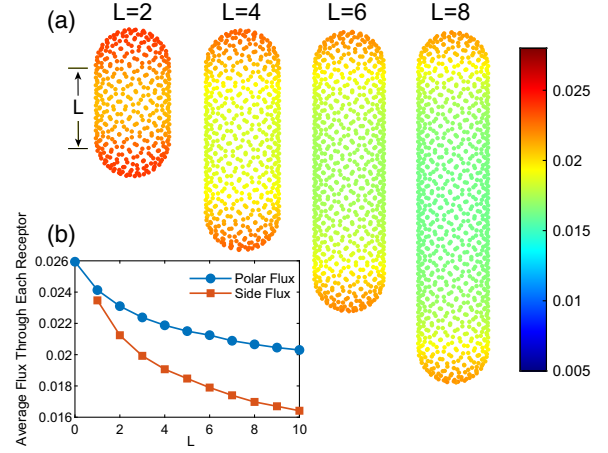


FIG. 2. (a) We uniformly sample N receptors on a rod-shaped cell, modeled as a cylinder with length L , capped with two half-spheres with radius $R = 1$. Here, we show the numerical results of four cells where $N = 400$ for $L = 2$, $N = 600$ for $L = 4$, $N = 800$ for $L = 6$, and $N = 1000$ for $L = 8$. (b) The average fluxes for receptors on the side and polar regions. As the cylinder length increases, the difference between the polar and side flux becomes more significant. In this Letter, we set the receptor radius $r = 0.01$ unless otherwise mentioned.

spherical cell with an invagination, the fluxes are the highest at the edge of the invagination. This observation aligns with the experimental observations that the PTS proteins are localized at the edge of the invagination in defective spherical *E. coli* cells [16]. Our theories unveil the benefit of such a localization pattern. For the spherical cell with a bud, the fluxes are highest at the tip of the bud and lowest in the neck, which connects the body and bud. The spatial dependence of fluxes leads us to wonder: if we allow the locations of receptors to change from a uniform distribution, what is the optimal distribution that maximizes the total flux?

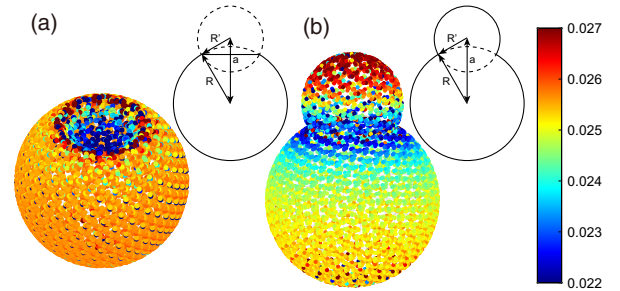


FIG. 3. (a) We uniformly sample $N = 407$ receptors on a defective spherical cell. We accumulate the results of 20 independent samplings to show the high fluxes at the invagination edge more clearly. (b) We uniformly sample $N = 400$ receptors on a spherical cell with a bud and accumulate the results of 20 independent samplings. The geometry of the cells in (a) and (b) is shown on the right of each figure, in which $\sqrt{3}R' = (\sqrt{3}/2)a = R = 2$.

The optimal distribution of receptors on an arbitrarily shaped cell—We seek the optimal distribution of receptors on an arbitrarily shaped cell that maximizes the total flux. For the optimal distribution, the flux through each receptor must be equal. If not, the cell can always let the receptors move toward the regions with higher fluxes to enhance the total flux. First, we point out a useful connection between the flux through a receptor and the concentration near the receptor: $c_i = J_i/4rD$. To see this, we let $\mathbf{x}_j$ be near $\mathbf{y}_i$ [$r \ll |\mathbf{x}_j - \mathbf{y}_i| \sim O(l)$] and take the difference between Eqs. (2) and (3), from which we obtain $c_i = J_i/4rD + O(1/l) \approx J_i/4rD$. Given the fact that $J_1 = J_2 = \dots = J$ for optimal receptor distributions, we have $c_1 = c_2 = \dots = (J/4rD)$ for all receptors. Since the concentrations near all receptors are the same, the concentration over the entire surface should be approximately constant as well, i.e., $c \approx (J/4rD)$. This allows us to simplify Eq. (A1) to

$$2\pi c_\infty = \frac{\pi}{2rD}J + \frac{J}{D} \sum_{k=1, k \neq i}^N \frac{1}{|\mathbf{y}_i - \mathbf{y}_k|} - \int_{\mathbf{y} \in \Gamma} \left(c_\infty - \frac{J}{4rD} \right) d\Omega_{\mathbf{y}}. \quad (5)$$

Here, $d\Omega_{\mathbf{y}} = (\partial/\partial n_{\mathbf{y}})(1/|\mathbf{y} - \mathbf{y}_i|)dS_{\mathbf{y}}$, the differential solid angle at $\mathbf{y}$ toward $\mathbf{y}_i$.

Let $\sigma(\mathbf{y})$ be the local density of receptors at $\mathbf{y}$. Using $\int_{\mathbf{y} \in \Gamma} d\Omega_{\mathbf{y}} = 2\pi$, we derive from Eq. (5) that $4rDc_\infty = \{1 + (r/\pi) \int_{\mathbf{y} \in \Gamma} [\sigma(\mathbf{y})/|\mathbf{y} - \mathbf{y}_i|] dS_{\mathbf{y}}\}J$. Thus, we find that for $\mathbf{x} \in \Gamma$

$$\int_{\mathbf{y} \in \Gamma} \frac{\sigma(\mathbf{y})}{|\mathbf{y} - \mathbf{x}|} dS_{\mathbf{y}} = \text{const}. \quad (6)$$

This corresponds to the isopotential condition of ideal conductors if we take $\sigma(\mathbf{y})$ as the charge density. Therefore, we predict that the density distribution of receptors maximizing the total flux is the same as the charge density distribution on an ideal conductor of the same shape.

To test this prediction, we simulate an evolutionary process on rod-shaped cells and cells with a bud, allowing the locations of receptors to evolve to maximize the total flux. At each step, we let a few receptors change their locations and accept the change if the total flux increases (see simulation details in SM). We confirm that the fluxes are approximately the same across different receptors for the optimal distributions (Fig. 4). We then compare the optimal receptor distribution with the charge density distribution on an ideal conductor of the same shape. For both rod-shaped cells and budding cells, the optimal receptor distributions are indeed the same as the charge density distributions (Fig. 4), confirming our prediction.

Discussions—In this Letter, we convert the problem of solving Laplace's equation with mixed boundary conditions to a set of linear equations. Our method shares a similar spirit with the collocation boundary element methods [26–28] with some important modifications tailored to

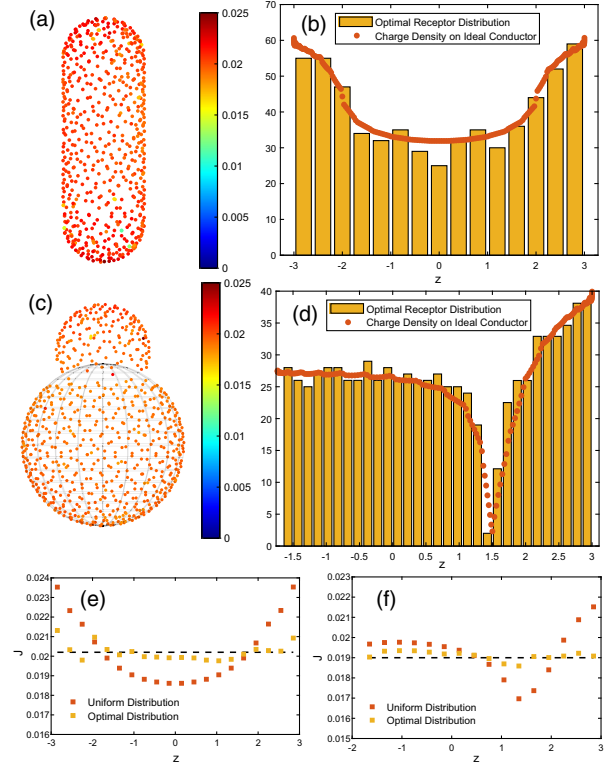


FIG. 4. Optimal distributions of receptors on a rod-shaped cell and a cell with a bud. (a),(c) The optimal receptor distribution on a rod-shaped cell (a) and a cell with a bud (c). We initially uniformly distribute 600 (a) and 710 (c) receptors, respectively, and let the locations of the receptors evolve to maximize the total fluxes. (b),(d) The optimal receptor distributions on the rod-shaped cell (b) and the cell with a bud (d) agree with the charge densities of ideal conductors of the same shapes. (e),(f) The fluxes J for receptors with different locations along the vertical direction of the rod-shaped cell (e) and the budding cell (f). For uniformly distributed receptors, the fluxes vary significantly. In contrast, the spatial heterogeneity of fluxes is much smaller for optimally distributed receptors.

our model (End Matter). We remark that the main novelty of our Letter lies in the biophysical insights it provides. Our calculations explain several spatial patterns of receptors observed in experiments, including localizations near polar regions [8–15] and invagination [16]. Remarkably, we demonstrate that for an arbitrarily shaped cell, the optimal distribution of receptors on a cell surface is precisely the charge density distribution on an ideal conductor of the same shape, which is a novel result as far as we realize. Our Letter predicts that for optimal molecule uptake efficiency, the receptors tend to be localized in high-curvature regions, just like the buildup of charge at sharp points on a conductor [31], in agreement with multiple experiments [8–16,18,19]. Our results are also relevant for a cell to sense the concentration of molecules surrounding it. It has been shown that the relative error in concentration sensing is $\Delta c_{\text{rms}}/\bar{c} \propto 1/\sqrt{J_{\text{tot}}}$, where J_{tot} is the total flux [22].

Therefore, the optimal receptor distributions we find also help cells to sense their surrounding molecule concentrations more accurately. We propose that in the presence of a concentration gradient, the optimal receptor patterns that maximize the total flux may be similar to the charge distribution on a conductor in the presence of an electric field, which requires further testing.

We provide an intuitive picture underlying the analogy between the optimal receptor distribution and the charge density of an ideal conductor. In the case of optimal receptor distributions, the fluxes through all receptors are the same. Therefore, if we average the fluxes of the receptors inside a patch of size ξ such that $l \ll \xi \ll R$, the direction of the average flux is perpendicular to the cell surface (if the fluxes of the receptors in this patch are unequal, the average flux would be tilted relative to the normal direction of the cell surface). Because the perpendicular nature of the mesoscopic fluxes agrees precisely with the perpendicular property of the electric field relative to the ideal conductor surface, we expect the receptor distribution to be the same as the charge density of an ideal conductor. One can also make an analogy between the receptor on the cell surface in the optimal case and a point charge on a conductor, where each point charge emits an electric field line corresponding to the constant molecule flux flowing into each receptor. We note that the analogy between the receptor distribution on the cell surface and the charge density on a conductor is only valid for the optimal case where the fluxes through each receptor are equal. We also note that for uniformly distributed receptors, the flux pattern differs from the charge distribution of a conductor of the same shape [Figs. 4(b), 4(d) and 4(e), 4(f)].

The presence of flow typically does not affect our main conclusions. The relative increment in the total flux due to cell motion for a nonspherical cell can be estimated as $(J_{\text{tot}} - J_{\text{tot},0})/J_{\text{tot},0} \sim UR/D$ from a dimensional analysis, where J_{tot} is the total flux with a small cell velocity $U \ll D/R$. $J_{\text{tot},0}$ is the total flux when $U = 0$. Here, R is the characteristic cell size, and D is the diffusion constant of the absorbed molecule. Taking the biologically relevant values for bacteria, $U = 10 \mu\text{m/s}$, $R = 1 \mu\text{m}$, and $D = 10^3 \mu\text{m}^2/\text{s}$, the relative flux increment is approximately 10^{-2} and negligible. We note that for a spherical absorber, different scalings between the flux increment and the Peclet number (UR/D) have been proposed [22,32].

Noted added—In a recent theoretical study [33], the authors investigated the receptor patterns that maximize the accuracy of sensing molecule concentration gradients. In contrast to our Letter, they considered three-dimensional spherical receptors and employed the free-space Green function for molecular diffusion. Interestingly, they found that the receptors cluster at high-curvature regions for optimal gradient sensing, a result similar to ours despite the optimized variables being entirely different. This accordance reveals how distinct optimization principles can

converge upon similar spatial strategies, revealing a deeper unity in the physics of biological absorption and sensing.

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Data availability—The data that support the findings of this article are openly available [34].

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End Matter

Derivation details of the linear equations—We take $\mathbf{x} = \mathbf{y}_i$ in Eq. (1), where $\mathbf{y}_i$ is the position of the center of receptor i and rewrite Eq. (1) as

$$2\pi c_\infty = - \int_{\mathbf{y} \in S_i} \frac{1}{|\mathbf{y}_i - \mathbf{y}|} \frac{\partial c(\mathbf{y})}{\partial \mathbf{n}_y} dS_y + \frac{1}{D} \sum_{k=1, k \neq i}^N \frac{J_k}{|\mathbf{y}_i - \mathbf{y}_k|} - \int_{\mathbf{y} \in \Gamma} (c_\infty - c(\mathbf{y})) \frac{\partial}{\partial \mathbf{n}_y} \frac{1}{|\mathbf{y}_i - \mathbf{y}|} dS_y. \quad (\text{A1})$$

Here, we use the definition of flux to replace the integrals over all the receptors except i by their fluxes. The first term on the right side of Eq. (A1) can be considered as the electric potential Ψ of a flat disk generated by the charge density $-\partial c(\mathbf{y})/\partial \mathbf{n}_y$; therefore, it is proportional to the flux, which can be considered as the total charge, by $J_i/D = - \int_{\mathbf{y} \in S_i} \partial c(\mathbf{y})/\partial \mathbf{n}_y dS_y = P\Psi$, where $P = 2r/\pi$ is capacitance of a thin conducting disk in the vacuum [35], leading to the first term on the left side of Eq. (A1). Using Eq. (1), we further find that

$$2\pi C_j = \frac{1}{D} \sum_{i=1}^N \frac{J_i}{|\mathbf{x}_j - \mathbf{y}_i|} - \int_{\mathbf{y} \in \Gamma} (c_\infty - c(\mathbf{y})) \frac{\partial}{\partial \mathbf{n}_y} \frac{1}{|\mathbf{x}_j - \mathbf{y}|} dS_y. \quad (\text{A2})$$

We approximate the integral over the cell surface in Eqs. (A1) and (A2) as a sum over the M auxiliary points, i.e., $\int_{\mathbf{y} \in \Gamma} (c_\infty - c(\mathbf{y})) (\partial/\partial \mathbf{n}_y) (1/|\mathbf{y}_i - \mathbf{y}|) dS_y \approx (S/M) \sum_{l=1}^M C_l (\partial/\partial \mathbf{n}_{x_l}) (1/|\mathbf{y}_i - \mathbf{x}_l|)$, where S is the total surface area. Combining Eqs. (A1) and (A2), we obtain the linear equations to solve the fluxes of all receptors, Eqs. (2) and (3). One should note that the $l = j$ term in the last term of the left side of Eq. (3) is negligible in the continuous case; therefore, it is not included in the discrete summation.

Comparison to collocation boundary element methods—In the collocation boundary element method (BEM), a surface is divided into multiple elements, with collocation points located at the centers of these elements. The simplest and most common approximation used by the collocation BEM is to assume that the potentials and flux densities are constant within each element, and the

integrals of the Green's function serve as parameters. There are some important differences between our method and the collocation BEM. In our model, we directly use the receptor centers as part of the collocation points, which have a clear physical interpretation. Since the flux density $[\partial c(\mathbf{y})/\partial \mathbf{n}_y]$ varies rapidly in space within each

receptor, we integrate it over the entire receptor to obtain the total flux J_i through the i th receptor. We treat this integral, $-\int_{y \in S_i} (1/|\mathbf{y}_i - \mathbf{y}|) [\partial c(\mathbf{y})/\partial \mathbf{n}_y] dS_y$ in Eq. (A1), by modeling the integral as the potential of a disk conductor with known capacitance.