Diffusion Fails to Make a Stink

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In this work we consider the question of whether a simple diffusive model can explain the scent tracking behaviours found in nature. For this behaviour to occur, both the concentration of a scent and its gradient must be above some threshold. Applying these conditions to the solutions of various diffusion equations, we find that a purely diffusive model cannot simultaneously satisfy the tracking conditions when parameters are in the experimentally observed range. This demonstrates the necessity of modelling odor dispersal with full fluid dynamics, where non-linear phenomena such as turbulence play a critical role.

I. INTRODUCTION

We live in a universe that not only obeys mathematical laws, but on a fundamental level appears determined to keep those laws comprehensible[1]. The achievements of physics in the three centuries since the publication of Newton's *Principia Mathematica*[2] are largely due to this inexplicable contingency. The predictive power of mathematical methods has spurred its adoption in fields as diverse as social science[3] and history[4]. A particular beneficiary in the spread of mathematical modelling has been biology[5], which has its origins in Schrödinger's analysis of living beings as reverse entropy machines[6]. Today, mathematical treatments of biological processes abound, modelling everything from epidemic networks[7,8] to biochemical switches[9], as well as illuminating deep parallels between the processes driving both molecular biology and silicon computing[10].

One of the most natural applications of mathematical modelling is to understand the sensory faculties through which we experience the world. Newton's use of a bodkin to deform the back of his eyeball[11,12] was one of many experiments performed to confirm his theory of optics[13–15]. Indeed, the experience of both sight and sound have been extensively contextualised by the mathematics of optics[16–19] and acoustics[20–23]. In contrast to this, simple models which adequately describe the phenomenological experience of smell are strangely lacking, belying the important role olfaction plays as nature's gas chromatograph[24]. A robust model describing scent dispersal is of some importance, as olfaction has the potential to be used in the early diagnosis[25] of infections[26] and cancers[27]. In fact, recent work using canine olfaction to train neural networks in the early detection of prostate cancers[28] suggests that future technologies will rely on a better understanding of our sense of smell.

In the face of these technological developments, it seems timely to revisit the mechanism of odorant dispersal, and examine the consequences of modeling it via diffusive processes. Here we explore the consequences of using the mathematics of diffusion to describe the dynamics of odorants. In particular, we wish to understand whether such simple models can account for the extraordinary capacity of organisms not only to detect odors, but to track them to their origin. In previous work, the process of olfaction *inside* the nasal cavity has been modeled with diffusion[29], but the question of whether purely diffusive processes can lead to spatial distributions of scent concentration that enable odor tracking has not been considered.

The phenomenon of diffusion has been known and described for millennia, an early example being Pliny the Elder's observation that it was the process of diffusion that gave roman cement its strength[30,31]. Diffusion equations have been applied to scenarios as diverse as predicting a gambler's casino winnings[32] to baking a cake[33]. The behaviour described by the diffusion equation is the *random spread* of substances[34,35], with its principal virtue being that it is described by well-understood partial differential equations whose solutions can often be obtained analytically. It is therefore a natural candidate for modelling random-motion transport such as (appropriately in 2020) the spread of viral infections[36] or the dispersal of a gaseous substance such as an odorant.

The rest of this paper is organised as follows - in Sec.II, we introduce the diffusion equation, and the conditions required of its solution to both detect and track an odor. Sec.III solves the simplest case of diffusion, which applies in scenarios such as a drop of blood diffusing in water. This model is extended in Sec.IV to include both source and decay terms, which describes e.g. a pollinating flower. Finally Sec.V discusses the results presented in previous sections, which find that the distributions which solve the diffusion equation cannot be reconciled to experiential and empirical realities. Ultimately the processes that enable our sense of smell cannot be captured by a simple phenomenological description, and models for the olfactory sense must account for the non-linear[37] dispersal of odor caused by secondary phenomena such as turbulence.

II. MODELLING ODOR TRACKING WITH DIFFUSION

We wish to answer the question of whether a simple mathematical model can capture the phenomenon of tracking a scent. We know from experience that it is possible to trace the source of an odorant, so any physical model of the dispersal of odors must capture this fact. The natural candidate model for this is the *diffusion equation*, which in its most basic (one-dimensional) form is given by[38]

$$\frac{\partial C\left(x,t\right)}{\partial t} - D\frac{\partial^2 C\left(x,t\right)}{\partial x^2} = 0 \tag{1}$$

where $C(x,t)$ is the concentration of the diffusing substance, and D is the diffusion constant determined by the microscopic dynamics of the system. For the sake of notational simplicity, all diffusion equations presented in this manuscript will be 1D. An extension to 3D will not change any conclusions that can be drawn from the 1D case, as typically the spatial variables in a diffusion equation are separable, so that a full 3D solution to the equation will simply be the product of the 1D equations (provided the 3D initial condition is the product of 1D conditions).

If an odorant is diffusing according to Eq.(1) or its generalisations, there are two prerequisites for an organism to track the odor to its source. First, the odor must be detectable, and therefore its concentration at the position of the tracker should exceed a given threshold or *Limit Of Detection* (LOD)[39]. Additionally, one must be able to distinguish relative concentrations of the odorant at different positions in order to be able to follow the concentration gradient to its source. Fig. 1 sketches the method by which odors are tracked, with the organism sniffing at different locations (separated by a length δ) in order to find the concentration gradient that determines which direction to travel in.

We can express these conditions for tracking an odorant with two equations

$$C(x) > C_T, \tag{2}$$

$$\frac{C(x)}{C(x+\delta)} > R \tag{3}$$

where $C(x)$ is the distribution of odor concentration, C_T is the LOD concentration, and R characterises the sensitivity to the concentration gradient when smelling at positions x and $x+\delta$.

The biological mechanisms of olfaction determine both C_T and R, and can be estimated from empirical results. While the LOD varies greatly across the range of odorants, the lowest observed thresholds are on the order of 1 part per billion (ppb)[40]. Estimating R is more difficult, but a recent study in mice demonstrated that a 2-fold increase in concentration between inhalations was sufficient to trigger a cellular response in the olfactory bulb[41]. We therefore assume that in order to track an odor, $R \approx 2$. Values of δ will naturally depend on the size of the organism and its frequency of inhalation, but unless otherwise stated we will assume $\delta = 1$m.

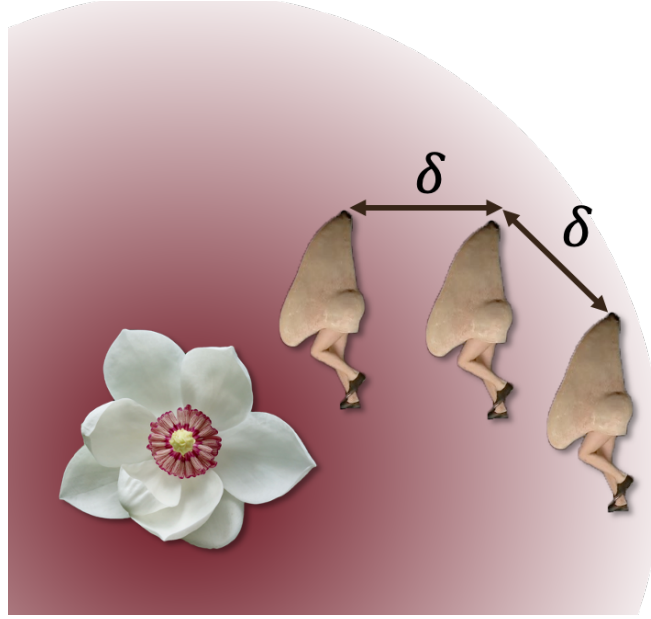

FIG. 1. **Tracking Odors** In order to trace an odor to its source, one sniffs at different locations separated by δ. If the concentration gradient is sufficiently large, it is possible to determine if one is closer or further from the origin of the smell. Image of the walking nose comes from the Royal Opera House's production of Shostakovich's 'The Nose'.

Having established the basic diffusion model and the criteria necessary for it to reflect reality, we now examine under what conditions the solutions to diffusion equations are able to satisfy Eqs.(2,3).

III. THE HOMEOPATHIC SHARK

Popular myth insists that the predatory senses of sharks allow them to detect a drop of its victim's blood from a mile away, although in reality the volumetric limit of sharks' olfactory detection is about that of a small swimming pool[42]. The diffusion of a drop of blood in water is nevertheless precisely the type of scenario in which Eq.(1) can be expected to apply. To test whether this model can be reconciled to reality, we first calculate the predicted maximum distance $x_{\max}$ from which the blood can be detected.

In order to find $C(x,t)$, we stipulate that the mass M of blood is initially described by $C(x,0) = M\delta(x)$. While many methods exist to solve Eq.(1), the most direct is to consider the *Fourier transform* of the concentration[43]:

$$\tilde{C}(k,t) = \mathcal{F}[C(x,t)] = \int_{-\infty}^{\infty} \mathrm{d}x\ \mathrm{e}^{-ikx} C(x,t). \tag{4}$$

Taking the time derivative and substituting in the diffusion equation we find

$$\frac{\partial \tilde{C}(k,t)}{\partial t} = D\int_{-\infty}^{\infty} \mathrm{d}x\ \mathrm{e}^{-ikx}\frac{\partial^2 C(x,t)}{\partial x^2}. \tag{5}$$

The key to solving this equation is to integrate the right hand side by parts twice. If the boundary conditions are such that both the concentration and its gradient vanish at infinity, then the integration by parts results in

$$\frac{\partial \tilde{C}(k,t)}{\partial t} = -Dk^2\tilde{C}(k,t). \tag{6}$$

This equation has the solution

$$\tilde{C}(k,t) = \tilde{f}(k)\mathrm{e}^{-Dk^2t} \tag{7}$$

where the function $\tilde{f}(k)$ corresponds to the Fourier transform of the initial condition. In this case (where $C(x,0) = M\delta(x)$), $\tilde{f}(k) = M$. The last step is to perform the inverse Fourier transform to recover the solution

$$C(x,t) = \mathcal{F}^{-1}[\tilde{C}(k,t)] = \frac{M}{2\pi}\int_{-\infty}^{\infty} \mathrm{d}k\ \mathrm{e}^{-Dk^2t+ikx}. \tag{8}$$

The integral on the right hand side is a Gaussian integral, and can be solved by first completing the square in the integrand exponent[38]:

$$-Dk^2t + ikx = -Dt(k + \frac{1}{2Dt}ix)^2 - \frac{x^2}{4Dt}. \tag{9}$$

Using this, we are finally able to express the solution to Eq.(1) as

$$C\left(x,t\right) = \frac{M}{2\pi}\mathrm{e}^{-\frac{x^2}{4Dt}}\int_{-\infty}^{\infty} \mathrm{d}k\ \mathrm{e}^{-Dk^2t} = \frac{M}{\sqrt{4\pi Dt}}\mathrm{e}^{-\frac{x^2}{4Dt}}. \tag{10}$$

This expression for the concentration is dependent on both time and space, however for our purposes we wish to understand the threshold sensitivity with respect to distance. To that end, we consider the concentration $C^*\left(x\right)$, *which describes the highest concentration at each point in space across all of time.* This is derived by by calculating the time which maximises $C(x,t)$ at each point in x:

$$\frac{\partial C\left(x,t\right)}{\partial t} = \frac{M}{\sqrt{4\pi Dt}}\mathrm{e}^{-\frac{x^2}{4Dt}}\left(\frac{x^2}{4Dt^2} - \frac{1}{2t}\right), \tag{11}$$

$$\frac{\partial C\left(x,t^*\right)}{\partial t} = 0 \implies t^* = \frac{x^2}{2D}. \tag{12}$$

Using this, we have

$$C^*\left(x\right) = C\left(x,t^*\right) = \frac{M}{\sqrt{2\pi e}x}, \tag{13}$$

where e is Euler's number. This distribution represents a "best-case" scenario, where one happens to be in place at the right time for the concentration to be at its maximum. Interestingly, this best case is entirely insensitive to the microscopic dynamics governing D - the maximum distance a transient scent can be detected is the same whether the shark is swimming through water or treacle!

The threshold detection distance $x_{\max}$ can be estimated from Eq.(2) using $x_{\max} = \frac{M}{\sqrt{2\pi e C_T}}$. For a mass of blood $M = 1$g and an estimated LOD of $C_T = 1$ppb $\sim 1\mu\mathrm{gm}^{-3}$. As we are working in one dimension we take the cubic root of this threshold to obtain $x_{\max} \approx 25$m. While this seems a believable threshold for detection distances, is it possible to *track* the source of the odor from this distance? Returning to Eq.(11), the ratio when the concentration is maximal at x is

$$\frac{C(x,t^*)}{C(x+\delta,t^*)} = \exp\left(\frac{\delta}{x} + \frac{\delta^2}{2x^2}\right). \tag{14}$$

Note that this expression assumes that the timescale over which the concentration changes is much slower than the time between inhalations, hence we compare the concentrations at x and $x+\delta$ at the *same* time t^*. Setting $\frac{C(x_{\max},t^*)}{C(x_{\max}+\delta,t^*)} = R$, we obtain

$$x_{\max} = \frac{\delta\left(1 + \sqrt{1 + 2\ln\left(R\right)}\right)}{2\ln\left(R\right)}. \tag{15}$$

For the sensitivity $R = 2$, $x_{\max} \approx 1.8\delta$. In order to track the scent, the shark has to start on the order of δ away from it, completely Fig.2 shows that to obtain a gradient sensitivity at comparable distances to the LOD distance for $\delta = 1$m would require $R \approx 1.04$. Clearly, the ability to distinguish and act on a 4% increase in concentration would require supernatural senses, suggesting either that the diffusion model is doing a poor job capturing the real physics of the blood dispersion, or the shark's ability to sense a gradient is somehow improved when odorants are at homeopathic concentrations.

IV. ADDING A SOURCE

The simple diffusion model in the previous section predicted that at any scent found at the limit of detection would have a concentration gradient too small to realistically track. This is clearly at odds with lived experience, so we now consider a more realistic system, where there is a continuous source of aromatic molecules (e.g. a pollinating flower). In this case our diffusion equation is

$$\frac{\partial C\left(x,t\right)}{\partial t} - D\frac{\partial^2 C\left(x,t\right)}{\partial x^2} + KC(x,t) = f\left(x,t\right) \tag{16}$$

where $f\left(x,t\right)$ is a source term describing the product of odorants, and K is a decay constant modelling the finite lifetime of aromatic molecules.

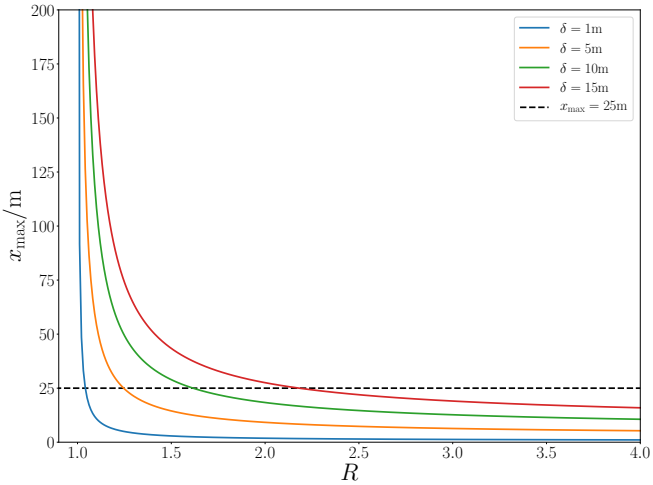

FIG. 2. **Gradient Sensitivity:** The maximum trackable distance depends strongly on both the minimum gradient sensitivity R and the spacing between inhalation δ. In order to obtain an $x_{\max}$ comparable with that associated with the LOD using $R = 2$, δ must be on the order of $x_{\max}$.

Finding a solution to this equation is more involved than the previous example, due to the inhomogeneous term $f(x,t)$. For now, let us ignore this term, and consider only the effect of the $KC(x,t)$ decay term. In this case, the same Fourier transform technique can be repeated (using the initial condition $C(x,0) = C_0\delta(x)$), leading to the solution $C_K(x,t)$:

$$C_K(x,t) = \frac{C_0}{\sqrt{4\pi Dt}} \mathrm{e}^{-\frac{x^2}{4Dt} - Kt}. \tag{17}$$

This is almost identical to our previous solution, differing only in the addition of a decay term Kt to the exponent.

Incorporating the source term $f(x,t)$ presents more of a challenge, but it can be overcome with the use of a *Green's function*[44]. First we postulate that the solution to the diffusion equation can be expressed as

$$C\left(x,t\right) = \int_0^\infty \mathrm{d}\tau \int_{-\infty}^{\infty} \mathrm{d}\xi \; G\left(x,\xi,t,\tau\right) f\left(\xi,\tau\right), \tag{18}$$

where G is known as the Green's function. In order for Eq.(18) to satisfy Eq.(16), G must itself satisfy:

$$\frac{\partial G\left(x,\xi,t,\tau\right)}{\partial t} - D\frac{\partial^2 G\left(x,\xi,t,\tau\right)}{\partial x^2} + KG\left(x,\xi,t,\tau\right) = \delta(t-\tau)\delta(x-\xi) \tag{19}$$

Note that the consistency of Eq.(18) with Eq.(16) can be easily verified by substituting Eq.(19) into it. At first blush, this Green's function equation looks no easier to solve than the original diffusion equation for $C(x,t)$. Crucially however, the inhomogeneous forcing term $f(x,t)$ has been replaced by a product of delta functions which may be analytically Fourier transformed. Performing this transformation on x, we find

$$\frac{\partial \tilde{G}\left(k,\xi,t,\tau\right)}{\partial t} - (Dk^2 - K)\tilde{G}\left(k,\xi,t,\tau\right) = \mathrm{e}^{-ik\xi}\delta(t-\tau). \tag{20}$$

We can bring the entirety of the left hand side of this expression under the derivative with the use of an *integrating factor*. In this case, we observe that

$$\frac{\partial}{\partial t}\left(\mathrm{e}^{-(Dk^2-K)t}\tilde{G}\left(k,\xi,t,\tau\right)\right) = \mathrm{e}^{-(Dk^2-K)t}\left[\frac{\partial \tilde{G}\left(k,\xi,t,\tau\right)}{\partial t} - (Dk^2-K)\tilde{G}\left(k,\xi,t,\tau\right)\right], \tag{21}$$

which can be substituted into Eq.(20) to obtain

$$\frac{\partial}{\partial t}\left(\mathrm{e}^{-(Dk^2-K)t}\tilde{G}\left(k,\xi,t,\tau\right)\right) = \mathrm{e}^{(Dk^2-K)t}\mathrm{e}^{-ik\xi}\delta(t-\tau). \tag{22}$$

Integrating both sides (together with the initial condition $C(x,0) = G(x,\xi,0,\tau) = 0$) yields the Green's function in k space:

$$\tilde{G}\left(k,\xi,t,\tau\right) = \theta_H(t-\tau)\mathrm{e}^{-(Dk^2-K)(t-\tau)}\mathrm{e}^{-ik\xi} \tag{23}$$

where $\theta_H(t-\tau)$ is the Heaviside step function. The inverse Fourier transform of this function is once again a Gaussian integral, and can be solved for in an identical manner to Eq.(8). Performing this integral, we find

$$G(x,\xi,t,\tau) = \theta_H(t-\tau)\frac{1}{\sqrt{4\pi D(t-\tau)}}\mathrm{e}^{-\frac{(x-\xi)^2}{4D(t-\tau)} - K(t-\tau)}. \tag{24}$$

Note that this Green's function for an inhomogeneous diffusion equation with homogeneous initial conditions is essentially the solution C_K given in Eq.(17) to the homogeneous equation with an inhomogeneous initial condition! This surprising result is an example of *Duhamel's principle*[45], which (roughly speaking) states that we can view the source term as the *initial condition* for a new homogeneous equation starting at each point in time and space. The full solution will then be the integration of each of these homogeneous equations over space and time, exactly as suggested by Eq.(18). From this perspective, it is no surprise that the Green's function is so intimately connected to the unforced solution.

Equipped with the Green's function, we are finally ready to tackle Eq.(18). Naturally, this equation is only analytically solvable when $f\left(x,t\right)$ is of a specific form. We shall therefore assume flower's pollen production is time independent and model it as a point source $f\left(x,t\right)$=$J\delta\left(x\right)$. In this case the concentration is given by

$$C\left(x,t\right) = \frac{J}{\sqrt{4\pi D}}\int_0^t \mathrm{d}\tau \; \frac{1}{\sqrt{\tau}}\mathrm{e}^{-\frac{x^2}{4D\tau} - K\tau}. \tag{25}$$

Now while it is possible to directly integrate this expression, the result is a rather ugly collection of error

functions[46]. For both practical and aesthetic reasons, we therefore consider the *steady state* of this distribution $C_s(x)$:

$$\lim_{t\to\infty} C(x,t) = C_s(x) = \frac{J}{\sqrt{4\pi D}} \int_0^\infty \mathrm{d}\tau \; \frac{1}{\sqrt{\tau}} \mathrm{e}^{-\frac{x^2}{4D\tau} - K\tau}. \tag{26}$$

This integral initially appears unlike those we have previously encountered, but ultimately we will find that this is yet another Gaussian integral in deep cover. To begin this process, we make the substitution $t = \sqrt{\tau}$:

$$\begin{aligned}\int_0^\infty \mathrm{d}\tau \; \frac{1}{\sqrt{\tau}} \mathrm{e}^{-\frac{x^2}{4D\tau} - K\tau} &= 2\int_0^\infty \mathrm{d}t \; \mathrm{e}^{-\frac{x^2}{4Dt^2} - Kt^2} \\ &= \int_{-\infty}^\infty \mathrm{d}t \; \mathrm{e}^{-\frac{x^2}{4Dt^2} - Kt^2}\end{aligned} \tag{27}$$

where the last equality exploits the even nature of the integrand. At this point we perform another completion of the square, rearranging the exponent to be

$$-\frac{x^2}{4Dt^2} - Kt^2 = -\left(\sqrt{K}t - \frac{|x|}{2\sqrt{D}t}\right)^2 - \sqrt{\frac{K}{D}}|x|. \tag{28}$$

Combining this with the substitution $t \to \left(\frac{|x|}{2kD}\right)^{\frac{1}{4}} t$, we can express the steady state concentration as:

$$C_s(x) = \frac{J\mathrm{e}^{-\sqrt{\frac{K}{D}}|x|}}{\sqrt{4\pi D}} \left(\frac{|x|}{2KD}\right)^{\frac{1}{4}} \int_{-\infty}^\infty \mathrm{d}t \; \mathrm{e}^{-\sqrt{\frac{|x|K}{2D}}\left(t - \frac{1}{t}\right)^2}. \tag{29}$$

It may appear that the integral in this expression is no closer to being solved than in Eq.(26), but we can exploit a truly marvelous property of definite integrals to finish the job.

Consider a general integral of the form $\int_{-\infty}^\infty \mathrm{d}x \; f(y)$, where $y = x - \frac{1}{x}$. Solving the latter expression, we see that x has two possible branches,

$$x_\pm = \frac{1}{2}\left(y \pm \sqrt{y^2+4}\right). \tag{30}$$

Using this, we can split the integral into a term integrating along each branch of x:

$$\begin{aligned}\int_{-\infty}^\infty \mathrm{d}x \; f(y) &= \int_{-\infty}^{0_-} \mathrm{d}x_- \; f(y) + \int_{0_+}^\infty \mathrm{d}x_+ \; f(y) \\ &= \int_{-\infty}^\infty \mathrm{d}y \; \left(\frac{\mathrm{d}x_-}{\mathrm{d}y} + \frac{\mathrm{d}x_+}{\mathrm{d}y}\right) f(y).\end{aligned} \tag{31}$$

Evaluating the derivatives, we find $\left(\frac{\mathrm{d}x_-}{\mathrm{d}y} + \frac{\mathrm{d}x_+}{\mathrm{d}y}\right) = 1$, and therefore

$$\int_{-\infty}^\infty \mathrm{d}x \; f(y) = \int_{-\infty}^\infty \mathrm{d}x \; f(x). \tag{32}$$

This remarkable equality is the *Cauchy-Schlömlich transformation*[47,48], and its generalisation to both finite integration limits and a large class of substitutions $y(x)$ is known as *Glasser's master theorem*[49].

Equipped with Eq.(32), we can immediately recognise Eq.(29) as a Gaussian integral, and evaluate it to to obtain our final result

$$C_S(x) = \frac{J\mathrm{e}^{-\lambda|x|}}{2\sqrt{DK}}, \tag{33}$$

where $\lambda = \sqrt{K/D}$ is the characteristic length scale of the system.

Having finally found our steady state distribution (plotted in Fig.3), we can return to the original question of whether this model admits the possibility of odorant tracking. Substituting $C_s(x)$ into Eqs.(2,3), we obtain our maximum distances for surpassing the LOD concentration

$$x_{\max} = \lambda^{-1} \ln\left(\frac{J}{2C_T\sqrt{DK}}\right) \tag{34}$$

and the gradient sensitivity threshold

$$R_{\min} = \mathrm{e}^{\lambda\delta}. \tag{35}$$

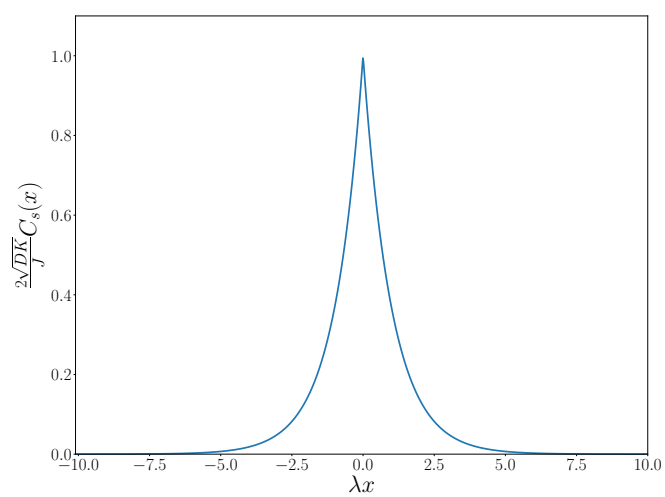

FIG. 3. **Steady state solution for a diffusing system with both source and decay**: While the source term J only determines the maximum concentration at the origin, the degree of exponential fall-off is strongly dependent on $\lambda = \sqrt{\frac{K}{D}}$.

Immediately we see that both of these thresholds are most strongly dependent on the characteristic length scale λ. For the LOD distance, the presence of a logarithm means that even if the LOD were lowered by an order of magnitude, $C_T \to \frac{1}{10}C_T$, the change in $x_{\max}$ would be only $\Delta x_{\max} \approx \frac{2.3}{\lambda}$. This means that for a large detection distance threshold, a *small* λ is imperative.

Conversely, in order for concentration gradients to be detectable, we require $R_{\min} \approx 2$. This means that $\lambda\delta \approx 1$, but as we have shown, a reasonable LOD threshold

distance needs $\lambda \ll 1$, making a concentration gradient impossible to detect without an enormous δ. It's possible to get a sense of the absurd sensitivities required by this model with the insertion of some specific numbers for a given odorant. Linalool is a potent odorant with an LOD of $C_T = 3.2\mu\text{gm}^{-3}$ in air[50]. Its half life due to oxidation is $t_{\frac{1}{2}} \approx 1.8 \times 10^7\text{s}$[51], from which we obtain $K = \frac{\ln(2)}{t_{\frac{1}{2}}} \approx 3.8\times10^{-8}\text{s}^{-1}$. To find the diffusion constant, we use the Stokes-Einstein relation[52]

$$D = \frac{k_B T}{6\pi\eta r}. \tag{36}$$

Taking the temperature as $T = 288K$. The molar volume of linalool in 178.9 mlmol^{-1}, and if the molecule is modelled as a sphere of radius r, we obtain:

$$r = \left(\frac{3}{4\pi N_A} \times 178.9 \times 10^{-6}\right)^{1/3} \text{m} = 4.13 \times 10^{-10}\text{m}, \tag{37}$$

where $N_A \approx 6.02\times10^{23}$ is Avogadro's number. At 288K, $\eta \approx 1.8 \times 10^{-5}\text{kgm}^{-2}\text{s}^{-1}$ and we obtain $D \approx 2.83 \times 10^{-8}\text{m}^2\text{s}^{-1}$, which is close to experimentally observed values[53]. Using these figures yields $\lambda = \sqrt{\frac{3.8}{2.8}}\text{m}^{-1} = 1.17\text{m}^{-1}$, which for $\delta = 1\text{m}$, gives

$$\frac{C_s(x)}{C_s(x+\delta)} = \text{e}^{1.17} = 3.22 \tag{38}$$

a figure that suggests an easily detectable concentration gradient.

As noted before however, a large concentration gradient implies that the LOD distance threshold $x_{\max}$ must be very small. Substituting the linalool parameters into Eq.(33) with $x_{\max} = 20\text{m}$ we find $J = 14\text{gs}^{-1}$, i.e. the flower must be producing a mass of odorant on the order of its own weight. If $x_{\max}$ is increased to 25m, then the flower must produce *kilograms* of matter every second! Fig.4 shows that even with an artificial lowering of the LOD, unphysically large source fluxes are rquired. Once again, the diffusion model is undermined by the brute fact that completely unrealistic numbers are required for odors to be both detectable and trackable.

Adding Drift

The impossibility of finding physically reasonable parameters which simultaneously satisfy both detection threshold and concentration gradients is due to the *exponential* nature of the concentration distribution, which requires extremely large parameters to ensure that both Eqs.(2,3) hold. One might question whether the addition of any other dispersal mechanisms can break the steady state's exponential distribution and perhaps save the diffusive model. A natural extension is to add a *drift velocity* to the diffusion equation, in order to model the effect of wind currents. The effect of this is to add a term

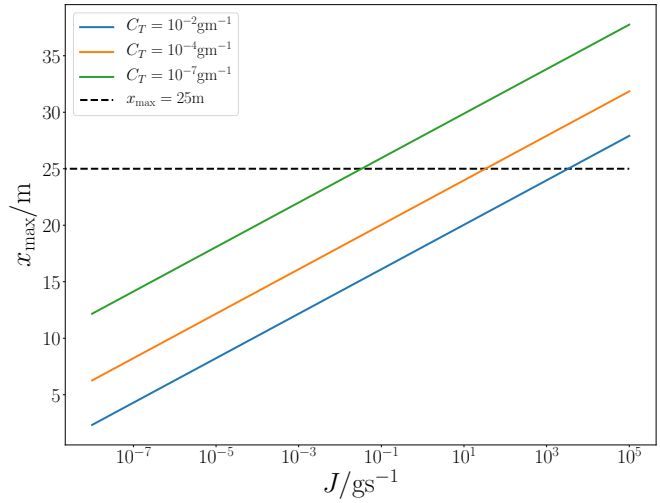

FIG. 4. **Maximum detection distance as a function of source flux**: Using the linalool parameters but varying the LOD threshold, we find that even in the case of $C_T = 10^{-7}\text{gm}^{-1}$ (which corresponds to only $\frac{10^{-21}\times N_A}{154.24} \sim 4$ molecules per cubic metre), one requires tens of milligrams of odorant being produced each second for detection at $x_{\max} = 25$ m. At realistic LOD thresholds, the source flux must increase to kilograms per second to reach the same detection distance.

$-v(x,t)\frac{\partial C(x,t)}{\partial x}$ to the right hand side of Eq.(16). For a constant drift $v(x,t) \equiv v$, and $v \gg D, K$ the steady state distribution becomes:

$$C_s(x) \approx \begin{cases} \frac{J\text{e}^{-\frac{K}{v}x}}{2v} & x > 0, \\ \frac{J\text{e}^{\frac{v}{D}x}}{2v} & x < 0. \end{cases} \tag{39}$$

Another alternative is to consider a stochastic velocity, with a zero mean $\langle v(t)\rangle = 0$ and Gaussian autocorrelation $\langle v(t)v(t')\rangle = \sigma\delta(t-t')$. In this case the average steady state concentration $\langle C_s(x)\rangle$ is identical to Eq.(33) with the substitution $D \to D + \sigma$.

In both cases, regardless of whether one adds a constant or stochastic drift the essential problem remains - the steady state distribution remains exponential, and therefore will fail to satisfy one of the two tracking conditions set out in Eqs.(2,3).

V. DISCUSSION

My Dog has no nose. How does he smell? Terrible.

In this paper we have considered the implications for olfactory tracking when odorant dispersal is modelled as a purely diffusive process. We find that even under quite general conditions, the steady state distribution of odorants is exponential in its nature. This exponent is characterised by a length scale λ whose functional form

depends on the whether the mechanisms of drift and decay are present. The principal result presented here is that in order to track an odor, it is necessary for odor concentrations both to exceed the LOD threshold, and have a sufficiently large gradient to allow the odor to be tracked to its origin. Analysis showed that in exponential models these two requirements are fundamentally incompatible, as large threshold detection distances require small λ, while detectable concentration gradients need large λ. Estimates of the size of other parameters necessary to compensate for having an unsuitable λ in one of the tracking conditions lead to entirely unphysical figures either in concentration thresholds or source fluxes of odorant molecules.

In reality, it is well known that odorants disperse in long, turbulent plumes[54,55] which exhibit extreme fluctuations in concentration on short length scales[56]. It is these spatio-temporal patterns that provide sufficient stimulation to the olfactory senses[57]. The underlying dynamics that generate these plumes are a combination of the microscopic diffusive dynamics discussed here, and the turbulent fluid dynamics of the atmosphere, which depend on both the scale and dimensionality of the modeled system[58]. This gives rise to a velocity field $v(x,t)$ that has a highly non-linear spatiotemporal dependence[59], a property that is inherited by the concentration distribution it produces. These macroscopic processes are far less well understood than diffusion due to their non-linear nature, but we have shown here that odor tracking strategies on the length scales observed in nature[60] are implausible for a purely diffusive model. It is by the subtraction of turbulent air flows that we find this phenomenon is the essential process enabling odors to be tracked.

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[1] Eugene P. Wigner, "The unreasonable effectiveness of mathematics in the natural sciences. richard courant lecture in mathematical sciences delivered at new york university, may 11, 1959," Communications on Pure and Applied Mathematics **13**, 1–14 (1960).
[2] Isaac Newton, *The Principia : mathematical principles of natural philosophy* (University of California Press, Berkeley, 1999).
[3] Wolfgang Weidlich, *Sociodynamics : a systemic approach to mathematical modelling in the social sciences* (Dover, Mineola, N.Y, 2006).
[4] Ingeborg van Vugt, "Using multi-layered networks to disclose books in the republic of letters," Journal of Historical Network Research **1**, 25–51 (2017).
[5] Joel E. Cohen, "Mathematics is biology's next microscope, only better; biology is mathematics' next physics, only better," PLoS Biol. **2** (2004), 10.1371/journal.pbio.0020439.
[6] Erwin Schödinger, *What is life? : the physical aspect of the living cell ; with Mind and matter ; & Autobiographical sketches* (Cambridge University Press, Cambridge New York, 1992).
[7] Herbert W Hethcote, "The Mathematics of Infectious Diseases (SIAM REVIEW)," SIAM Rev. **42**, 599–653 (2000).
[8] Cornelia M. Ulrich, H. Frederik Nijhout, and Michael C. Reed, "Mathematical modeling: Epidemiology meets systems biology," Cancer Epidemiol. Biomarkers Prev. **15**, 827–829 (2006).
[9] Rosa D. Hernansaiz-Ballesteros, Luca Cardelli, and Attila Csikász-Nagy, "Single molecules can operate as primitive biological sensors, switches and oscillators," BMC Syst. Biol. **12**, 1–14 (2018).
[10] Neil Dalchau, Gregory Szép, Rosa Hernansaiz-Ballesteros, Chris P. Barnes, Luca Cardelli, Andrew Phillips, and Attila Csikász-Nagy, "Computing with biological switches and clocks," Nat. Comput. **17**, 761–779 (2018).
[11] Olivier Darrigol, *A history of optics : from Greek antiquity to the nineteenth century* (Oxford University Press, Oxford New York, 2012).
[12] Bill Bryson, *A short history of nearly everything* (Broadway Books, New York, 2003).
[13] Isaac Newton, *Opticks* (CreateSpace, Lexington, Ky, 2012).
[14] Michael Nauenberg, "Newton's theory of the atmospheric refraction of light," American Journal of Physics **85**, 921–925 (2017).
[15] Sascha Grusche, "Revealing the nature of the final image in newton's experimentum crucis," American Journal of Physics **83**, 583–589 (2015).
[16] H. W. White, P. E. Chumbley, R. L. Berney, and V. H. Barredo, "Undergraduate laboratory experiment to measure the threshold of vision," American Journal of Physics **50**, 448–450 (1982).
[17] James L. Hunt, "The roget illusion, the anorthoscope and the persistence of vision," American Journal of Physics **71**, 774–777 (2003).
[18] Rudolf Karl Luneburg, *Math. Anal. Binocul. vision.* (Princeton University Press, Princeton, NJ, US, 1947) pp. vi, 104–vi, 104.
[19] James A. Lock, "Fresnel diffraction effects in misfocused vision," American Journal of Physics **55**, 265–269 (1987).
[20] W Rutherford, "A New Theory Of Hearing," J. Anat Physiol. **21**, 166–168 (1886).

[21] Francesca M. F. Mascarenhas, C. M. Spillmann, John F. Lindner, and D. T. Jacobs, "Hearing the shape of a rod by the sound of its collision," American Journal of Physics **66**, 692–697 (1998).

[22] D. Gabor, "Acoustical Quanta And The Theory of Hearing," Nature **159**, 591 (1947).

[23] Olan E. Kruse, "Hearing and seeing beats," American Journal of Physics **29**, 645–645 (1961).

[24] Charles Sell, *Fundamentals of fragrance chemistry* (Wiley-VCH, Weinheim, Germany, 2019).

[25] L. R. Bijland, M. K. Bomers, and Y. M. Smulders, "Smelling the diagnosis A review on the use of scent in diagnosing disease," Neth. J. Med. **71**, 300–307 (2013).

[26] Marije K. Bomers, Michiel A. Van Agtmael, Hotsche Luik, Merk C. Van Veen, Christina M.J.E. Vandenbroucke-Grauls, and Yvo M. Smulders, "Using a dog's superior olfactory sensitivity to identify Clostridium difficile in stools and patients: Proof of principle study," BMJ **345**, 1–8 (2012).

[27] Bogusław Buszewski, Tomasz Ligor, Tadeusz Jezierski, Anna Wenda-Piesik, Marta Walczak, and Joanna Rudnicka, "Identification of volatile lung cancer markers by gas chromatography-mass spectrometry: Comparison with discrimination by canines," Anal. Bioanal. Chem. **404**, 141–146 (2012).

[28] Claire Guest, Rob Harris, Karen S. Sfanos, Eva Shrestha, Alan W. Partin, Bruce Trock, Leslie Mangold, Rebecca Bader, Adam Kozak, Scott Mclean, Jonathan Simons, Howard Soule, Thomas Johnson, Wen-Yee Lee, Qin Gao, Sophie Aziz, Patritsia Stathatou, Stephen Thaler, Simmie Foster, and Andreas Mershin, "Feasibility of integrating canine olfaction with chemical and microbial profiling of urine to detect lethal prostate cancer," bioRxiv (2020), 10.1101/2020.09.09.288258.

[29] Intaek Hahn, Peter W. Scherer, and Maxwell M. Mozell, "A mass transport model of olfaction," J. Theor. Biol. **167**, 115–128 (1994).

[30] Pliny, *Natural history, a selection* (Penguin Books, London, England New York, NY, USA, 1991).

[31] Marie D. Jackson, Sean R. Mulcahy, Heng Chen, Yao Li, Qinfei Li, Piergiulio Cappelletti, and Hans-Rudolf Wenk, "Phillipsite and Al-tobermorite mineral cements produced through low-temperature water-rock reactions in Roman marine concrete," American Mineralogist **102**, 1435–1450 (2017).

[32] Cedric J. Gommes and Joe Tharakan, "The pclet number of a casino: Diffusion and convection in a gambling context," American Journal of Physics **88**, 439–447 (2020).

[33] Edward A. Olszewski, "From baking a cake to solving the diffusion equation," American Journal of Physics **74**, 502–509 (2006).

[34] Cyril Domb and Elmer L. Offenbacher, "Random walks and diffusion," American Journal of Physics **46**, 49–56 (1978).

[35] Kingshuk Ghosh, Ken A. Dill, Mandar M. Inamdar, Effrosyni Seitaridou, and Rob Phillips, "Teaching the principles of statistical dynamics," American Journal of Physics **74**, 123–133 (2006).

[36] Paulo H. Acioli, "Diffusion as a first model of spread of viral infection," American Journal of Physics **88**, 600–604 (2020).

[37] John D. Ramshaw, "Nonlinear ordinary differential equations in fluid dynamics," American Journal of Physics **79**, 1255–1260 (2011).

[38] K. F. Riley and S.J. Hobson, M.P. Bence, *Mathematical methods for physics and engineering* (Cambridge University Press, Cambridge, 2006).

[39] Jacques Nicolas and Anne-Claude Romain, "Establishing the limit of detection and the resolution limits of odorous sources in the environment for an array of metal oxide gas sensors," Sensors and Actuators B: Chemical **99**, 384 – 392 (2004).

[40] Zhen Ding, Shifu Peng, Weiwen Xia, Hao Zheng, Xiaodong Chen, and Lihong Yin, "Analysis of five earthy-musty odorants in environmental water by HS-SPME/GC-MS," International Journal of Analytical Chemistry **2014**, 1–11 (2014).

[41] Ana Parabucki, Alexander Bizer, Genela Morris, Antonio E. Munoz, Avinash D.S. Bala, Matthew Smear, and Roman Shusterman, "Odor concentration change coding in the olfactory bulb," eNeuro **6**, 1–13 (2019).

[42] Tricia L. Meredith and Stephen M. Kajiura, "Olfactory morphology and physiology of elasmobranchs," J. Exp. Biol. **213**, 3449–3456 (2010).

[43] Lawrence Evans, *Partial differential equations* (American Mathematical Society, Providence, R.I, 2010).

[44] Tom Rother, *Green's functions in classical physics* (Springer, Cham, Switzerland, 2017).

[45] A. N. Tikhonov, *Equations of mathematical physics* (Dover Publications, New York, 1990).

[46] K. F. Riley, M. P. Hobson, and S. J. Bence, *Mathematical Methods for Physics and Engineering: A Comprehensive Guide*, 2nd ed. (Cambridge University Press, 2002).

[47] A.L. Cauchy, *Ouevre Completes D'Augustin Cauchy* (De L'Académie Des Sciences, 1823).

[48] T. Amdeberhan, M. L. Glasser, M. C. Jones, V. Moll, R. Posey, and D. Varela, "The cauchy–schlömilch transformation," Integral Transforms and Special Functions **30**, 940–961 (2019).

[49] M.L. Glasser, "A remarkable property of definite integrals," Math Comp **40**, 561–563 (1983).

[50] Shaimaa A. Elsharif, Ashutosh Banerjee, and Andrea Buettner, "Structure-odor relationships of linalool, linalyl acetate and their corresponding oxygenated derivatives," Front. Chem. **3**, 1–10 (2015).

[51] Maria Sköld, Anna Börje, Elma Harambasic, and Ann Therese Karlberg, "Contact allergens formed on air exposure of linalool. Identification and quantification of primary and secondary oxidation products and the effect on skin sensitization," Chem. Res. Toxicol. **17**, 1697–1705 (2004).

[52] A. Einstein, "Über die von der molekularkinetischen theorie der wärme geforderte bewegung von in ruhenden flüssigkeiten suspendierten teilchen," Annalen der Physik **322**, 549–560 (1905).

[53] Cláudio A. Filho, Carlos M. Silva, Marintho B. Quadri, and Eugénia A. Macedo, "Infinite dilution diffusion coefficients of linalool and benzene in supercritical carbon dioxide," Journal of Chemical & Engineering Data **47**, 1351–1354 (2002).

[54] John Murlis, Mark A. Willis, and Ring T. Cardé, "Spatial and temporal structures of pheromone plumes in fields and forests," Physiol. Entomol. **25**, 211–222 (2000).

[55] Paul Moore and John Crimaldi, "Odor landscapes and animal behavior: Tracking odor plumes in different physical worlds," J. Mar. Syst. **49**, 55–64 (2004).

[56] K. R. Mylne and P. J. Mason, "Concentration fluctuation

measurements in a dispersing plume at a range of up to 1000 m," Quarterly Journal of the Royal Meteorological Society **117**, 177–206 (1991).

[57] Neil J Vickers, Thomas A Christensen, Thomas C Baker, and John G Hildebrand, "Odour-plume dynamics influence the brain's olfactory code," Nature **410** (2001).

[58] M. J. Weissburg, D. B. Dusenbery, H. Ishida, J. Janata, T. Keller, P. J.W. Roberts, and D. R. Webster, "A multidisciplinary study of spatial and temporal scales containing information in turbulent chemical plume tracking," Environ. Fluid Mech. **2**, 65–94 (2002).

[59] Grzegorz Lukaszewicz, *Navier-Stokes equations : an introduction with applications* (Springer, Switzerland, 2016).

[60] Christodoulos Lytridis, Gurvinder S. Virk, Yann Rebour, and Endre E. Kadar, "Odor-based navigational strategies for mobile agents," Adapt. Behav. **9**, 171–187 (2001).

[61] Not that one.