Density Fluctuation in Brownian Motion and its Significance in Olfaction

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Abstract—Sensory perception might be defined, in part, as that activity whereby changes in the environment are detected. From this point of view, fluctuations in a stimulus are more important than the mean stimulus intensity. In this paper, we are concerned primarily with the chemical senses in which the stimulus consists of molecules undergoing random motion in a fluid. We extend Smoluchowski's model of Brownian motion to include an analysis of the variance of observed density fluctuations (variance because we are concerned with changes rather than mean values). A computer simulation of Brownian motion in two dimensions was developed and run on the Cray supercomputer. It is shown that density fluctuations in the computer-simulated data fall within the constraints calculated from the analysis of variance, but that published experimental data deviate somewhat from the theoretical constraints. We then apply the computer simulations to show that successive density measurements by olfactory cells are probably highly correlated, which can produce an olfactory "illusion" during the early moments of the process of smelling.

INTRODUCTION

The sensory response to a stimulus can be measured physiologically by the frequency of action potentials in a sensory neuron (a nerve fiber issuing from a sensory receptor such as a light detector or taste bud), or psychophysically as the magnitude of a sensation (e.g., the brightness of a light or the perceived intensity of an odor). Usually, the sensory response is related to some mathematical function of the stimulus intensity, and various characteristic functions have been nominated [1]. However, sensory response diminishes and frequently vanishes when the stimulus is held constant, a process known as adaptation. A changing stimulus continues to be perceived, while a steady stimulus soon fades from the sensorium. Such considerations led to the formulation of a theory of sensation in which stimulus fluctuation, rather than stimulus magnitude, is the initiator of the sensory process [2]. When we consider these changes for the

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chemical senses (taste and smell) on a microscopic scale, it would seem to make little difference whether one regards mean density or fluctuation in density as the stimulus intensity, since for gases or dilute solutions densities are distributed in space in a Poisson distribution where mean is equal to variance. Therefore, whether a chemical receptor is more sensitive to mean density or fluctuation in density would seem to be unimportant. However, at the onset of the process of sensation there may, indeed be a significant difference.

If the receptor samples the density of its stimulus sufficiently rapidly, there may be strings of density values (say samples \(n, n+1\) and \(n+2\)) that will exhibit a degree of correlation—that is, will not be totally independent of each other. This correlation between density values, particularly during the early milliseconds of the process of sensation, will result in speciously low values of density fluctuation. Within the new view of perception, where change rather than prevailing stimulus strength is the primary actuator of the process of sensation, these early, specious, low values in density fluctuation will be perceived as a weak stimulus signal. The question is, how long does the initial phase of density correlations last? In the microsecond range, it would have little significance, but if correlation persists into the millisecond range, it will modify the sensation of taste or smell, producing a kind of natural illusion during the early moments of sensation.

Smoluchowski [3] produced a model of density fluctuations for particles undergoing Brownian motion, and his model is used, virtually unchallenged, to the present time. We felt it necessary, however, to test the Smoluchowski model rather intensively before applying the results physiologically and drawing inferences from it. We shall outline, very briefly, the development of the Smoluchowski model in the following section. We shall then extend the model to include an expression for the variance of a quantity which is measurable in the laboratory. We then test the extended model

(a) on published experimental data, and
(b) by computer simulation.

With some knowledge of the confidence limits to this model, we apply it to olfactory phenomena.

**BACKGROUND: SMOLUCHOWSKI'S MODEL**

In this section, we outline the development of a model which relates an experimentally observable quantity to one that can be calculated from the physical properties of particles undergoing Brownian motion. If we make sequential measurements of the densities of such particles by observing a small volume element of the space in which the particles are distributed, we may then calculate \((\Delta^2)\), the mean square of the differences between observed densities as they fluctuate in time. We must then relate this measured quantity to the diffusion coefficient of the particles and the boundary constraints of the volume element. We shall then be able to compare theory with “observation” both in the computer model and in the laboratory.

We consider a small element of volume in a fluid in which particles are engaged in Brownian motion. \(P(t)\) is defined as the probability that a particle in a volume of fluid subject to the above conditions will have emerged from it in time \(t\). Based on \(P\), it is clear that we can derive the probability \(A^n_i\) that some \(i\) particles will have emerged in the time, \(t\), from which \(n\) particles were present. The complementary probability is \(C^n_j\), the probability that \(j\) particles remain in the specified volume:

\[
C^n_j = \frac{n!}{j!(n-j)!} (1 - P)^j P^{n-j}, \quad (0 \leq j \leq n),
\]

a Bernoulli distribution.

Under equilibrium conditions, particles are equally likely to enter as they are to leave the volume. Accordingly, the probability \(B_i\) that \(i\) particles have entered in time \(t\) is the probability that \(i\) particles have emerged on some arbitrary occasion. That is, \(B_i = (A^n_i)\), where \(A^n_i\) is
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It can be shown that $B_i$ is a Poisson distribution [4]:

$$B_i = \frac{e^{-\nu P}(\nu P)^i}{i!}, \quad (0 \leq i < \infty),$$

where $\nu$ is the average observed particle density.

Smoluchowski introduced a transition probability, $W(n; m)$, that $m$ Brownian particles will be counted in a small volume of fluid at a time $t$ from the instant when $n$ particles were observed. He then combined $C_j^m$ and $B_i$ to obtain an expression for the transitional probability:

$$W(n; m) = \sum_{i+j=m} C_j^m B_i.$$  

The mean and variance of this distribution, conveniently, are the sum of the means and variances, respectively, of the component Bernoulli and Poisson distributions. Using this property of $W(n; m)$ as the “sum” of two distributions, we can evaluate $\Delta_n = (m - n)$, the difference in current particle density from the initial particle count of $n$, and $\langle \Delta_n^2 \rangle$, the mean square differences of particle density:

$$\langle \Delta_n^2 \rangle = P^2 [n^2 - n] + (n + \nu) P.$$

If we further average this quantity over all values of $n$, we obtain the desired equation predicting mean square differences, irrespective of the initial density:

$$\langle \Delta^2 \rangle = 2\nu P.$$

That is, the mean square difference in particle density is a function only of $\nu$, which is easily measured, and $P$. The probability $P$ can be calculated directly from the equation of diffusion for any simple boundary conditions. The above calculations have been developed fully by Chandrasekhar [4].

The classical development of the model goes no further. While Equation (5) permits us to check the expectation of experimental and simulated data, it does not allow for the scatter of experimental $\langle \Delta^2 \rangle$-data about the expectation curve. It was, therefore, necessary to extend the model.

**VARIANCES OF MEAN DENSITY FLUCTUATIONS**

The quantity $\langle \Delta^2 \rangle$ implies a mean value of the squares of differences in particle densities, for example the mean of $(7 - 5)^2 + (3 - 1)^2 + \ldots$ Let us now consider the mean value of the squares of differences in particle densities for the specific case in which the initial particle density has the value $n$. That is, we consider sums of the form $\sum_{m=1}^{\infty} f_m (m - n)$, where $f_m$ is the frequency of occurrence of the terminal density $m$. We shall represent this mean square difference by $\langle \Delta_n^2 \rangle$, while $\langle \Delta^2 \rangle$ will imply averaging over all initial densities or $n$'s.

We may obtain an expression for the variance of the distribution of which $\langle \Delta_n^2 \rangle$ is the mean by using the usual relation

$$\sigma^2 = \langle (\langle \Delta_n^2 \rangle)^2 \rangle - \langle (\Delta_n^2) \rangle^2.$$  

Substituting equations (4) and (5) reduces $\sigma^2$ to

$$\sigma^2 = \langle (P^2 [n^2 - n] + (n + \nu) P)^2 \rangle - \langle (\Delta^2) \rangle^2,$$

$$= \langle (P^2 [n^2 - n] + (n + \nu) P)^2 \rangle - (2\nu P)^2.$$
Expanding terms we get

$$\sigma^2 = P^4((v - n)^2 - n) + (n + \nu) P^2 + P^2((n + \nu)^2)$$

$$+ 2P^3((v - n)^2 - n(n + \nu)) - 4\nu^2 P^2$$

$$= P^4\left\{\nu^4 - (2\nu^2 + 4\nu^2)(n) + (1 + 4\nu + 6\nu^2)(n^2) - (2 + 4\nu)(n^3) + (n^4)\right\}$$

$$+ P^2\left\{\nu^2 + 2n(n) + (n^2)\right\} + 2P^3\left(\nu^3 - (\nu + \nu^2)(n) - (1 + \nu)(n^2) + (n^3)\right) - 4\nu^2 P^2.$$  \hspace{1cm} (9)

$n$ is distributed in accordance with the Poisson distribution with mean $\nu$ and, thus, the remaining averages are evaluated using moment generating functions. Substituting

$$\langle n \rangle = \nu,$$  \hspace{1cm} (11)

$$\langle n^2 \rangle = \nu + \nu^2,$$  \hspace{1cm} (12)

$$\langle n^3 \rangle = \nu + 3\nu^2 + \nu^3,$$  \hspace{1cm} (13)

$$\langle n^4 \rangle = \nu + 7\nu^2 + 6\nu^3 + \nu^4,$$  \hspace{1cm} (14)

we obtain

$$\sigma^2 = P^4(2\nu^2) + 2P^3(0) + P^2(4\nu^2 + \nu) - 4\nu^2 P^2,$$  \hspace{1cm} (15)

or

$$\sigma^2 = 2\nu^2 P^2 + \nu P^2.$$  \hspace{1cm} (16)

This is the expression we sought for the variance of our distribution.

Thus, in equations (5) and (16), we have the mean and variance of the variable $\Delta t$, for a particular time interval $t$ between observations. Recall that what we are seeking is the expected statistical variation in an average of, say, $N$ mean square difference values we shall use in estimating $P$. The dependence on $t$ enters through $P(t)$.

The variance of an average is

$$\text{Var} \left[ \frac{\sum_{i=1}^{N} \Delta t_i}{N} \right] = \frac{\sigma^2}{N}.$$  \hspace{1cm} (17)

The above quantity is just $\sigma^2$ divided by the number of values used in the average. The greater the number of differences, the closer to mean is the resulting $P$-value.

We shall now proceed to test the model of Brownian motion, first using experimental data and then by computer simulation.

### EXPERIMENTAL TESTS OF MEAN AND VARIANCE OF THE MODEL

Equation (5) for the mean square fluctuation was tested experimentally by Svedberg and Inouye [5] and more completely by Westgren [6,7] many years ago. But lacking the computational facilities to make the thousands of calculations necessary (about 100,000 arithmetic operations are necessary), the test was incomplete. To our knowledge, the predicted variance of fluctuations from the mean has never been tested. Since Westgren published his data in numerical form, it is possible now to complete the evaluation of the model.

Westgren used a microscope to record, at regular intervals, the number of colloidal gold particles in a small volume of water. The density of the particles fluctuated as particles moved into and out of the observed volume as a result of Brownian motion. The motion of the particles is governed by the diffusion equation. The point source solution to this equation provides a probability density function for the appearance of a given particle within an element of volume (e.g., beneath the
objective lens of the microscope) at any time $t$. Using this density function, one can calculate the value of $P(\tau)$, which is the probability that a particle residing in the element of volume at time $t = 0$ will be outside the volume at time $t = \tau$. The calculation is straightforward [4] and provides the solution. By means of a double integration of the point source solution to the diffusion equation we obtain,

$$P(t) = 1 - \frac{2}{(\pi)^{1/2}} \int_0^\infty e^{-x^2} \, dx + \frac{1}{\alpha(\pi)^{1/2}} \left(1 - e^{-\alpha^2}\right),$$

(18)

where

$$\alpha = \frac{h}{2(Dt)^{1/2}}.$$  

(19)

$h$ is the height of the volume layer under observation, $D$ is the coefficient of diffusion, and $x$ is the direction of primary diffusion. The theoretical curves which we calculate agree precisely with those reported by Westgren.

The method used to obtain the experimental measure of $P(t)$ is straightforward. From equation (5),

$$P(t) = \frac{\langle \Delta^2 \rangle}{2\nu}.$$  

(20)

**EXAMPLE.** Consider a sequence consisting of 10 measured density values:

$$d_1, d_2, d_3, d_4, d_5, d_6, d_7, d_8, d_9, d_{10}.$$  

The measurements are separated by equal intervals of time $\tau$.

We can obtain a measure of $\langle \Delta^2 \rangle$, $t = \tau$, by averaging

$$(d_2 - d_1)^2, (d_3 - d_2)^2, \ldots, (d_{10} - d_9)^2 \text{ [9 differences]}.$$  

Similarly, we can measure $\langle \Delta^2 \rangle$, $t = 2\tau$, by averaging

$$(d_3 - d_1)^2, (d_4 - d_2)^2, \ldots, (d_{10} - d_8)^2 \text{ [8 differences]}.$$  

$$\vdots$$  

$$\langle \Delta^2 \rangle, t = 9\tau, \text{ from } (d_{10} - d_1)^2 \text{ [1 difference]}.$$  

In this way, experimental points for times $t = \tau, t = 2\tau, \ldots, t = 9\tau$, can be added systematically to a graph.

We can now compare the limited validation offered by Westgren with the more exhaustive validation permitted by the computer. Westgren’s analysis is reproduced in Figure 1. The smooth curve is given by Equation (18) issuing from the diffusion equation. The measured data have been converted to $P$-values using Equation (20) issuing from Smoluchowski’s model. Experiment matches the theory closely, but no indication of expected deviation from the theory was given. The exhaustive reanalysis of Westgren’s data is shown in Figure 2. The smooth curves are identical to those of Figure 1. Again, agreement appears to be fair. The encircled points correspond to those calculated by Westgren. Comparison of Figures 1 and 2 shows that our points deviate somewhat from those of Westgren. Presumably, the differences arise because Westgren’s plotted points were calculated from fewer density values. Use of all available data gives rise to approximately 1400 squared difference values that are averaged to produce one plotted point. Curiously, though, Westgren’s experimental points lie, for the most part, closer to their theoretical curves than the recalculated points shown in Figure 2.

Figures (3a), (3b) and (3c) depict the points of Figure 2 along with associated theoretical points and standard deviations. The latter, of course, provide the criteria by which one can judge how closely Smoluchowski’s theory is confirmed by Westgren’s measurements. One can see that the correspondence between model and experiment is not completely satisfactory.
Figure 1. The probability that a colloidal particle present in the observed volume will emerge during the time, \( t \), is plotted against \( t \) for different heights, \( h \), of the volume layer.

\[
\Delta h = 2.73 \text{ \mu m} \\
\square h = 8.56 \text{ \mu m} \\
\blacksquare h = 11.15 \text{ \mu m}
\]

The solid curves have been calculated from the equation of diffusion. The data points are those of Westgren [6], calculated from the experimental observations using Equation (20).

Figure 2. Reanalysis of Westgren's experimental data. The smooth curves are identical with those in Figure 1, and data points are calculated as in Figure 1 using Westgren's data. All possible data points have been calculated, both those made by Westgren and reported in Figure 1 (circled), and those not made by him. Notice, by comparison with Figure 1, that the circled values differ somewhat from those calculated by Westgren.

**COMPUTER SIMULATIONS**

To confirm Brownian motion theory under Smoluchowski's assumptions, particle movements were simulated on the CRAY X-MP/22 supercomputer. Most Brownian motion algorithms function by calculating a particle's displacement over successive time intervals \( \Delta t \), based on a dynamical equation of motion [8,9]. The most appropriate equation for computer simulation, the Langevin equation, is simply an expression of Newton's law equating change in momenta \( m \dot{v} \) to forces acting on the particles [10]. It reads

\[
m \dot{v} = -m \gamma v + F + A(t), \tag{21}
\]

where \( m \) is mass, \( v \) velocity and \( \gamma \), the coefficient of friction [8].

Consider the terms on the right hand side of the Langevin equation. The first term is the friction term, acting to decrease particle energy. It includes the indirect interaction of particles
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(a) $h = 2.73$ µm. □ are points calculated from Westgren's data. † indicate theoretical points and ± one standard deviation, calculated from Equations (16) and (17).

(b) $h = 6.56$ µm. □ and † as in (a).

(c) $h = 11.15$ µm. □ and † as in (a).

Figure 3. Reanalysis of Westgren's data and statistical variation from the theory. The $P$-values of Figure 2 are reproduced together with the corresponding theoretical points, indicating one standard deviation above and below theory. The units of time are $\tau$, the time interval between observations. $\tau$ is 0.61s for the $h = 2.73$ µm experiment and 1.39s for the other experiments. We expect almost 70% of values to lie within one standard deviation from theory. However, barely 20% of points meet this criterion.
on each other through the perturbation of the velocity of the fluid molecules. It is followed by $F$, the direct forces term. Direct forces include, per example, the effects of field forces and interparticle forces. The last term $A(t)$ constitutes the random force exerted on a particle by the surrounding fluid—i.e., the Brownian motion component of the equation of motion. It tends to increase particle energy [10].

The Langevin equation can be rewritten as

$$\frac{dy}{dt} = -\frac{1}{\gamma} \frac{d\mathcal{H}}{dt} + \frac{F}{\gamma m} + \frac{A(t)}{\gamma m},$$

where $y$ specifies particle position in three dimensions.

A system is essentially diffusive if the medium has a high viscosity, as is always the case with liquid solutions. Under these conditions, the velocity distribution relaxes much more quickly than the position distribution and the velocity term of equation (22) can be neglected [8]. In the absence of any direct forces, the corresponding term may also be dropped. Choosing to represent particle movement in a single direction, leaves us with

$$\frac{dy}{dt} = \frac{A(t)}{\gamma m},$$

where $y$ and $A$ being now one-dimensional. Integration of equation (23) leads us to a simple difference equation which can be used to simulate the movement of Brownian particles in the diffusive regime:

$$y_{n+1} = y_n + N(y; 0, 2D\Delta t),$$

where $N$ symbolizes a Gaussian-distributed random variable. The position values $y_{n+1}$ and $y_n$ are separated by time $\Delta t$. The last term of (24) is the zero-mean, $(2D\Delta t)$-variance Gaussian variable.

The computer simulation algorithm is described by equation (24); it iteratively calculates a particle's position at times $\Delta t$, $2\Delta t$, $3\Delta t$, … Even though the current particle position is dependent on its past position, the change in position is determined stochastically. Therefore, the displacement is independent and a sequence of displacement values are qualified as stationary (i.e., governed by identical distributions).

The prominent feature of (24) is that the particles move in accordance with normally distributed displacements. The Polar Marsaglia method [12], an exact method that avoids the need for evaluating time-consuming trigonometric functions, was used to generate normal random numbers.

Densities were recorded in the simulation at 0.1 second intervals in layers of height 2.73 and 6.56 $\mu$m (refer to Equation (19)) with respect to the subvolume element. These heights correspond to the dimensions of the first two of Westgren's experiments, represented by the top curves in Figures 1 and 2. The simulated densities were processed in the same manner as Westgren's observations and resulting $P$ curves plotted, with theoretical prediction and variance, in Figures (4a) and (4b). Both experimental and simulated $P$'s were based on approximately the same number of densities, facilitating comparison to the points in Figure 3.

Figure 4 paints a picture remarkably consistent with statistical theory. In both simulations, approximately 70% of values lie within one standard deviation and almost all values within two standard deviations of theory.

**DISCUSSION OF THE PHYSICAL THEORY**

The experimental $P$-points computed from the totality of Westgren's data are the most accurate estimates possible based on the number of measurements made. And yet, these points, in general, deviate further from their respective theoretical curves than implied by Westgren. The
laws of chance do not prohibit the possibility of a subsequence of the available observations producing a more accurate set of $P$-values. However, it seems unlikely since a mean square difference based on fewer points would have a correspondingly larger variance $\sigma^2/N$.

With reference to Figure 3, it is apparent that most experimental points deviate from theoretical values by at least two standard deviations and 80% lie greater than one standard deviation from theory. We conclude that statistical randomness is not a sufficient explanation of the deviation of experiment from theory.

From Figure 4, we see that, by and large, the Cray-simulated data do lie within one standard deviation of the expected $P$-curve. This result essentially confirms the validity of the model equations and the computer simulation.

![Figure 4](image-url)

(a) $h = 2.73$ µm.

(b) $h = 6.56$ µm.

Figure 4. Computer simulations of some of Westgren's experiments. The jagged curve shows data simulated using the Cray computer. The central smooth curve is the corresponding theoretical curve from Equations (18) and (19). The outer smooth curves define ± one standard deviation and ± two standard deviations from the central theoretical curve. Careful examination reveals that about 70% of the simulated curve lies within ± one standard deviation and 95% within ± two standard deviations, conforming well to statistical prediction.

How can one interpret the deviation of the experimental results from those of the computer simulation? Experiments support the general trend predicted by theory. However, there is a degree of variation in density fluctuation data not accounted for by applying Smoluchowski's equations to experiment. Deviation of experimental values from theory is due either to errors...
inherent in the experiments themselves, to inadequacies in the physical postulates in the theory, or to improper application of the theory to experiment. For example, inter-particle forces may not be negligible, as assumed by the theory. Or constraint of diffusion to a single dimension, as used in the mathematical derivation of the $P$-curve may have introduced more error than expected.

The computer simulations of density fluctuations confirm the fidelity of the theoretical treatment of Brownian motion to the modern view of molecular motion in liquids or gases. The statistical analysis of density variations was also confirmed by the simulations. It also proved possible, using the computer, to extract considerably more information, and to extract information more accurately, from previously analyzed experimental data.

**IMPLICATION FOR OLFACTION**

Our motivation for carrying out the tests on the validity of the physical model was primarily to justify its use in computing the degree to which density fluctuations are correlated in samples of an odorant drawn during a very brief interval of time. Certainly we could obtain a measure of correlation using a standard autocorrelation technique. The autocorrelation function for velocity of particles in Brownian motion is a negative exponential derived from the frictional coefficient $\gamma$ of the Langevin equation [13]. A more modern method for evaluating density correlation functions is by means of neutron or X-ray scattering by the Brownian particles [14]. In principle time-dependence of density correlation could be obtained as well. A theoretical value of density correlation, however, is obtained very simply using the $P(t)$-function which is derived directly from the diffusion coefficient, which can be determined empirically, and which we have just validated.

The human olfactory epithelium, in which the olfactory receptors are located, is bathed in two mucous layers. The outer mucous layer has a lower viscosity, and the inner layer has a higher viscosity. The receptors lie in the high viscosity layer. Unfortunately, both the exact thicknesses of the layers and their respective viscosities are not known precisely for the human being. The thickness $h$ of the deep mucous layers is 30 $\mu$m for frogs and salamanders but only 5$\mu$m for higher vertebrates such as cats and dogs [15-17]. The values for viscosity in the human being must be inferred. The viscosity of the superficial mucous layer is usually taken as that of water, or 0.01 poise [18,19,20]. The viscosity of the deep mucous layer has been taken as approximately that of canine tracheal mucus, which has a value of 200 $p$. For a more detailed review, please refer to the thesis by Aebersold [21].

For diffusion within the deep mucous layer, $P(t)$ rises slowly to its asymptotic value (state of absence of correlation) during a period in the order of one second, as implied in the computer simulation of Figure 5. This one-second value implies, using the entropic or fluctuation theory of sensation, that during the early milliseconds of the process of olfaction, neural activity is lower than expected from the mean density of the odorant. That is, neural discharge rate would be expected to increase during the early phases of olfaction. One does, in fact, have some evidence of this effect from the work Mozell [22]. At the conscious level, one would expect a natural illusion in which the intensity of smell would build up over a period of a few seconds (conscious apprehension of events is delayed and protracted with respect to neural events at the sensory periphery). This correlational delay in sensation would add to the mechanical delay produced by convection and attainment of diffusional equilibrium within the mucous layers and would serve to further limit the speed at which one could detect an odor.

**SUMMARY**

The Smoluchowski model of Brownian motion has been expanded to allow an experimental check on the variance of density fluctuation about their expected value. The model is confirmed to a point. Using the model, we have found that during the early period of the olfactory or
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Figure 5. \( h = 0.2 \mu m \), which is approximately the diameter of one cilium. For comparison with earlier simulations, where viscosity equaled 1.5 p, we include this computer simulation, run with the same boundary conditions, but with viscosity equal to 900 p, corresponding to the best guess for deep mucous layer of the olfactory epithelium. \( P(t) \), the probability that a particle has left the observed volume element, is plotted against time. The lower curve corresponds to the case of zero convective flow, and the upper curve to the more realistic case of convective flow rate equal to 0.1 mm s\(^{-1}\).

Smelling process, densities of the odorant are probably significantly correlated, which may have interesting consequences for the physiology and psychophysics of olfaction.

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