ATMOSPHERIC ODOUR RESPONSE OF HUMAN NOSES

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Abstract

Human noses are sensors that respond to volatile molecules in the air from some odour source. The sense of smell is able to identify many odours and assign the strength of odour for useful awareness of the environment, including foraging for food and alerts to dangers. In modern society the amenity of our environment is a high priority and offensive odours are regulated and mitigated. The understanding required for regulation depends on the exposure to odours carried on the winds, but also on the complex biological processes that convert atmospheric signals into brain signals and our perception of smell. The molecules are carried in a stream of air into noses, to a surface of sensor cells where molecules are identified and released and electrical signals from excited neurons passed into the brain. The complex process acts on time scales determined by the atmospheric structure of chemical signals, the fluid flow process of passing chemicals through the nose onto a surface, the molecular absorption/desorption, and the progress of excited electrical signals into the brain. These are linked to the time scales of sniffing, determining that chemical fluctuations averaged over about one second are the key to the sampling. A simple Gaussian plume is found to describe the chemical input to the olfactory sensor cells based on straining flows in the nose on sniffing time scales and flow rates.

Keywords: Olfaction, neurons, sensors, stagnation flow.

1. Introduction

1.1. Olfaction

Human olfaction is both an example and shares many characteristics of more general mammalian odour sensing. While often regarded as grossly inferior compared to dogs and rats, human odour perception is an important sensing function (Gilbert 2008). The importance for humans can be gauged by industries like perfumes and fragrances, food additives and preparations, and simple pleasures like ‘smelling the roses’. On the other hand, our amenity can be severely impacted by bad odour, and foul smells constitute a considerable environmental nuisance in all cultures and societies (Vance 2008).

The remarkable reality about odour and the sense of smell, despite the long standing link to science Aristotle (350 B.C.), is that our scientific understanding of odour sensing, perception and prediction is poor. Partly this is because of great complexity, including the turbulent nature of the wind-borne chemical signal, but also the chemical complexity of typical odours (many types of molecules) and the corresponding complexity of the olfactory receptors cells and the complex ‘wiring’ into neurons, and axons into the brain. However, most of us reliably use the sense of smell to identify, locate and estimate our olfactory environment. In other words, from all the constituent complexity there is an emergent sense of smell that we collectively and reproducibly share as humans.

In this paper we describe some of the detail of the complex components, hopefully to explain the working of the sense of smell and provide clarity on a number of questions:

- First, the relevant time scale for sampling the chemicals in the atmosphere.
- Second, the link to sniffing as our natural sampling process.
- And third, the scope for physiological differences in individual perception of odour.

These details can be usefully understood with some simple models of the physiology, the neural wiring, and the flow in an idealised nose.

For the purpose of this paper we largely ignore the problem atmospheric scientists mostly focus on which is the prediction of odour fluctuations for given source emissions in air and the relationships with meteorology, source emissions, dispersion and

mixing. These characteristics and influences are assumed to be known at the nose on which our attention is focussed.

1.2. Odour Signals

In figure 1 we show a typical graph of the concentration of an odourant in air downwind of a constantly emitting point-source modelled as a sequence of puffs with turbulent wind time series used as the instantaneous source-wind for each puff. The wind is modelled in neutral-stability conditions with a mean wind of 2 m/s at source height and 5% turbulent-wind intensity.

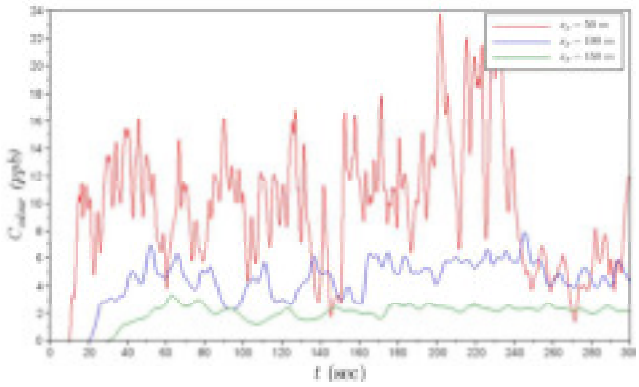

Figure 1. Typical Atmospheric Odour Time Series

The up-and-down fluctuations are entirely due to turbulent wind fluctuations which randomly blows odourant, generally downwind, but laterally and vertically as well. Far downwind, these filtered puff fluctuations are weaker, as shown in the figure, with time series at three downwind distances from the odour source. For many problems it is large peak concentrations of odour, at least close to the source, which are important for the sense of smell.

The signals shown in figure 1 are generated with a filtering process with a band-width of one-second averaging over the signal nearest to the source. The required understanding of the nose responses are answers to the questions: can the nose respond to the large but short one second peaks or is it an accumulation over longer time scales like 30 seconds to a minute that is important? Intuitively, we expect the typical one second sample sniff to be our appropriate odour sampling event but the analysis below helps to understand why this is the case and importantly why and how the nose sensing recovers in between sniffs.

2. The Human Nose

2.1. The nasal passages and olfaction sensing cells

Most of us see our own noses in a mirror on a daily basis, but probably do not know what lurks within. Figure 2 shows a schematic of the nose and considerable effort in understanding the details of nasal flow are currently underway (Rennie *et al* 2011). For our purposes many simplifications can be made: in profile the nostrils are opening to a nasal cavity with effectively slot like chambers progressing into skull, which terminate at the top of the slots at a surface which deflects the inflow into exit 'exhaust manifold'. At the deflecting surface at the apex of the nasal cavity, the inflow jets from the nostrils decelerate normal to the surface and spread laterally. Approximately at the stagnation point is where a 2 cm^2 patch of olfactory sensory cells reside in an epithelial layer with a thin mucous covering – more detail is given below.

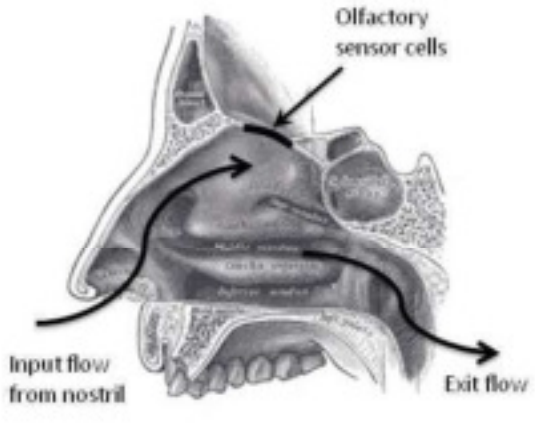

Figure 2. Schematic of nasal air flow, impacting on epithelial olfactory sensor cells at the apex of the nasal cavity.

The complicating intrusions mainly control recirculation in the nasal cavity. The overall design is to facilitate an in-flow onto the sensor cells and effective removal of that air to allow a new inflow not contaminated by the prior input.

Some of the key characteristics of the nasal cavity are:

- Distance from the nostril to the sensor cells is about 8 cm in an adult.
- The nasal cavity is a slot like cavity with width (normal to the page in figure 2) of about 1 cm
- A jet from the nostril impacts directly onto the sensor cells protruding from a bony substrate which deflects the flow at right angles.

Simple approximations are used later to estimate the chemical concentration exposure at the sensor cells for a given atmospheric concentration at the nostrils. For simplicity we use a model for chemical sensing with direct absorption/desorption at the epithelial layer (allowing for minimal time lag for diffusion through the mucous layer) and with no

mass exchange, that is to say the molecules at the epithelial layer effectively couple with the sensor cells and then are released and diffuse back out of the mucous layer and are swept away by the remnant sniffing flow.

The time scale for molecular exchange is of the order of ten milli-seconds and is effectively instantaneous from the perspective of odour perception. The molecules therefore enter and exit the nasal cavity, but leave an electrical imprint from the depolarisation of the sensor cells which will be described below.

2.2. The Olfactory Sensing Cells and Neural Wiring

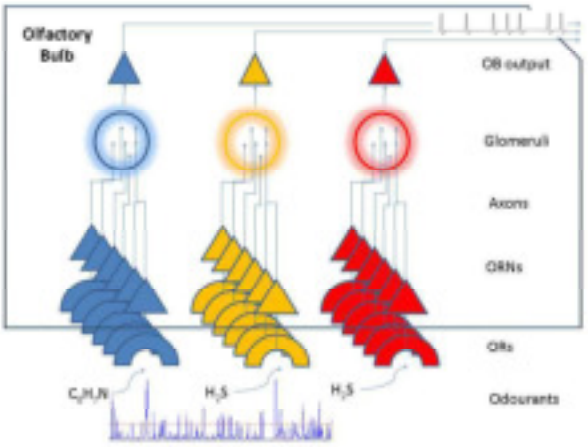

Figure 3. Schematic of the olfactory sensor cells and wiring to receptor neurons and higher order synapse and olfactory bulb 'repeater' neurons.

At the top of the nasal cavity resides a small patch of cells as indicated in Figure 2. In this patch are distributed the odour receptors, which are a family of trans-membrane proteins that protrude from the cell wall into the epithelial mucous layer and interact with molecules that diffuse into the mucous layer. The trans-membrane proteins are drawn from a family of a thousand or so types which have known mapping onto genetic code (Buck 1996). In humans about 350 different proteins are expressed, that is to say, the epithelial layer typically has 350 different types of protein receptors which interact with different odourant molecules and at different concentrations of those molecules.

2.2.1. Odour Receptors (ORs)

In figure 3 the receptor cells (ORs) are shown at the bottom of the schematic interacting with odourant molecules, for illustration listed as hydrogen sulphide and indole (faeces odour).

The response is a *threshold* response, so that for some odourants only a sufficiently high concentration will excite enough receptors for a net response. Below the threshold there is no perception of smell. In the epithelial layer there are enormous numbers of receptor trans-membrane protein cells, up to a million for a single type of protein. There are hundreds of millions of possible odourant interaction sites in the epithelial layer and the diversity of different types makes it possible to respond to a diverse array of odourant molecules Sell (2006).

For a simple case, a single odourant chemical may excite a subset of the receptor cells. Exposure to the chemical for a short finite time has odourants adsorb onto the trans-membrane protein for the relevant subset of receptors. The receptors compete for the odourants, so that those with the highest binding energy are extracted first and only if enough molecules remain (for high enough concentrations) will binding sites at lower energy be occupied.

2.2.2. Odour Receptor Neurons

Each cluster of activated OR cells of a single type triggers a known signalling pathway (Buck & Axel 1991) along dendrites connected to an odour receptor neuron (ORN) for each family. These are shown in figure 3 as triangles and there are about one million neurons of this type. Therefore each colour coded receptor neuron (the triangles) connect to many OR cells of a single type, on average a hundred. When sufficient of these cells excite the odour receptor neuron it then fires a nerve impulse along an axon into the olfactory bulb.

2.2.3. Glomeruli Synapses and Mitral Neurons

The odour receptor neuron axons all converge into a site where synaptic connections are made in a bundle called a glomeruli node, and when sufficient excitation of these nodes (which number 350 for the 350 different types of receptors) occurs, a linked neuron (the mitral neuron also shown as a triangle in figure 3) generates an action-potential impulse along an axon exiting the olfactory bulb as input into the brain. 350 channels of signals for the different receptor types are possible inputs into the brain each effectively an on-off indicator of stimulation by an odourant associated with its linked OR protein.

The convergence occurs at two levels, with dendrite connections of OR cells to an OR neuron, at about 100 to one, and a second convergence from the ORNs to the glomeruli of about 30000 to one. This amplifies and correlates the stimulus from an odourant to indicate the threshold presence of an odour and, when present in high enough concentrations, at higher and higher thresholds to indicate the intensity of an odour, which is discussed below. If the stimulus is too large or persists for too long, olfactory fatigue may occur,

when the sensor cells, neurons and glomeruli are unable to respond to any additional odour stimuli. Recovery requires flushing with clean non-odorous air, and with time for the chemical and electrical balances to be restored.

3. A Model for Odour Recognition and Intensity

3.1. Odour Recognition

For the nose described above, the process of odour perception begins with air containing an odourant passing over the epithelial layer and exciting a signal from the olfactory bulb conveying information about the odour.

At very low concentrations nothing occurs, but above a first threshold the simplest case is the excitation of one member of the family of odour receptors, which sends a coded impulse for that receptor to the brain. If each odourant has a single unique receptor then our library of odours is comprised of just 350 smells, but this is far fewer than estimated in studies of olfaction. Table 1 gives a very small sample of the variety of smells and for the range of odourant threshold concentrations (Sell 2006).

Volatile Compound	Smell Identification	Threshold Concentration
Acetone	Pungent	10 ppm
Indole	Putrid,fecal	140 ppb
Damascenone	Roses	0.002 ppb
Dimethyl sulphide	Rotten Cabbage	20 ppb

Table 1. Some common smell characteristics.

The range of sensitivity to threshold concentration varying over many orders of magnitude is simply related to how likely the molecule is going to bind with a receptor and, for that particular receptor, how many receptor cells there are and how much convergence of dendrites and axons occur.

However, given the diversity of smell descriptions possible, up to 10000 distinct smells according to Gilbert (2008), the threshold concentrations listed above are likely to require multiple receptor types to be excited. Clearly, if a single compound requires more than a single receptor for identification, then the number of possible smells is reduced unless each receptor binds with multiple odourants.

A simple way for accounting for this diversity is if the family of 350 OR types is comprised of 12 subfamilies of about 30 different receptors. If these 12 different family channels are excited as binary signals from the olfactory bulb, i.e. a set of 12 zeros and ones to indicate the presence or not of an odourant, then 2^{12}=4096 differently coded smells exist. The most simply encoded smells only require a single receptor input (a one) with all other receptors failing to fire and give a zero. So the most sensitive odours would correspond to those simple codings. On the other hand, in this model some odours will require up to twelve different receptor systems to 'fire' simultaneously and register a detection to the brain. These are most likely to require much higher concentrations to register this clear identification of the odour.

3.2. Odour Intensity

A second attribute of odour is the intensity of the perception of the odour, or just how strong we think the odour is. Sensory perception is a difficult science, but for odour a common tool has been the Weber-Fechner scale of odour intensity, related to the logarithm of concentration for large concentrations (Nagata 2003). In the context of the olfactory receptors, if we achieve identification then at higher intensity we expect just more sensor cells and sensor neurons to be firing within the same family. It is natural to associate the intensity of perception with the amount of neural activity stimulated and progression as a logarithmic law can be related to scaling from information theory for efficient extraction of information from a concentration signal, i.e. the nose is designed for maximum extraction of information from chemical signals in the environment (Borgas 2013).

The number of olfactory neurons firing at the level of glomeruli in figure 3, which produce the signal for the brain, can be approximated by the simple relationship (Nagata,2003 ; Sell, 2006)

$$k_n = k \log\left(C/C_{thresh}\right) \quad , C \geq C_{thresh} \quad . \quad (1)$$

For a suitable scale, the intensity of smell is proportional to the number of neurons firing (k_n) for odour concentrations, C, above the detection threshold C_{thresh} .

Important odours for human well being can encode in parallel so that the constant, k , in (1) is larger and a more intense odour is possible for concentrations near the threshold of detection. This means that multiple neurons are excited at the same concentration, or within a narrow band of concentrations. On the other hand, the sensitivity may be encoded by having low threshold concentrations with many receptors readily binding with the relevant odourant molecule.

In general, the parameters in (1) have to be determined empirically (Nagata 2003), and no practical theory exists for estimating the complex chemistry of odour-protein binding, electrical cell excitation and synaptic excitation in the glomeruli.

3.3. Timescales of Odour Perception

The processes of molecular binding with receptor cells and the associated electrical/chemical signalling in the olfactory bulb is typically measured in milli-seconds, perhaps fitting with our intuitive expectation of instant recoil from an offensive odour. However, is it realistic to expect that we respond to a millisecond instantaneous puff of odour in the atmosphere? In fact we expect such signals to be random because of turbulent mixing, and therefore have a probability distribution of concentration. Odour problems are often framed in the context of peak-to-mean ratios (Barry 1971). Because of long-tailed distributions this begs the question that since the molecular apparatus of the nose can respond to millisecond samples of atmospheric odour, do we need peak-to-mean ratios for as short an averaging time as ten milli-seconds, or 100 milli-seconds or is a one-second average the fundamental driver of olfaction? The answer to these questions is provided not by the molecular and neural time scales, but by the function of human sniffing and odour transport within the nasal cavity (Laing 1983).

4. A Nasal Cavity Flow Model

4.1. Two dimensional approximation

The span-wise thinness of the nasal cavity slots means the flow in the cavity is approximately two-dimensional. The inflow is generated by the sniff by inhaling into the lungs sucking air into the nostril. A typical sniff has duration of about one-second, and is of sufficient strength to draw air into the nasal cavity, over the epithelial sensor layer and out of the exit manifold.

It is clear that the sniff is a critical functional part of the sense of smell (Laing, 1983). This is because molecular diffusion on its own can only transport molecules from the nostril to epithelial layer in a time scale of around 5 minutes and atmospheric winds obviously play no role inside the nose.

The main characteristics of the nasal cavity flow are captured by a simple stagnation point flow on the surface containing the epithelial layer and where the line along the bridge of the nose inside the cavity is effectively a plane of symmetry.

The idealised flow is represented by figure 4 below. The input pulse at the nostril is blown down onto to the surface containing the odourant sensors. The idealised straining flow (outside a thin diffusion layer) is very simple

$$u = \sigma x,\ v = -\sigma z \qquad (2)$$

for the straining parameter, σ, which can be estimated as $\sigma \approx 8\ s^{-1}$ so that a one second sniff locates the pulse at the nostril within the diffusion layer at the surface (for a diffusivity of $\nu \approx 0.15\ cm^2 s^{-1}$). This can be estimated because the solution of the straining flow is represented by

$$x = x_0 \exp(\sigma t),\ z = z_0 \exp(-\sigma t), \qquad (3)$$

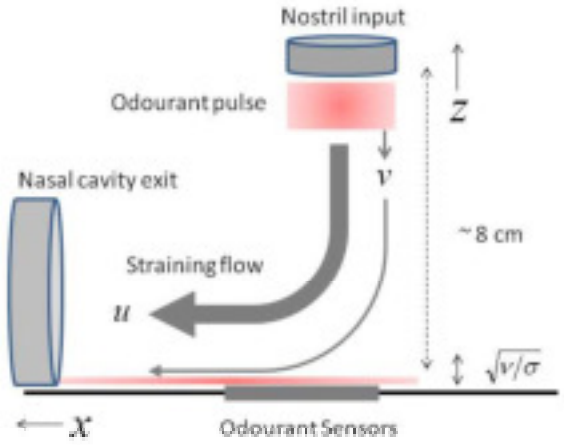

Figure 4. Schematic of the straining flow in the nasal cavity. The dashed line is a plane of symmetry aligned with the bridge of the nose.

with the initial positions, at time t=0, in the input pulse, so that assuming a half-second impact time,

$$\sqrt{\nu/\sigma} = z_0 \exp(-\tfrac{1}{2}\sigma) \Rightarrow \sigma - \log\sigma = 6\ . \qquad (4)$$

The inlet velocity at the nostril for this value of strain is 70 cm/s, so that a one second sniff inhales about 300 ml of air, which is typical for humans at normal inspiration rates (Rennie *et al.* 2011).

A straining flow has a number of key features, first there is effectively no spanwise dependence of the pulse concentrations as it is advected down onto the surface, so the precise position of the sensor cells relative to the nostril is not important. The straining flow also stretches the pulse and compresses it vertically so it becomes ever thinner as it approaches the surface as shown in the figure. Effectively the full one-second duration input pulse is compressed into the diffusion layer during the sniff. The input concentration is conserved in this non-diffusive model, however all finer-scale structure in the atmospheric concentration field is compressed and effectively lost during the sniff.

In the Appendix a simple diffusion model is used to simply describe the straining flow deposition process. The concentration exposure at the epithelial layer for nostril-pulse width σ_0 is

$$\frac{C}{C_0} = 2\frac{\sigma_0}{\bar{z}_0}\lambda e^{-\frac{1}{2}\lambda^2}, \quad \lambda = \frac{\bar{z}_0}{\sqrt{\sigma_0^2 + 2\kappa t e^{2\sigma}}} \quad . \quad (5)$$

For a typical nose, and for an input pulse of a few centimetres in scale we obtain the concentration plots shown below in figure 5.

The straining flow rate was selected for a half-second advection time from the nostril onto the sensor's diffusion layer, and this characteristic is clear in figure 5 for the more detailed calculations of the 'Gaussian plume' model given in the Appendix.

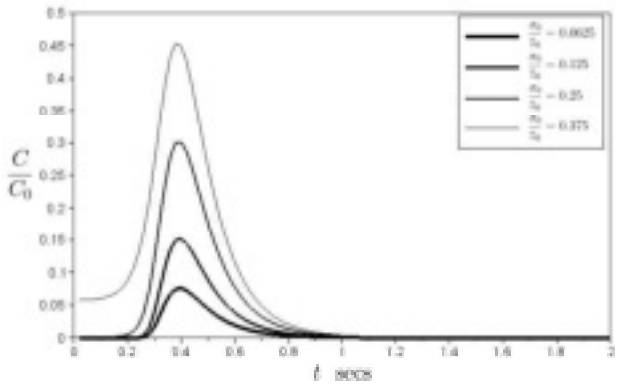

Figure 5. Concentration response at the epithelial sensors for different pulse thicknesses.

The flow in the diffusion layer and the overlying mucous layer can also be analysed in detail, but the effect is a modest time lag added to time response described by the sniffing Gaussian puff. The overall fluid mechanics of sniffing indicate that the key time scale of the odour perception process is on the order of one to two seconds. The near instantaneous molecular and electrical responses once odourant molecules engage with receptor proteins and the associated neural signalling are not the rate controlling processes in odour perception.

Finally, the rapid flushing of odour from the epithelial layers at the end of the sniff is an important characteristic of odour sensing. If the atmosphere has broad smooth distributions of odour, then a pulse of odour is the incorrect conceptual model and instead the odour sensors are flooded constantly with odour molecules and odour fatigue occurs. In this case the molecular processes are overwhelmed by odour sensing and cannot recover between sniffs for the pulse-sniff scenario described above. The process of useful odour perception clearly requires the distribution of odour in air to be patchy and localised enough for significant recovery time between sniffs, and for the post-sniff peak rapid flushing as shown in figure 5.

5. Odour Sampling for Regulation

Odour regulation, for example using German VDI standards use a regimented protocol for sniffing, with distributed sampling over an hour with an odour-hour defined if a sufficient number of sniffs sense positively for odour. To model these processes, it is clearly most effectively done with one-second averaged concentration samples. This is because shorter time scale pulses are all accumulated within the sniffing process and cannot be differentiated. On the other hand broader scale fluctuations are only ever sampled by a one to two second sniffing process and if it is possible to model concentrations down to a few seconds averaging time fidelity, this is indeed the key to understanding the frequency of odour sensing in the environment.

6. Summary

A simplified understanding of odour perception in humans is provided and details for nasal cavity flow are shown to regulate the time scales of sniffing and odour perception. The sniffing time scale of one to two seconds is linked to the statistical peak-to-mean fidelity needed when using atmospheric concentration distributions to model environmental odour responses. The complexity of odour perception and distribution need not be an insurmountable challenge to better regulation.

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Appendix: A Gaussian Sniff

In this Appendix we consider the diffusion and advection of a odourant pulse at the nostril under the influence of a steady straining flow and molecular diffusion of the odour. The equations describing this process are

$$\begin{aligned} dx &= \sigma x + \sqrt{2\kappa}\, dW_x \\ dz &= -\sigma z + \sqrt{2\kappa}\, dW_z \end{aligned} \qquad \text{(A1)}$$

for white noise stochastic diffusion for molecular diffusivity κ and the solution for a pulse takes the form as a consequence of advective straining

$$\begin{aligned} \bar{x} &= \exp(\sigma t) x_0 \\ \bar{z} &= \exp(-\sigma t) z_0 \end{aligned} \qquad \text{(A2)}$$

and with odour mass per unit nostril span q,

$$C = \frac{q}{2\pi\sigma_x\sigma_z}\exp\left(-\tfrac{1}{2}\frac{(x-\bar{x})^2}{\sigma_x^2}-\tfrac{1}{2}\frac{(z-\bar{z})^2}{\sigma_z^2}\right) + \frac{q}{2\pi\sigma_x\sigma_z}\exp\left(-\tfrac{1}{2}\frac{(x-\bar{x})^2}{\sigma_x^2}-\tfrac{1}{2}\frac{(z+\bar{z})^2}{\sigma_z^2}\right) \qquad \text{(A3)}$$

together with the diffusive dispersion

$$\begin{aligned} \sigma_x^2 &= 2\kappa t e^{2\sigma t} \\ \sigma_z^2 &= 2\kappa t e^{-2\sigma t} \end{aligned} \quad . \qquad \text{(A5)}$$

For odour pulses that have significant spanwise extent (in the x direction) we simply have

$$C = \frac{q}{\sqrt{2\pi}\sigma_z}\exp\left(-\tfrac{1}{2}\frac{(z-\bar{z})^2}{\sigma_z^2}\right) + \frac{q}{\sqrt{2\pi}\sigma_z}\exp\left(-\tfrac{1}{2}\frac{(z+\bar{z})^2}{\sigma_z^2}\right) \qquad \text{(A6)}$$

which, curiously, is in mathematical form effectively equivalent to a Gaussian-plume distribution for an elevated source. For a finite size pulse initially (also with a Gaussian distribution centred at $\bar{z}_0$ with vertical pulse spread σ_0), the final 'Gaussian plume' solution takes the form

$$C = \frac{q' e^{-\sigma t}}{\sqrt{2\pi}\tilde{\sigma}_z}\exp\left(-\tfrac{1}{2}\frac{\left(z-\bar{z}_0 e^{-\sigma t}\right)^2}{\tilde{\sigma}_z^2}\right) + \frac{q' e^{-\sigma t}}{\sqrt{2\pi}\tilde{\sigma}_z}\exp\left(-\tfrac{1}{2}\frac{\left(z+\bar{z}_0 e^{-\sigma t}\right)^2}{\tilde{\sigma}_z^2}\right) \qquad \text{(A7)}$$

where $\tilde{\sigma}_z^2 = \sigma_0^2 e^{-2\sigma t} + \sigma_z^2$.

The concentration at the epithelial layer is $(z = 0)$

$$C = \frac{2q e^{-\sigma t}}{\sqrt{2\pi}\tilde{\sigma}_z}\exp\left(-\tfrac{1}{2}\frac{\bar{z}_0^2 e^{-2\sigma t}}{\tilde{\sigma}_z^2}\right) \qquad \text{(A8)}$$

giving the peak concentration at the epithelial layer about half a second after the start of the sniff of

$$\frac{C_{peak}}{C_0} \approx 1.2\frac{\sigma_0}{\bar{z}_0} \quad (\sigma_0 < 0.8\bar{z}_0), \qquad \text{(A9)}$$

where the peak initial-pulse concentration is $C_0 = q/\sqrt{2\pi}\,\sigma_0$. For the current parameters, after a further half a second of straining flow the epithelial concentration is negligible, having been flushed away.

Expression (A9) means that larger pulses give a sniffing concentration peak close to the peak atmospheric concentration pulse. However, for smaller pulses (finer 'filaments' of odour) the compression onto the epithelial layer leads to a dilution of the pulse and, for example, for patches of odour of coherent spatial extent of 1 cm, dilutes the peak exposure of odour to about 15% of the atmospheric peak. Finer scale peaks are generally the high concentration events, so there is effectively a cap on the exposure concentration experienced at the epithelial layer.

This simple Gaussian plume sniff model has many gross simplifications including geometry and steadiness of the straining flow, i.e. an instantaneous on-off with uniform strain maintained. In addition the viscous sub-layers are ignored, but these are thin and more detailed models can be solved with viscous mechanics, but no new insights are added.

Nevertheless, the key salient features of the sniffing flow are represented by the idealised model, and more detailed modelling with advanced computational fluid dynamics models appear not to be warranted for our purposes.

The self-consistency of the parameter choices with known attributes of human sniffing and nasal geometry suggest that the model is not grossly

incorrect, and with the time-scale estimate, with precision of around a second or two, giving a fundamentally useful guide, more precision than this is unlikely to be helpful for olfactory modelling.