The biomechanical design of an insect antenna as an odor capture device

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21.1 Introduction

Insect antennae are renowned for the specificity and sensitivity with which they detect airborne chemicals. Our ability to evaluate how antennae function is improving due to increasing appreciation of the role of physical factors such as air speed or antennal size and geometry on odorant capture. In engineering terms, this exchange of material between the environment and an object is called “mass transfer.” The interception of airborne chemicals by sensory hairs on insect antennae may be treated as a mass transfer problem using a fluid mechanical approach. This approach is applicable to air because “fluids” include both gases and liquids. The utility of such an approach is that it results in quantitative predictions of the interception rate of these potentially informative molecules, i.e. odorants. Such predictions provide a null hypothesis against which to compare the actual performance of a sensory structure. That is, this approach will allow us to estimate the rate at which relevant molecules will reach a sensory surface, and with what kind of spatial or temporal pattern. It also allows us to make predictions about the functional consequences of behaviors (such as flight or wing fanning) or morphological attributes that will affect air flow in the vicinity of the antenna.

In the biomechanical approach taken here it is assumed that any molecules that will eventually be interpreted as a chemical stimulus must first make physical
contact with the surface of the sensory hairs on an antenna. Alternative mechanisms that would allow molecules to be detected in the absence of physical contact, such as the detection theories of Callahan (1975), are not generally accepted due to problems with interpretation and lack of corroborative evidence with other observations (Dienendorf, 1977a, b). The fluid mechanical approaches described in this chapter will be used to make estimates of rates of interception of airborne molecules, where “interception” is defined as the physical contact of the external surfaces of sensory structures by chemical stimulus molecules. The subsequent travel by the molecules as they enter pores in the sensory hairs and eventually contact the neurons will not be discussed in this chapter.

Some of the different ways of estimating interception rates will be described, with example calculations provided. Past treatments of this problem (Adam and Delbrück, 1968; Murray, 1977; Funfelle, 1984; Loudon and Koehl, 2000) have focused on calculations of interception for sensory hairs on the antenna of the domestic silkworm moth, Bombyx mori. Choice of this species was stimulated by the rather extraordinary research effort that has taken place over a period of several decades on this and related species (Schneider, 1964; Steinbrecht, 1970, 1987; Kaissling, 1971, 1986; Schneider, 1974; Keil, 1982, 1999). The example calculations in this chapter will consider both pectinate (feathery) and filiform antennae. Thus, we will be primarily concerned with cylindrical geometry. Unfortunately a cylindrical geometry in mass transfer can generate some formidable mathematics (e.g. Bessel functions may appear in the solutions to the differential equations) but this need not be paralyzing, as algebraic approximations are available in a few cases, as will be shown. It is hoped that the introduction to the concepts and approaches provided here will make it easier for biologists to enter the physical literature in search of helpful solutions. This chapter is written for chemical ecologists or insect physiologists who wish to understand the physical bases for making estimates of chemical interception rates and may wish to do some of their own “back of the envelope” estimates or even tackle more involved approaches. A “back of the envelope” level of calculation is often the most appropriate in many cases where a more detailed analysis is not justified due to the uncertainties in sensor geometry or air flow patterns. Many insights may be gained from a relatively simple approach.

21.2 Chemoreception treated as a mass transfer problem

21.2.1 Rate at which molecules in a gas strike a solid surface

Molecules in air are in constant motion, regularly striking each other as well as any surfaces extending into the air. Therefore, an antenna in air will be regularly struck by molecules in the air (including any potential chemical stimulus molecules) at a rate that follows directly from physical laws. Ideal gas laws predict that the
number of molecules (N) striking a surface will be directly proportional to the area of the surface (A) and the time (t) over which the collisions are counted: 
\[ N = c_i A t \]  
(21.1)
The constant of proportionality, \( c_i \), is 
\[ c_i = \frac{\beta}{4} \sqrt{\frac{8 k_B T}{\pi m}} \]  
(21.2)
where \( n \) is the number of molecules per volume, \( k_B \) is Boltzmann's constant \( (1.381 \times 10^{-23} \text{ J/K}) \), \( T \) is temperature (K), and \( m \) is the mass of a single molecule (inconveniently in kg, equation 4.56c from Taber, 1979). Combining equations (21.1) and (21.2), pooling constants, and changing units results in 
\[ \frac{N}{t} = 36.3 \text{ molecules cm}^{-2} \text{ s}^{-1} \]  
(21.3)
where \( M \) is the molecular mass of the molecule of interest (now in amu or g/mole) and the rest of the variables are as defined above. This relationship (equation 21.3) is the simplest way to make a quick and straightforward estimate of the rate (N/t) at which odorant molecules available at a given concentration (c) will be striking a sensor or sensory hairs (of surface area A). These estimates should be treated as approximations, keeping in mind that any deviations of molecular behavior from that assumed of ideal gases will make its application less exact.

21.2.1 Example calculation using equation (21.3)
Consider the case of pheromone molecules striking a single cylindrical sensory hair that is 100 \( \mu \text{m} \) long and 2 \( \mu \text{m} \) in diameter (the geometry for long sensilla trichodea of the silkmoth moth *Bombyx mori*; Steinbrecht, 1970). The surface area, A, of a single hair exposed to the surrounding air is \( 6.31 \times 10^{-10} \text{ m}^2 \) (from \( 2\pi r h + \pi r^2 \), the side and distal end of a cylinder with \( r = 1 \times 10^{-6} \text{ m} \) and \( h = 100 \times 10^{-6} \text{ m} \)). Assuming that the pheromone is bombykol (238 amu or g/mole), the temperature is 25°C (298 K), and the concentration of bombykol in the air is \( 10^9 \text{ molecules/m}^3 \) (1000 molecules/cc, a threshold concentration reported by Schneider, 1974), then substituting those numbers into equation (21.3) results in the number of bombykol molecules hitting the hair every second: 
\[ \frac{N}{t} = (36.3)(10^9)(6.31 \times 10^{-10} \text{ m}) \sqrt{\frac{298}{238}} = 26 \]  
(21.4)
or about 26 molecules per second (equation 21.4). This number is much larger than would be expected on the basis of other approaches. For example, treating the sensory hair as a perfectly absorbing cylinder in non-moving homogeneous air at the same initial concentration of bombykol results in a prediction of about
0.2 molecules/hair over the first second (Loudon and Koehr, 2000). These numbers differ so much in part because the concentration of bombykol in the air will be decreasing in the latter case of the adsorbing surface, as molecules are removed from the air after contact with the surface. That is, if the molecules were not adsorbing onto the surface, the expectation would be about 26 molecular collisions between bombykol molecules and the sensory hair every second. These collisions will not all be with different individual bombykol molecules. From the point of view of the insect’s sensory system, a molecule should be counted only once regardless of how many times it struck the hair before being finally captured, as multiple counts of single molecules are not informative (Dusek, 1992).

A prediction based on equation (21.3) provides an upper limit for molecular capture rate, because the molecules cannot be captured more often than they hit the surface in the first place. In practice, predictions based on equation (21.3) are likely to be an overestimate of what can be achieved by a real sensor, even by a couple of orders of magnitude as shown above. An overestimate will occur when the concentration $(n)$ used to calculate the capture rate exists only momentarily before being decreased to (unknown) lower levels as the chemical stimulus molecules are removed from the air. Usually one wants an average interception rate over some biologically meaningful but somewhat arbitrary time interval, such as a second or a fraction of a second. However, if the interception rate is changing during this time, then different choices of time interval will result in different estimates for the average interception rate. For these unsteady-state cases where rates are changing with time, it is important to define the time interval over which the interception rate has been estimated in order to avoid problems of interpretation.

There is no term in equation (21.3) for air flow. External air flow around organisms is sufficiently slow (subsonic) that it may usually be treated as incompressible (Vogel, 1994). This incompressibility means that the concentration of chemical stimulus molecules $(n)$ will not be increased noticeably by the pressures that develop adjacent to insect sensory hairs or antennae due to moving air (or moving antennae). The replacement of any captured molecules by the arrival of fresh odorant-laden air is the primary reason why air flow has such a dramatic effect on interception rate. One way of considering the influence of air flow is that if the flow brought the interception rate closer to the limit predicted by equation (21.3), in order to discuss approaches more complex than that provided by equation (21.3), we have to consider the physical bases for molecular movement: diffusion and convection.

21.2.2 Processes of mass transport: diffusion and convection

There are two physical processes involved in the movement of molecules from one place to another (such as from the air to the surface of a sensory structure) – the molecules may walk themselves, or they may be pushed. Diffusion is the
net movement of a species of molecule due to randomly directed thermal movements of individual molecules, while convection is the net movement of molecules by an air current resulting from a pressure gradient. These two processes occur at the same time, so while the molecules are being convected from one location to another they are also undergoing small-scale random walks. "Max transport" refers to the net movement of a species of molecule regardless of the underlying physical cause, and therefore includes both diffusion and convection.

Obviously a randomly moving molecule will spend much of the time heading in the "wrong" direction away from a sensor. This is one of the reasons why a "reduction in dimensionality" when an odorant molecule makes contact with a sensory hair was such an appealing idea when first proposed (Adams and Delbrück, 1966). The idea is that an odorant molecule in air moving in three-dimensional space will change to two-dimensional diffusion after reaching a sensory hair and becoming lightly adsorbed onto its surface. However, the diffusion coefficient for odorant molecules on the surface is likely to be orders of magnitude smaller than the diffusion coefficient of the same odorant molecules in air. Therefore, an increase in the rate or efficiency with which odorant molecules contact pores will only occur with this two-dimensional path if the geometric gains are not completely offset by the lowering of the diffusion coefficient. Berg and Purcell (1977) have shown that a randomly moving molecule is likely to thoroughly explore an area once reached, suggesting that one does not have to invoke two-dimensional surface diffusion, because an odorant molecule is likely to strike a sensory hair many times (Fortelle, 1984). Odorants with different chemical properties may take slightly different routes to the pores; larger, more hydrophobic molecules would execute a path somewhat closer to the adsorbed two-dimensional ideal path if the surface is waxy. It is clear that at least some odorants do adsorb well onto the surfaces of sensory hairs (Kanaujia and Kässling, 1985). The exact route taken by an odorant molecule between reaching the sensory hair and entering a pore in the hair's surface will not affect consideration of the mass transport from the air to the sensory surface and will not be considered further.

Insights about convection from fluid mechanics are immediately applicable to chemoreception by insect antennae. First, the "no-slip" condition that exists between any solid and an adjacent moving fluid precludes that the air immediately adjacent to the sensors' surface is not moving with respect to the sensory surface (Figure 21.1). In addition, the small size scale relevant to chemoreception by insect antennae limits the behavior of the air flow in ways that have implications for chemoreception. The smaller the object and the slower the flow, the thicker the velocity boundary layer is relative to the size of the object (Figure 21.1A). By definition, the velocity boundary layer extends from the surface of the object to the point where the velocity has reached 99 percent of ambient; Vogel (1888) suggests that an alternative standard of 90 percent would suit the purposes of most biologists. One consequence of this fluid behavior is that microscopic
sensory hairs will be surrounded by very slowly moving air to a distance of many diameters away. In addition, the small size scale means that the air flow will be laminar, and there will not be any turbulent mixing. The way in which chemical molecules will reach the sensory hair surface is by their random thermal movements (diffusion) (Figure 21.1B). The physical world of microscopic organisms is well described by Parcell (1977). An overview of the small-scale fluid-dynamics of olfactory antennae (treated as cylindrical arrays) may be found in Koehl (1996).

21.2.3 Fick’s law vs mass transfer coefficients – why are there two approaches and which should be used?

There are two completely different approaches to calculating mass transport rate: one approach starts with a mathematical equation (Fick’s law) and searches for an analytical or numerical solution. The other approach starts with data which are used to generate mass transfer coefficients and then predictive equations. Cussler (1997) devotes the first chapter of his book to discussing the pros and cons of the two approaches. He argues persuasively that although the Fick’s law approach may seem more legitimate because it is based on underlying physical principles, the mass transfer coefficient approach may be preferable in cases where the system has complex geometry or boundary conditions.

After introducing Fick’s law and dimensional analysis using mass transfer coefficients, the most useful solutions will be presented. The solutions will be
divided into steady-state (not changing in time) and unsteady-state cases, both with and without air flow. Some implications of these relationships for chemoreception will then be briefly discussed.

21.2.3.1 Fick’s law

In order to predict mass transport due to diffusion, one usually turns to Fick’s law as the most fundamental underlying mathematical statement of how the rate of diffusion scales with concentration and geometry. A one-dimensional form of Fick’s law is usually stated as

\[ J = -DA \frac{\partial c}{\partial x} \]  \hspace{1cm} \text{or} \hspace{1cm} J = -DA \frac{\Delta c}{\Delta x} \tag{21.5} \]

or for radial diffusion in cylindrical coordinates as

\[ J = -DA \frac{\partial c}{\partial r} \]  \hspace{1cm} \text{or} \hspace{1cm} J = -DA \frac{\Delta c}{\Delta r} \tag{21.6} \]

where \( J \) is the flux (mass/time) that crosses an area, \( c \) is concentration, \( D \) is the diffusion coefficient for the diffusing species, and \( x \) and \( r \) are spatial coordinates. Rewriting equation (21.6) in the variables already defined results in

\[ \frac{N}{I} = -DA \frac{\partial n}{\partial r} \] \hspace{1cm} \tag{21.7} \]

The apparent simplicity of equations (21.5)–(21.7) can be misleading: the number of exact solutions is small, and while approximate solutions fill books (e.g., Crank, 1975), their application can be problematic. Seemingly small differences in the boundary conditions will completely change the character of the solution, as will be seen below, and identification of the appropriate boundary conditions is not easy. However, in practice one can make an educated guess about the approximate boundary conditions, or can estimate the interception rate for different kinds of possible boundary conditions. Below are a number of solutions that are the most useful for the geometry most relevant to insect antennae, the cylinder.

Either sensory hairs or filiform antennae can be approximated as cylindrical in shape.

21.2.3.2 Mass transfer coefficients, dimensional analysis, and dimensionless numbers

By definition, the mass transfer coefficient (\( k \)) relates the rate of mass transport (\( N/\Omega \)) to a difference in concentration at two identifiable locations:

\[ \frac{N}{\Omega} = kA(n_2 - n_1) \] \hspace{1cm} \tag{21.8} \]

Thus, the investigator needs only to be able to estimate the molecular concentration at two identifiable points in space, rather than estimate the concentration gradient
Dimensionless numbers are combinations of variables in which all units cancel. These numbers are named after scientists and are used in the physical sciences to summarize causal relationships between variables and processes. One convenience of expressing these physical relationships in dimensionless terms is that large amounts of data may be collapsed into a single relationship. Cusdler (1997, p. 232) describes what typically happens after first exposure to dimensionless numbers: at first one thinks that a tool has been found that will solve all problems, followed by disillusionment after a first difficulty in application, and finally, renewed enthusiasm if one perseveres.

Dimensionless numbers are very simple to calculate, although proper interpretation is dependant on the choice of variables such as which length to use for the characteristic length. The magnitudes of the dimensionless numbers are predictors of physical behavior. In addition, the functional relationships written in term of the appropriate dimensionless numbers are extremely powerful because they will be valid for that geometry and boundary conditions for a wide range of variable combinations. In chemoreception there are six dimensionless numbers that are particularly important (Re, Pe, Sh, Fo, Sc, and Po).

The most important dimensionless number in fluid mechanics is the Reynolds number (Re), which is defined as

\[ Re = \frac{UL}{\nu} \]  

(21.9)

where \( p \) is the density of the fluid, \( U \) is characteristic velocity, \( L \) is characteristic length, \( \mu \) is the dynamic viscosity of the fluid, and \( \nu \) is the kinematic viscosity of the fluid (\( \mu / p \)). The magnitude of \( Re \) indicates the ratio of the factors that tend to keep the fluid moving to those that tend to slow the fluid motion, i.e., the ratio of inertial to viscous effects. In the case of chemoreception by insect antennae, both the velocity (\( U \)) and the size (\( L \), usually the diameter for cylindrical geometry) are small, and hence the flow may be considered low \( Re \) flow.

The Sherwood number (Sh) is a dimensionless form of the mass transfer coefficient and is

\[ Sh = \frac{m}{D} \]  

(21.10)

where \( k, L, \) and \( D \) are already defined. The magnitude of the Sherwood number may be considered as the ratio of the molecular mass transport resistance to the convective mass transport resistance of the fluid. In steady-state cases, the Sherwood number is typically a function of the \( Re \) and the Péctel number (Pe) which is

\[ Pe = \frac{UL}{D} \]  

(21.11)
Sh and Pe are not synonymous, despite unfortunate misstatements in Vogel (1994) and Denny (1993), which otherwise provide informative reviews of the importance and interpretation of Pe (referred to in their texts as Sh).

The Fourier number (Fo) is an estimate of the temporal extent of diffusion and is

\[ Fo = \frac{D t}{L^2} \]  

(21.12)

The magnitude of Fo is often used as a dimensionless time (to estimate how long diffusion has proceeded). The Schmidt number (Sc) is simply the ratio of the Pe to Re and is

\[ Sc = \frac{\nu}{D} \]  

(21.13)

The magnitude of the Schmidt number indicates the relative thicknesses of the velocity and concentration boundary layers under some conditions, such as laminar low Re flow. And finally, the Womersley number (Wo) which tells us to what extent an unsteady or oscillating pressure gradient will be reflected in unsteady flow between hairs on an antenna:

\[ Wo = \frac{L}{2} \sqrt{\frac{2 \pi f}{\nu}} = \frac{L}{2} \sqrt{\frac{\pi f}{2 \nu}} \]  

(21.14)

where \( f \) is frequency in Hz (Loudon and Tordjman, 1998).

Note that the characteristic length \( L \), that appears in many of these dimensionless numbers is defined differently depending on whether the flow is external or internal. \( L \) is usually measured on a solid in the case of external flow and measured in a fluid in internal flow. For the case of flow around cylinders (external flow), the convention in comparative biomechanics is to use the diameter for \( L \) (e.g., Vogel, 1994) and that will be the convention used here. In the physical literature, the radius rather than the diameter is sometimes used for \( L \), which then makes some of the dimensionless numbers appear to be off by a factor of two if one is not careful. Similarly, for cases of internal flow, \( L \) will be based on the diameter or width of fluid-filled gaps or openings. Complex morphologies such as seen in pectinate antennae may be characterized with a set of \( Re \), with the different characteristic lengths referring to the width of a whole antenna, hair diameter, branch diameter, and gap width, and each \( Re \) has different meaning and physical significance.

21.2.3.3 Steady-state solutions for diffusion to a cylinder (no flow)

(a) A cylinder with its surface held at constant concentration and constant concentration at infinity – no air flow. There is no solution for this most obvious and simple case (Figure 21.2A). This is worth pointing out because the lack of a solution is often not explicitly noted. The lack of a solution is not due to the
need for some new mathematical approach to crack this difficult problem, but because the predicted flux to the cylinder keeps changing indefinitely with time. A solution does exist for the same boundary conditions for a spherical body, which has been used extensively in the context of mass transport to microorganisms and single cells (Berg and Purcell, 1977; Wiegel, 1991; Berg, 1993).

(b) A cylinder surrounded by a cylindrical outer boundary—still air. This situation is for a cylinder (of radius $a$ and surface held at a constant molecular concentration $n_x$) with an outer cylindrical boundary (at $b$) held constant at $n_x$:

$$
N = \frac{2\pi DL_{a,b}(n_x - n_e)}{\ln(b/a)}
$$

(21.15)

where $L_{a,b}$ is the length of the cylinder (Figure 21.2B; equation (21.15) modified from equation 5.5 in Crank, 1975). This may be used as an approximation for a cylinder surrounded by a velocity boundary layer where the outer cylindrical boundary represents the constantly refreshed air sample.

21.2.3.4 Unsteady-state solutions

(a) A cylinder initially surrounded by a homogeneous cloud of molecules—still air. In this case, a cylindrical sensor is suddenly (at $t = 0$) surrounded by a homogeneous cloud of molecules at molecular concentration $n_i$ (Figure 21.2C).

The exact solution to equation (21.71) is expressed as combinations of Bessel functions or complex error functions for which Crank (1975) has supplied approximate simple algebraic expressions:
\[ \frac{N}{t} = 2\pi DL_{\text{crit}}(n_{1} - n_{2})[4\pi\tau]^{-0.5} + 0.5 - 0.50(\tau/n)^{0.5} + 0.50\tau - \ldots \] (21.16)

for small times \((\tau < 1)\) and

\[ \frac{N}{t} = 4\pi DL_{\text{crit}}(n_{1} - n_{2})\left[ \frac{1}{\ln(16\tau)} - \frac{\gamma}{\ln(16\tau)} - \frac{\gamma^{2}}{2}\tau \right] \ldots \] (21.17)

for longer times \((\tau > 1)\) where \(\tau\) is dimensionless time \((D/t)\) and \(\gamma\) is Euler's constant (equation 21.16–17 modified slightly from equations 5.80 and 5.81 in Crank, 1975). Note these equations allow one to predict the instantaneous rate of interception, not the accumulated number of captured molecules. To estimate the accumulated capture at some point in time, such as one second after the initial boundary conditions, the incremental captures for the successive time intervals need to be summed. This was how the accumulated capture was estimated for single hairs in Lould and Kochl (2000).

21.2.3.5 Steady-state solutions for diffusion/convection

When the air is moving, it becomes more difficult to calculate the interception rate. The mass transfer under these circumstances is generally expressed in dimensionless terms. Adam and Delbrück (1968) were able to generate a formula by making the simplifying assumption that the velocity of the air as it passed around the hair was everywhere constant \((U)\) and very similar to the ambient air flow far away \((U_{0})\):

\[ \frac{N}{t} = \frac{2\pi DL_{\text{crit}}(n_{1} - n_{2})}{\ln(Pe U/U_{0}) + \gamma} \] (21.18)

where \(Pe\) is assumed to be 0.4 (equation 21.18) modified slightly from equation 47 in Adam and Delbrück, 1968). In practice it is difficult to apply this formula, as the choice of ambient air velocity \((U_{0})\) is not obvious, particularly for the case of apiculate antenna. Note that as \(U\) gets smaller and smaller (relative to \(U_{0}\)), the logarithmic term gets very large, and the formula may no longer be applied. However, this formula does provide important physical insights into chemoreception by insect antennae: in particular this formula predicts that there will be relative insensitivity of the interception rate \((N/t)\) to changes in the air flow.

Murray (1977) uses the same formula (equation 21.13) to predict interception rates of sensory hairs on insect antennae, but provides an additional insight in its application. As long as \(Pe < 1\) (where \(L\) is hair diameter), the odorant molecules may be assumed to strike the hair anywhere. As \(Pe\) becomes larger \((Pe > 1)\), the interception rate will differ more with downstream/upstream location on the cylinder. The same logic may be used to estimate the potential for spatially dependent interception by a filiform antenna.
In the physical literature, functional relationships for mass transport can be found for a few cases of low Re, but unfortunately the actual range of dimensionless numbers for which the formulas are valid are often either not provided or can be somewhat misleading. For example, Clift et al. (1978) provide the following formula for a “spheroid” in “creeping flow” (Re << 1):

\[
Sh = 0.991(K/Pe)^{1/3}
\]  

(21.19)

where the constant K must be read from a graph (Figure 4.14 in Clift et al., 1978). Note that in this case, the interception rate (Sh) is predicted to go to zero as the air flow gets slower and slower (as Pe goes to zero), but this would be a misapplication of the formula because the derivation was based on the assumption that Pe is very large (Pe → ∞).

A formula for the case of air flow perpendicular to a cylinder (assuming low Re and low Pe) is

\[
Sh = \frac{2}{\ln \left( \frac{8}{Pe} \right) - \gamma} \left[ 1 - \frac{\alpha_l}{\left( \frac{8}{Pe} \right) - \gamma} \right]^{1/2}
\]  

(21.20)

(equation 4-71 in Clift et al., 1978), but there is an unknown coefficient, \( \alpha_l \), which “must be evaluated numerically.” Equation (21.20) is considered a “solution” even though it is not immediately possible to use it to make a quantitative estimate for molecular interception by an insect antenna or sensory hair. However, similar to what was seen earlier, the relationship between the variables again predicts relative insensitivity of the interception rate to changes in air flow. The magnitude of the unknown coefficients in these formulas is being addressed empirically with physical modeling to directly estimate the mass transfer coefficients (Loudon et al., unpublished).

Having summarized the most useful of the solutions available for mass transport to cylinders, a few examples of applications of this mass transfer approach will be considered.

21.3 Applications of mass transfer approach

21.3.1 Morphology

Insect antennae vary tremendously in size and shape, but two common forms are filiform (a single cylinder) and pectinate (feathery arrays of many cylinders). Most of the published morphological information on insect antennae concentrates on sensory hairs (e.g. Zachariak, 1985; Steinbrecht, 1987, 1989; Zachariak and Shields, 1991). Descriptions of sensory hair morphology are necessary for biomechanical analyses and interpretation, but it is equally important to have
estimates of the sizes of gaps between sensory hairs as well as their three-dimensional arrangement in space, because these factors will significantly influence the air flow around the sensory hairs arrayed on the antennae (Oheer and Kochl, 1987a, b).

The size and shape of the antennae will affect chemosensation in a couple of ways - by changing the pattern of the air flow and by determining the surface area in contact with the air. The usual functional interpretation for larger antennae or for a larger number of sensory hairs is that the larger surface area will increase the interception rate of airborne chemicals. A direct proportionality between surface area and interception rate is predicted by equation (21.3). However, an increase in surface area per se will not necessarily increase the interception rate, because (a) different areas can interfere with each other (e.g., one hair might catch molecules that could be caught by another hair), (b) greater surface area may lead to higher drag thus lessening the volume of air processed, or (c) increases in the surface area may be functionally irrelevant (such as some microscopic sculpturing).

Quantifying the surface area of the sensory hairs or antennal surface leads to the same problem encountered in the famous analysis of the coastline of Britain in fractal studies; as one increases the magnification of the surface, the area becomes larger and larger without limit as successively smaller ripples become noticeable (Figure 21.3). While a mathematical limit may not exist, a physically meaningful limit does. From the point of view of odorant interception from the air, any ripples that are smaller than the mean free path of the diffusing molecules in air (the average distance traversed by molecules between collisions, about 70 nm) may be disregarded, and ripples slightly larger than this are unlikely to add significantly to the "capture" area. This reasoning assumes that the sensory surface is acting like a "sink" such that any incoming odorant molecule is not affected by the presence of odorant molecules already on the surface. It is possible that extensive surface sculpturing could increase odorant absorption by decreasing

Figure 21.3 Molecules in air strike a surface at a rate directly proportional to the surface area. (A) The surface area is easier to estimate for a smooth surface. (B) Real surfaces often have surface ripples at any arbitrary level of magnification, making it more difficult to estimate the surface area.
interaction between adsorbed odourant molecules, but that is unknown at this point.

Sensory hairs may compete for the same molecules (and hence decrease each other’s interception rates) when an odourant molecule passing through the gap between hairs is likely to strike either hair. This interference between hairs will occur when the hairs are sufficiently close and the air flow between them is slow. For the pectic antennae that have been analyzed so far (B. mori, Actias luna), it is clear that the sensory hairs are exhaustively sampling much if not all of the air that passes through the spaces between hairs (Kausling, 1971; Vogel, 1983; Loudon and Koell, 2000). For a different case, such as sensory hairs projecting from a filiform antenna, the dimensionless numbers introduced above give us a way to approximate when these sensory hairs will be competing for the same molecules. If the Fourier number (equation 21.12) is greater than one in magnitude when the gap width between hairs (g) is used as the characteristic length, then the molecules have time to “walk” across the gap between the hairs during the characteristic time:

\[
\frac{Dg}{\nu} > 1
\]  \hspace{1cm} (21.21)

One estimate for characteristic time (t) may be obtained by dividing the hair diameter by the average air velocity through the gap (L/U), and therefore represents the time during which that air sample is passing directly between the hairs. Making this substitution results in

\[
\frac{Dg}{\nu} = \frac{D\ln(L/U)}{g^2} = \frac{D\ln(L)}{g^2} > 1
\]  \hspace{1cm} (21.22)

21.3.1.1 Example calculation using equation (21.22)

Consider sensory hairs 2 \( \mu m \) in diameter that are 20 \( \mu m \) apart. Inserting these values into equation (21.22) and assuming that \( D = 2.5 \times 10^{-9} \text{ m}^2/\text{s} \) (the diffusion coefficient for bombbykol, the main component of the commercial silkworm sex pheromone; Adam and Debreci, 1968) results in the prediction that these hairs are likely to interfere with each other’s odorant interception when the air speed between the hairs is below 0.0125 \( \text{m/s} \). This is not a discontinuous function – the sensory hairs will interfere with each other more at slower speeds and less at faster speeds. Another way of appreciating what this means quantitatively is to recognize that the root mean square displacement of a molecule (considering movement in one dimension) is

\[
s < s >_{rms} = \sqrt{2Dt}
\]  \hspace{1cm} (21.23)

Displacements due to molecular diffusion are normally distributed and therefore equation (21.23) is an estimate of the standard deviation of the displacements in
time \( t \). From the known characteristics of the normal distribution, 50 percent of the molecules will have gone as far as or farther than 0.67 times the standard deviation or

\[
0.67 \times \sqrt{2 \Delta t} = \sqrt{T} \tag{21.24}
\]

This result (equation 21.24) helps us interpret the magnitude of \( \text{Foc} \) when \( \text{Fo} = 1, L = \left( \text{Df} \right)^{1/3} \) (from equation 21.12), or about 50 percent of the molecules will have gone as far as or farther than \( L \) in time \( t \) in any direction (equation 21.24).

For \( \text{Fo} > 1 \), more than 50 percent of the molecules, and for \( \text{Fo} < 1 \), fewer than 50 percent of the molecules will have gone as far as or farther than \( L \) in time \( t \) in any direction.

A decrease in the interception rate for individual sensory hairs does not necessarily imply that the total interception rate for the antenna has decreased, if there is a larger number of hairs. Increasing sensory hair number and decreasing spacing between them may tend to decrease the interception rate for single hairs while increasing the total interception rate for the antenna, at least within the range of sensory hair number and spacing seen in nocturnal antennae (Loudon and Koch, 2000). Therefore functional interpretations of the consequences of insect antennal morphology must consider these opposing tendencies.

Other morphological forms, such as the lamellate antennae of beetles, have unknown airflow patterns adjacent to the sensory surfaces. For these non-cylindrical cases there are few mathematical options other than the application of equation (21.3) to estimate an upper limit for the interception rate. These more complex morphologies may be tackled with other methods, including measurements using microsensors (Schneider et al., 1998a, b) and physical modeling to estimate the mass transfer coefficients for those geometries (Loudon et al., unpublished). The microsensor method has been used to demonstrate that the sexually dimorphic (filiform) antennae of Manduca sexta perturb the airflow in different ways, such that the sensory hairs on male and female antennae will intercept odorant molecules with a different temporal pattern from the same plume (Schneider et al., 1998a).

21.3.2 Airflow In the context of chemoreception, air movement is important in replacing the sampled air adjacent to the sensory surfaces with fresh odorant-laden air. Moving air may be generated by the insects (flying or moving its antennae) or the environment (wind). The relevant air speed (that acts on sense organs above as \( U \)) is considered from the spatial frame of reference of the insect's body. In a natural setting, insects are constantly changing their speed and orientation, such as a moth flying upwind in a zigzag manner to a pheromone source, making it challenging to identify the sensory input and the mechanisms of control for this behavior (Willis and Arbas, 1998).
A sensory hair measures flux, not concentration directly (i.e. molecules/time reaching the surface, not molecules/volume). Increasing the air flow can to a certain extent compensate for a low concentration of odorant molecules in the air. For example, a sensory surface would hypothetically be unable to differentiate between the number of odorant molecules delivered by a rapidly passing but dilute airstream and a slow but concentrated airstream, in the absence of accompanying mechanosensory information about the air flow. The extent to which mechanosensory input from the antennae modifies the response to chemosensory input is not clear, although electrophysiological recordings from interneurons show that mechanosensory and chemosensory information is integrated in the brain (e.g. Iwagaki and Hildebrand, 1990).

A change in interception rate with air flow has been identified as a characteristic of "flux detectors" such as insect sensory hairs (Kaisling, 1998). However, in some instances (low Pe), an increase in flow will have only a negligible impact on the flux rate, even for a "flux detector." This was shown by Herg and Purcell (1977) in the context of cells swimming through a liquid environment. That is, the flow rate doesn't matter if the molecules can walk themselves around just as quickly. For single cylindrical sensors (isolated hairs or filiform antennae), the slower the flow (the lower the Re and Pe), the less the interception rate is expected to increase with an increase in air speed (equations 21.18 and 21.20).

A different relationship between interception rate and ambient air speed exists for an otherwise identical sensory hair in an array, such as a sensory hair in a pectinate antenna. For a hair in an array, the interception rate is directly proportional to the airflow through the antenna because the air passing through the antenna is expected to be sampled almost exhaustively. A pectinate antenna allows only a small fraction of the approaching air to pass through, but the fraction increases with ambient air speed (Vogel, 1983). Excessively sampling an increasing fraction of oncoming air leads to a disproportionate increase in the interception rate with the ambient air flow, such as a 50% increase in interception rate predicted for a 15x increase in ambient air flow (Loudon and Koehl, 2000). Thus, the anticipated influence of ambient air flow on the interception rate by a sensory hair is completely different if the hair is isolated or is part of an array.

Unfortunately, the air flow in the vicinity of these microscopic sensory hairs is extremely difficult to calculate. Cheer and Koehl (1987b) provide a solution for the flow field in the vicinity of two parallel and infinitely long cylinders. Even for this simple geometry, the solution (expressed as a stream function) has enough terms that it takes up most of a printed journal page, and the reader must differentiate the provided stream function with respect to the spatial variables in order to solve for the velocities at different points in space. Finite hairs usually experience less flow between them than predicted assuming infinite length because fluid can go around the tips as well as the sides of an array (Koehl, 2001).
21.3.3 Spatial and temporal characteristics of interception

As an air stream passes by an insect antenna, the air may be slowed, distorted, or possibly even mixed, which will affect the rate at which molecules reach the sensory surface. These modifications will be perceived at the level of the sensory hairs as changes in the rate at which molecules strike the sensory hairs. Air flow patterns adjacent to cylinders may be predicted based on the magnitude of $Re$ (using the diameter of the cylinder for $L$; equation 21.9; Figure 21.4). While turbulence will not occur because of the small size scale (and small $Re$), attached vortices (rotating fluid structures) will develop downstream of isolated cylinders when $10 < Re < 40$ (Vogel, 1994). This $Re$ range requirement would seemingly prevent attached vortices near sensory hairs, as this would require unreasonable ambient speeds of 75 m/s for 2 μm diameter sensory hairs (Figure 21.4). However, stable, attached vortices can exist adjacent to cylinders that are in arrays for very low $Re$ (such as seen for $Re = 0.01$ in Figure 15 in Van Dyke, 1982). Therefore, it is possible that attached vortices may exist adjacent to sensory hairs in pedicellate antennae, or the branches that support them, although their existence (and the consequences for chemoreception) have not yet been evaluated. An attached vortex could hypothetically increase the rate of interception by giving a sensor another chance to capture molecules from a vortex rotating in its vicinity, but this would also prolong the time during which an "old" and increasingly irrelevant stimulus may be sensed. A complex morphology such as a pedicellate antenna has several different cylindrical sizes (the main stalk, the side branches, and the sensory hairs), and each of these structures will reach a transitional $Re$ range at different air speeds. Complex interactions can be seen in such porous structures, such as the pulsatile flow generated through cylindrical arrays by vortex shedding of the whole array (Leonard, 1992).

![Figure 21.4](image-url)

Figure 21.4 The air flow behavior around an isolated cylinder will depend on the magnitude of $Re$ (equation 21.9, $L$ is cylinder diameter). Combinations of air speed and cylinder diameter are shown that lead to vortex shedding ($Re > 40$), attached vortices ($10 < Re < 40$), or laminar flow without vortices ($Re < 10$) (dynamic viscosity of air is assumed to be $15 \times 10^{-6}$ m²/s).
Antennal morphologies that slow the air flow in the vicinity of the sensory hairs, such as pectinate antennae that typically pass only about 10 percent of the approaching air, will distort the flow in a particular way – they will cause spreading (divergence) of the air stream as it approaches an antenna. This distortion of the air means that a small patch of odorant molecules will strike a much larger number of sensory hairs than would be predicted on the basis of the undistorted patch size (London and Davis, unpublished).

If a chemical stimulus consists of multiple chemical components which differ in the magnitude of their diffusion coefficients, it is of interest to consider whether or not these components will be intercepted by the sensory hairs at the ratios in which they are available in the air. This question may be addressed using the equations supplied above.

21.3.3.1: Example calculation for diffusion of multiple chemicals
Consider a mix of chemicals that differ greatly in molecular mass (and hence in their diffusion coefficients), such as a 3:1 ratio of ethanol:hexadecanol in the air surrounding a sensory hair or filiform antenna. The 16-carbon alcohol will be approximately eight times as massive as the 2-carbon alcohol. The diffusion coefficients (\(D\)) are \(1.32 \times 10^{-5}\) m\(^2\)/s for ethanol (Welty et al., 1984) and \(2.5 \times 10^{-6}\) m\(^2\)/s for hexadecanol (using the value for bombykol), both in air at 298 K. What will be the rate of interception be at the level of a sensory hair for these two chemicals? The answer (and choice of equation) depends on the boundary conditions.

If the sensory hair is suddenly immersed in a homogeneous air sample that contains the two chemicals, the ratio of the rates at which the hair takes up the two compounds will be directly proportional to the product of their molecular concentrations and the square root of the ratio of the diffusion coefficients (approximating using the first term in equation 21.16). That is, if ethanol and hexadecanol had similar diffusion coefficients, the 3:1 ratio in their molecular concentration would be reflected in an expected 3:1 ratio in interception by the hair. The diffusion coefficients actually differ by a factor of 5.3, and therefore the odorant with the smaller diffusion coefficient (ethanol, in this case), will be taken up at a rate of approximately 2.3 times what would be expected on the basis of their molecular concentrations. Thus, the 3:1 ethanol:hexadecanol ratio would be expected to result in an interception ratio of 6.9:1. This boundary condition corresponds approximately to the case of a filiform antenna suddenly immersed in a cloud of odorant in still air.

On the other hand, if approximate steady-state conditions may be assumed, such that the two chemicals are held at a fixed concentration at some distance from the sensory surface, then the difference between the fluxes to the surface turns out to be directly proportional to the ratio of the diffusion coefficients (equation 21.15). That is, for this case where the two chemicals differ in the
magnitude of their diffusion coefficients by a factor of 5.3, they are expected to reach the surface of a cylindrical sensory surface at rates that differ by a factor of 5.3 (the surface of the hair will be struck by 5.3 times as many of the smaller molecules per unit time, assuming that the hair can adsorb all of these molecules). Surprisingly, this result is independent of the distance at which the concentrations are held constant, as long as they are the same for the two compounds. So in this case, the more rapidly diffusing ethanol would actually be striking the surface at a rate 16 times more frequently than hexadecanol even though it is really only three times as common.

Therefore, when compounds differ greatly in their molecular masses (which will be reflected in a smaller difference in the magnitudes of their diffusion coefficients), a modest difference in interception rates may be expected, particularly when the concentration of the compounds may be approximated as constant at some distance from the surface.

21.4 Concluding remarks

The purpose of this biochemical analysis of chemoreception is to help us understand how antennae intercept molecules from the environment — what the likely rate of odorant interception will be under different conditions of odorant concentration and air speed, and how morphological attributes will constrain or modify odorant interception. Any behaviors that modify the air flow, such as wing flapping, oscillation of the antennae, locomotor movements, changing posture, or microhabitat selection, will all greatly influence odorant interception rates. It is increasingly clear that fine-scale spatial or temporal heterogeneity in odorant interception is processed by the brain and affects behavior (Mitsui-Neto and Cardé, 1994; Baker et al., 1998; Vickers et al., 2001), and this fluid mechanical approach should allow greater predictive ability for how the chemicals strike the sensory hairs on antennae in the first place. The air flow patterns around insect antennae and individual sensory hairs are still virtually unknown except in the few cases described here, and fluid visualization techniques will be invaluable in addressing these unknowns. In addition, the growing interest in small-scale flow applications such as microfabrication systems (Rens et al., 1999) is providing information about the complications of (non-turbulent) mixing and vortex formation at the spatial scale relevant to chemoreception by insect antennae.

Acknowledgements

This research was funded by a grant from the National Science Foundation (IBN 9984475). Thanks to Dr Ward Thompson, a physical chemist, for useful discussion.
on molecular diffusion, and to Dr Brian Smith for suggesting the example calculation on ratios of compounds. J. Botz, E. Davis, and G. Miller made suggestions that improved the text.

List of symbols

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description/Formula</th>
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<tbody>
<tr>
<td>A</td>
<td>area (m²)</td>
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<tr>
<td>a</td>
<td>radius of cylinder (m)</td>
</tr>
<tr>
<td>b</td>
<td>distance to boundary (m)</td>
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<tr>
<td>c</td>
<td>concentration (kg/m³)</td>
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<tr>
<td>D</td>
<td>diffusion coefficient (m²/s)</td>
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<tr>
<td>f</td>
<td>frequency (Hz)</td>
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<tr>
<td>F₀</td>
<td>Fourier number (D₁/D₁)</td>
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<td>g</td>
<td>gap or space between surfaces (m)</td>
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<td>h</td>
<td>length of cylinder (m)</td>
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<td>J</td>
<td>flux (kg/s)</td>
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<tr>
<td>k</td>
<td>mass transfer coefficient (m/s)</td>
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<td>kₜ</td>
<td>Boltzmann’s constant (1.381 x 10⁻²³ J/K)</td>
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<td>L</td>
<td>length (m)</td>
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<tr>
<td>L₁</td>
<td>length of cylinder (m)</td>
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<tr>
<td>m</td>
<td>mass of a single molecule (kg)</td>
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<td>M</td>
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<td>dimensionless time (D₁/D², F₀)</td>
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References


