SMALL-SCALE FLUID DYNAMICS OF OLFACTORY ANTENNAE

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A critical step in the process of olfaction is the arrival at the surface of a chemosensory structure of chemical signals from the environment. Many organisms use appendages bearing arrays of microscopic hairs to pick up chemical signals from the surrounding water or air. In this study a general model of fluid flow between neighboring hairs in an array is used to explore the effects of hair size, spacing, and speed on flow near olfactory hairs. If an array of hairs is moved more rapidly: 1) the volume flow rate through it rises, causing higher molecule encounter rates even though a smaller proportion of the odorants passing through the array have time to diffuse to hair surfaces, and 2) velocity gradients along hair surfaces become steeper, causing greater sensitivity to changes in odorant concentration. The more closely-spaced the hairs, the less sensitive they are to these effects of changing speed.

INTRODUCTION

The first step during olfaction is the arrival at the surface of a chemosensory structure of chemical signals from the environment. A diversity of organisms, including many zooplankton, use appendages bearing arrays of microscopic hairs to pick up chemical signals from the surrounding water or air (e.g., Atema, 1987; Laverack, 1988). The fluid flow field in the immediate vicinity of a sensory hair determines the rates at which molecules are captured. However, analyses of how these animals extract information from odor plumes, and efforts to characterize the kinetics of their olfactory neurons, will be compromised until we know more about how antennal morphology and motion determine small-scale fluid flow near (and hence the arrival of odorant molecules at) receptors. By elucidating basic rules about how morphology affects flow through arrays of olfactory hairs, we can also provide useful guidelines for the design of man-made chemical sensors, and for the analysis of other important biological structures bearing arrays of hairs, such as locomotory, filter-feeding, and gas-exchange appendages.

Importance of Fluid Motion to Olfaction

A critical step in the process of olfaction is the arrival of chemical signals from the environment to the surface of a chemosensory structure. This involves 1) the convection of odorant in the fluid from the source to the region of the sensor, and 2) diffusion from the bulk fluid to the surface of the sensor (DeSimone, 1981).

Odor plumes in the environment: Turbulent fluid motion on the scale of meters to centimeters determines the patchy structure of odor plumes in the environment (e.g. Csanady, 1973; Okubo, 1980), hence chemical signals in the fluid downstream from an odor source fluctuate (Aylor, *et al.*, 1976; Miksad and Kittredge, 1979; Murlis and Jones,

1981; Elkinton and Cardé, 1984; Atema, 1985; 1987; 1988; Murlis, 1986; Moore and Atema, 1988; 1991; Zimmer-Faust, et al., 1988; Moore, et al., 1989; 1991b; 1992; Murlis, et al., 1992). The behavior of various aquatic and terrestrial animals in odor plumes has been studied, and the ways in which organisms might use the information in odor plumes has received much attention (e.g. Bossert and Wilson, 1963; Hamner and Hamner, 1977; Reeder and Ache, 1980; David, et al., 1982; Devine and Atema, 1982; Bursell, 1984; Cardé, 1984; McPhie and Atema, 1984; Atema, 1985; 1988; Baker, 1989; Brady, et al., 1989; Moore, et al., 1991b; Murlis, et al., 1992; Willis, et al., 1991; 1994; Willis and Baker, 1994; Basil and Atema, 1994). However, the ability of a sensor to sample changes in odorant concentration as it moves relative to a plume depends on small-scale fluid flow near the sensory hairs, which is still poorly understood.

Small-scale fluid flow in the vicinity of sensory hairs: The number of molecules (N) captured per unit time (t) by an array of sensory hairs is given by:

$$N/t = (V/t)CP \tag{1}$$

where V is the volume of fluid moving through the array, C is the number of molecules per volume in the fluid, and P is the proportion of the molecules in the fluid that are captured. Both V/t and P depend on the small-scale fluid flow in the vicinity of the hairs.

Reynolds number (Re) represents the relative importance of inertial to viscous forces for a particular flow situation:

$$Re = LU/\nu, \tag{2}$$

where L is a linear dimension such as hair diameter, U is fluid velocity relative to the hair, and ν is fluid kinematic viscosity. The Re's of olfactory hairs on a variety of crustaceans and insects are low: 10^{-4} to 10 (Loudon, et al., 1994). Although inertial effects cannot be ignored at the upper end of this Re range, the viscous flow near sensory hairs is laminar (i.e. fluid motion is smooth and orderly, with no turbulent mixing between adjacent streamlines or random fluctuations in velocity; Happel and Brenner, 1965; Vogel, 1994).

When fluid flows past a solid surface, the fluid in contact with the surface does not slip and a velocity gradient (boundary layer) develops in the fluid between the surface and the freestream flow (Figure 1, A). At low Re's, such boundary layers are thick relative to the dimensions of the object. There is no turbulent mixing in a laminar boundary layer, hence molecular diffusion is the mechanism that moves odorants across streamlines towards or away from the sensor's surface. The distance travelled by a diffusing molecule is proportional to time $^{1/2}$ (Berg, 1993), so molecules in a streamline 10 times farther from the surface of a sensor than another streamline will take 100 times longer to arrive at the sensor's surface by diffusion.

Olfactory antennae often bear arrays of sensory hairs. Fluid can flow through or around a group of hairs. The leakiness (defined in Figure 1, B) of an array of hairs determines the volume flow rate (V/t) of fluid through the array (Figure 1, C). A row of hairs with low leakiness does not process much fluid per time, but the reduction of fluid velocity between neighbouring hairs allows a longer time for molecules to diffuse onto the hairs, thereby increasing the proportion (P) of the molecules in the fluid that are caught (e.g. Fuchs, 1964; Davies, 1973; Pich, 1966; Rubenstein and Koehl, 1977; Murray, 1977; Shimeta and Jumars, 1991). However, although they are good at capturing a large percentage of the molecules in the fluid, hairs surrounded by thick boundary layers are insulated from rapid changes in the concentration of molecules in the ambient flow, as
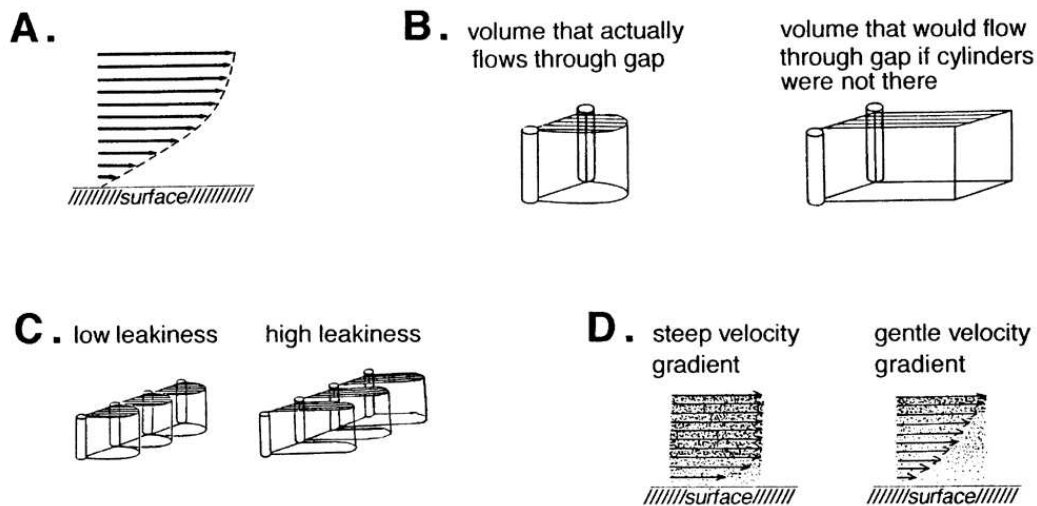
Figure 1 A. Diagram of a laminar boundary layer in the fluid moving with respect to a solid surface, such as the surface of a sensory hair. Arrows represent fluid velocity vectors at different heights above a point on the object. This represents the flow seen from the frame of reference of the object, and hence could represent flow past a stationary structure, or flow relative to an object moving through the fluid. B. "Leakiness" is defined as the ratio of the volume of fluid that actually moves between a pair of cylinders of unit length in a unit of time (shown on the left), to the volume of fluid that would move at freestream velocity ($U\infty$) through a gap of that width if the cylinders were not there to slow the flow (shown to the right). C. The flow rate (volume per time) of fluid moving through a leaky row of hairs (diagram on the right) is greater than through a less leaky row moving at the same velocity (diagram to the left). D. Diagram of a steep (left) and gentle (right) velocity gradient along a surface. The density of stippling in the fluid indicates the concentration of odorant molecules. In this example, a patch of light concentration odorant is being carried by in the ambient flow across the surface of a hair that had been in odorant-free fluid. The only way the molecules can reach the surface through these laminar velocity boundary layers is via molecular diffusion. Note that the surface with the gentle velocity boundary layer is "insulated" from this odor patch by a layer of slowly-moving "old" water.

illustrated in Figure 1, D. These trade-offs illustrate the importance of understanding the factors that determine the small-scale flow around sensory hairs if we are to understand how antennae of different designs sample their fluid environments.

Importance of fluid transport of odorants to olfactory neurobiology: Although many efforts have been made to characterize the response characteristics (adaptation, flicker-fusion, dose-response, response threshold) of olfactory neurons of marine organisms such as crustaceans (e.g. Borroni and Atema, 1988; Voigt and Atema, 1990; Marscall and Ache, 1989; Moore, 1994), our lack of understanding of how small-scale flow affects arrival of odorant molecules makes these data difficult to interpret. Do the measurements reflect the properties of the nerves, or of the boundary layer around the sensor? Indeed, Moore, *et al.* (1991a) have lamented the lack of proper stimulus control in olfactory electrophysiological experiments.

While several authors have suggested that the time course of the initial phases of neural responses to odorants might be determined by the transport of molecules to the receptor (Getchell and Getchell, 1977; DeSimone, 1981; Nachbar and Morton, 1981; Getchell, *et al.*, 1984; Moore, *et al.*, 1989; 1991b), others have argued that molecular diffusion may not be a limiting barrier to access to odor molecules (Boeckh, *et al.*,

1965; Futrelle, 1984; Mankin and Mayer, 1984). This issue has been addressed by a number of calculations of the diffusion of odor molecules to the surfaces of receptors (Adam and Delbrück, 1968; Berg and Purcell, 1977; Murray, 1977; DeSimone, 1981; Berg, 1983; Futrelle, 1984; Getchell, *et al.*, 1984; Kaissling, 1987). However, in spite of the importance of small-scale fluid flow to this process, information has been lacking about velocity profiles near hairs with neighbors. Therefore, various flow fields (such as flow around an isolated sphere or cylinder) have been assumed in these models that are not necessarily appropriate for antennae, hence applicability of model conclusions to various organisms is not yet clear.

Gleeson (1982) and Atema (1985) have pointed out that the morphology of the antennules of various decapod crustaceans with densely-packed hairs appears to inhibit flow and odor access, as corroborated by microelectrode measurements of reduced molecule fluxes within aesthetasc tufts on lobster lateral antennules, (Moore, *et al.*, 1989; 1991a), but not near smooth medial antennules. Antennal vibrating by insects (Schneider, 1964) and antennule flicking by crustaceans have been recognized as potential mechanisms of reducing boundary layer thickness, thereby increasing access of odors to receptor cells (e.g. Snow, 1973; Schmidt and Ache, 1979; Atema, 1985). Schmidt and Ache (1979) found that flicking enhanced the response of lobster olfactory receptors to changes in odor concentration, and Moore, *et al.* (1989; 1991a) found that pipette squirts to mimic flicking increased penetration of molecules into tufts of aesthetascs. Such periodic "sniffing" might provide a mechanism to get around the physical trade-off (mentioned above) between having a high P versus having a rapid response to a patch of odorant (i.e. "old" fluid can be "stripped off" olfactory hairs during a flick, yet fluid can be held between hairs when the antennule is not flicking, thereby allowing more of the molecules in that fluid the time to diffuse to receptors on the hairs' surfaces).

How Does the Morphology of an Array of Hairs Affect the Small-Scale Fluid Motion Through the Array?

We have used a combination of mathematical models (Cheer and Koehl, 1987a; 1987b) and dynamically-scaled physical models (Koehl, 1992; 1995; Loudon, *et al.*, 1994) to elucidate how the leakiness (Figure 1, B) of an array of hairs depends on factors such as hair diameter, spacing, length, speed relative to the fluid, and motion relative to nearby body surfaces. Such models enable us to vary one morphological or behavioral parameter at a time to ascertain the effects of each on performance. Since such controlled exploration of parameter space is not possible in comparative studies of different species, and since the small-scale flow around delicate, uncooperative, or very small organisms can be technically difficult to measure, models provide a useful complement to experiments with real organisms. Although the details of velocity profiles are difficult to measure around tiny hairs on living animals, the overall leakiness (which depends on those profiles) can sometimes be assessed to test the applicability of a model to the organism. The few measurements that have been made of the leakiness of arrays of hairs on arthropod appendages are consistent with the predictions of our mathematical and physical models (Koehl and Strickler 1981; Craig and Chance, 1982; Vogel 1983; Cheer and Koehl 1987b; Koehl 1992; 1995). Our predictions match measured leakinesses very closely for hairs operating at Re's of 10^{-1} and higher, and our physical models indicate that our under-estimation of the leakiness

of copepod hairy appendages whose setae operate at lower Re's (Koehl, 1992) is due to the interaction of those appendages with the body surface next to which they flap (Loudon, *et al.*, 1994).

The purpose of this study is to consider the general case of fluid flow between neighboring hairs to identify how hair size, speed, and spacing affect several aspects of fluid flow that are directly related to the performance of olfactory hairs: volume flow rate through an antenna, steepness of velocity gradient adjacent to a hair, and relative importance of fluid motion and molecular diffusion in getting odorant molecules to the surface of a sensory hair. Identifying such basic rules is a first step towards understanding the functional morphology of olfactory antennae, and may help us analyze the olfactory capabilities of planktonic animals whose sensors are technically difficult to study directly.

MATERIALS AND METHODS

I have employed velocity profiles calculated using the model of Cheer and Koehl (1987a) in order to estimate simple measures of various aspects of the performance of arrays of sensory hairs: leakiness and volume flow rate through the array, velocity profile steepness near the surface of an individual hair, and relative importance of fluid motion and of molecular diffusion in getting odorant molecules to the surface of a sensory hair. I have used these estimates of performance to explore the consequences of changing the behavior (velocity) or the morphology (inter-hair gap width) of rows of sensory hairs.

Model of Fluid Flow Between a Pair of Cylinders

Of the various methods that have been used to calculate the flow through arrays of hairs (reviewed in Koehl, 1995), the model of Cheer and Koehl (1987a) gives the best match to empirical data for biological antennae of finite width (Cheer and Koehl, 1987b). The details of this two-dimensional analytical model of fluid movement between a pair of circular cylinders at Re's of 0.5 and lower are given in Cheer and Koehl (1987a). Fluid velocities far from the cylinders were calculated using Oseen's low-Re approximation of the Navier-Stokes equations (which includes inertial effects), velocities near the cylinders were calculated in bipolar coordinates using Stoke's low-Re approximation, and these two flow fields were put together using a matched asymptotic expansion technique. The fluid motion relative to the hairs (due either to motion of the antenna through the surrounding fluid, or to ambient wind or water currents past the antenna) was assumed to be normal to the plane of the row of hairs. The velocity vectors of the fluid moving between neighboring cylinders were used in all the calculations described below.

Leakiness

The "leakiness" of the gap between neighboring hairs was calculated as illustrated in Figure 1, B (Cheer and Koehl, 1987a).

Although such dimensionless indices as leakiness and Re are useful for seeing general patterns in the physical behavior of arrays of hairs, the performance consequences of changes in the morphology or motion of an array of hairs can be more easily illustrated

by considering their effects on absolute flow rates and velocities for specific cases. Therefore, I have worked out the following examples for sensory hairs that are 1 μm in diameter.

Volume Flow Rate

An estimate of the volume (V) of fluid per time (t) moving through a unit area (A) normal to the flow direction of a filter or antenna composed of a row of hairs was calculated as:

$$V/(tA) = U_\infty Le\ g/(g + d),\qquad(3)$$

where g is the width of the gap between neighboring hairs and d is the diameter of a hair. All calculations were done for a hair 1 μm in diameter.

Steepness of Velocity Gradient

The position closest to the surface of a hair for which velocity was calculated was 0.3 μm from the hair. The velocity of the fluid at that position ($U_{0.3\mu m}$) was used as an indicator of the steepness of the velocity gradient next to the hair. Calculations were done for hairs 1 μm and 0.1 μm in diameter.

Relative Importance of Fluid Flow and Diffusion in Molecule Encounter by a Hair

I used two simple indices to estimate the relative importance of fluid motion and of molecular diffusion in getting odorant molecules to the surface of a sensory hair in an array: Péclet number, and "diffusive spread" (both defined below).

Péclet number represents the importance of convection (i.e. fluid motion) relative to molecular diffusion for a particular mass transfer situation (Kaissling, 1987; Murray, 1977; Vogel, 1994). Péclet number (Pé) is given by

$$\text{Pé} = dU_\infty/D,\qquad(4)$$

where d is hair diameter, U_∞ is freestream fluid velocity relative to the hair, and D is the diffusion coefficient of the molecule of interest in the fluid. All calculations were done for a small molecule having a diffusion coefficient (D) of 10^{-9} m^2/s in water at room temperature (Berg, 1993), and for hairs 1 μm in diameter. Péclet number plays a role in convective-diffusional mass transport processes somewhat comparable to the role of Re in inertial-viscous momentum transfer processes (Murray, 1977). Futrelle (1984) offered an intuitive description of Pé saying it could be interpreted roughly as the ratio of the actual cross-sectional area of a hair to the effective cross-section of fluid from which a diffusing molecule has a "reasonable" chance of hitting the hair. The higher the Péclet number, the more important water flow is relative to molecular diffusion in getting molecules to the surface of the olfactory hair. However, because this rough measure does not take into account the effect of inter-hair gap width on velocity profiles along hair surfaces, I also utilized another rough estimate of the importance of diffusion relative to fluid flow in hair encounter by molecules, "diffusive spread".

As molecules in a patch diffuse via random thermal motion, their mean position does not change, but their spread about that mean increases with time. One measure of such diffusive spread of molecules along an axis is the root mean square displacement of those
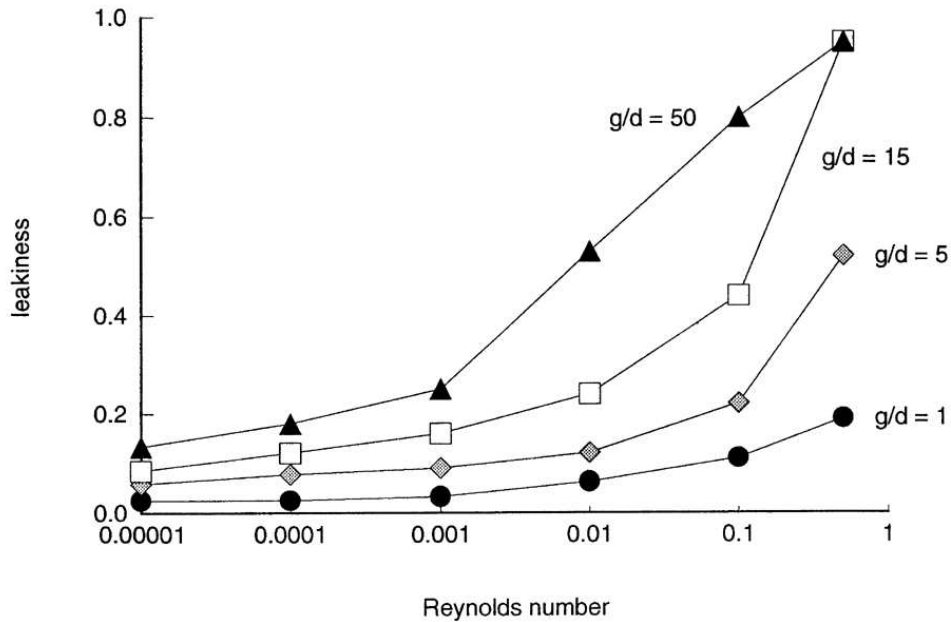
Figure 2 "Leakiness" (defined in Figure 1, B) plotted as a function of Reynolds number (log scale) for hairs at different distances apart. Each line represents a different gap (g = distance between neighboring hairs) to diameter (d = hair diameter) ratio.

molecules at some time (r.m.s. displacement = $[2D\ t]^{1/2}$, where D is the diffusion coefficient and t is time); it represents the distance at which the chances are 32% that a molecule has wandered that far or farther (Berg, 1993). I calculated a rough estimate of how much diffusive spread there is away from a streamline during the time that a parcel of water in that streamline is "near" a hair. I focused on the streamline 0.3 μm from the hair's surface, and I estimated the time "near" a hair as the time (Δt) that it takes for a parcel of water in that streamline to travel the distance of the diameter (d) of the hair. I estimated "diffusive spread" (S) as the root mean square distance that molecules in that streamline could diffuse in Δt:

$$S = [2D\ d/U_{0.3\mu m}]^{1/2}, \tag{5}$$

where $U_{0.3}\mu$m is the velocity in the streamline at 0.3 μm from the surface of the hair. The greater this diffusive spread, the greater the likelihood that molecules arriving in a parcel of water in that streamline might diffuse to the surface of the hair. All calculations of S were done for hairs 1 μm in diameter and for small molecules having a diffusion coefficient (D) of 10^{-9} m^2/s in water at room temperature.

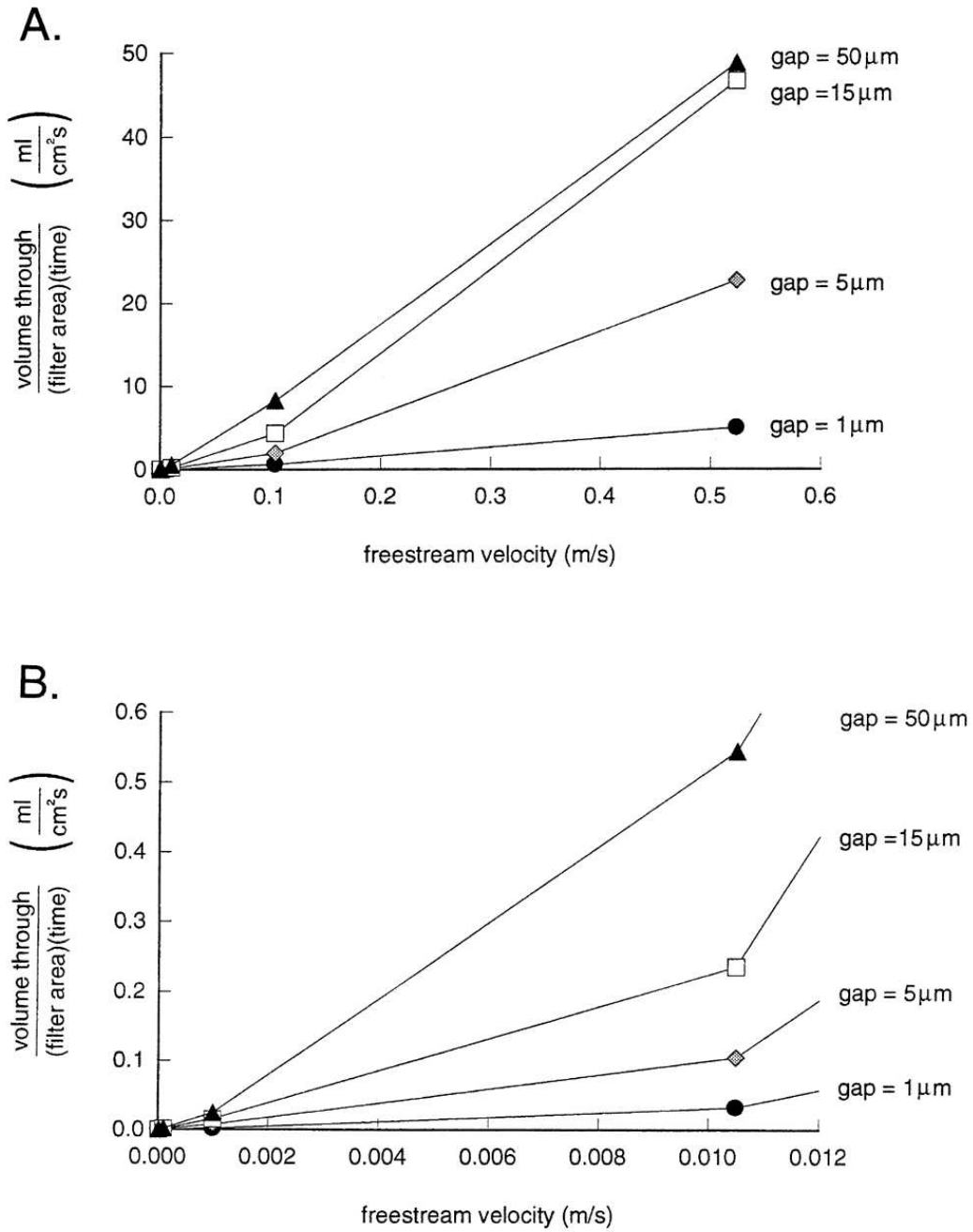**Figure 3** A. Volume (ml) of fluid per time (s) moving through a unit area (cm²) of a filter or antenna composed of a row of hairs that are 1 μm in diameter, plotted as a function of freestream velocity (m/s; the velocity of the fluid in the environment relative to the antenna). Each line represents a different width of gap (μm) between neighboring hairs. B. Same as in A., but focusing on low freestream velocities.
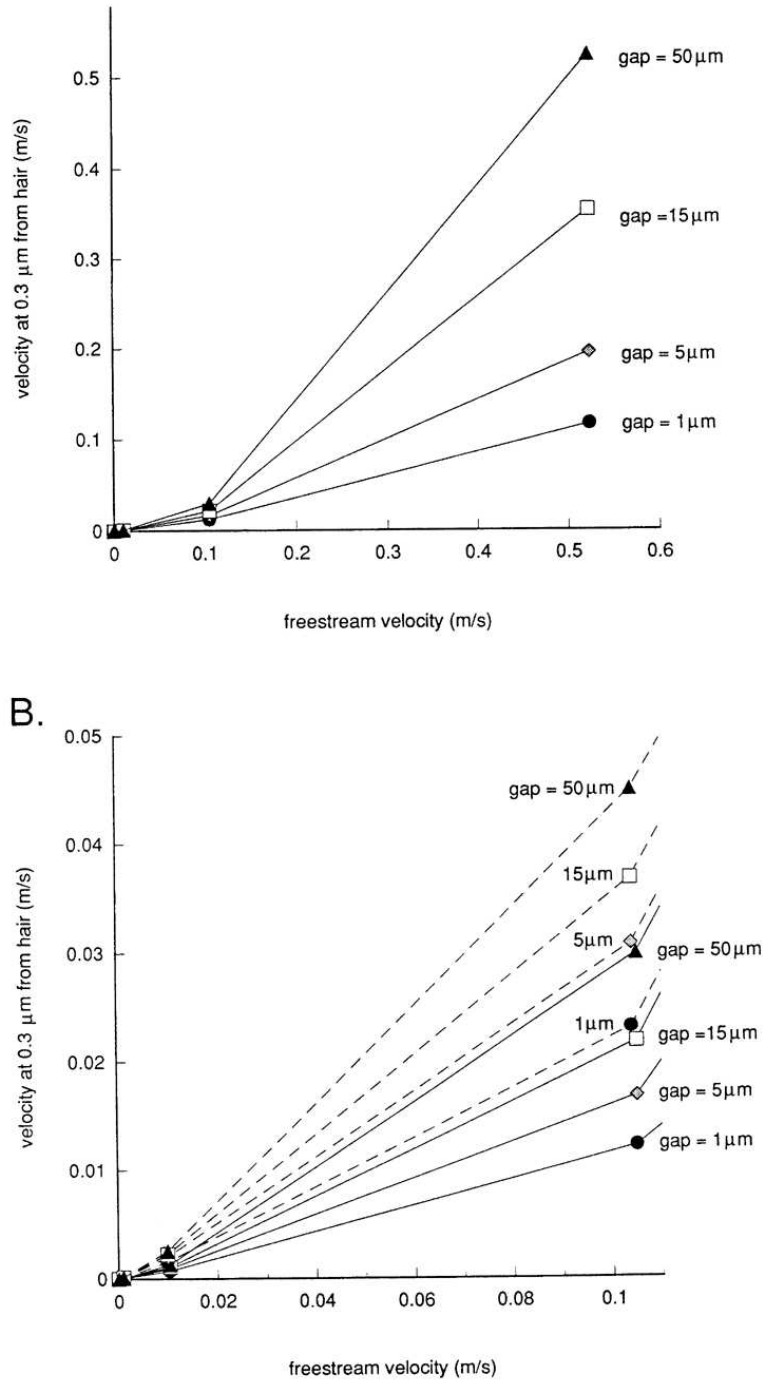
Figure 4   A. Velocity (m/s) in the fluid at a distance of 0.3 μm from the surface of a hair that is 1 μm in diameter, plotted as a function of freestream velocity (m/s). Each line represents a different width of gap (μm) between neighboring hairs. The higher the velocity at 0.3 μm from the hair, the steeper the velocity gradient along the surface of the hair. B. Same as in A, but focusing on low freestream velocities. Solid lines represent hairs that are 1 μm in diameter, and dashed lines represent hairs that are 0.1 μm in diameter.

RESULTS AND DISCUSSION

Effects of Morphology and Motion on Flow Between Hairs in an Array

The calculations described above reveal some general features about the design and deployment of appendages such as olfactory antennae composed of arrays of small hairs.

Leakiness: The leakiness of an array of hairs depends on Reynolds number (Re), as illustrated in Figure 2. At very low Re (10^{-3} and lower; i.e. for very small or slowly-moving sensory hairs) little fluid moves through the gap between neighboring hairs and the antenna behaves more like a paddle than like a sieve. In contrast, at higher Re's (i.e. for larger or more rapidly-moving hairs), the array is leakier. At Re approaching 1, little fluid is dragged along with the hairs as they move and a hair-bearing antenna should be sieve-like. The Re of a sensory hair is modified if the hair changes in size (e.g. via growth of an individual, or through evolutionary change within a lineage) or if the fluid velocity relative to an antenna is altered (e.g. via swimming at a different speed, flicking the antenna, or moving to an area of different ambient current). Leakiness is changed little as Re is altered for hairs operating at very low Re's, hence there is permission for variation in size or behavior without consequences to leakiness. In contrast, changing Re between 10^{-2} and 1 can lead to drastic changes in leakiness. Similarly, changes in the gap-to-diameter ratio (g/d) of a row of hairs has little effect on leakiness at very low Re, whereas moving hairs closer together can lead to drastic decreases in leakiness at higher Re's. However, at Re's approaching 1, hairs must be quite close together before gap width affects leakiness (for example, leakiness is the same for g/d's of 15 and 50, but is much lower for a g/d of 5; Figure 2).

Volume flow rate: Obviously, the volume of fluid that can be processed per unit time by an antenna of a given area is increased if the velocity at which the sensory hairs are moved through the surrounding fluid is increased. The effect of velocity is more pronounced for arrays of hairs that have wide between-hair gaps (Figure 3). At high velocities, increasing the gap width increases the volume flow rate per area through the antenna if the hairs are very close together, but makes little difference if the hairs are farther apart (Figure 3, A). In contrast, at lower velocities, altering gap width alters volume flow rate per area through the antenna even for widely-spaced hairs (Figure 3, B).

Steepness of velocity gradient: As illustrated in Figure 1, D, the steeper the velocity gradient next to the surface of a sensory hair, the more quickly a change in ambient concentration of some odorant molecule will translate into a change in the rate of molecules arriving at the surface of the hair. Velocity gradients become disproportionately steeper as the velocity at which an antenna moves through the surrounding fluid is increased (Figure 4). The sensitivity of velocity gradient steepness to changes in antenna velocity is greater for arrays of hairs that are widely spaced than for those with narrow gap widths. Furthermore, for a given gap width and velocity, slim hairs have steeper velocity gradients along their surfaces than do wider hairs (Figure 4, B).

Relative importance of fluid flow and diffusion in molecule encounter by a hair: The slower the flow through an antenna, the greater the probability that an odorant molecule in the fluid moving through the antenna will have time to diffuse to the surface of an olfactory
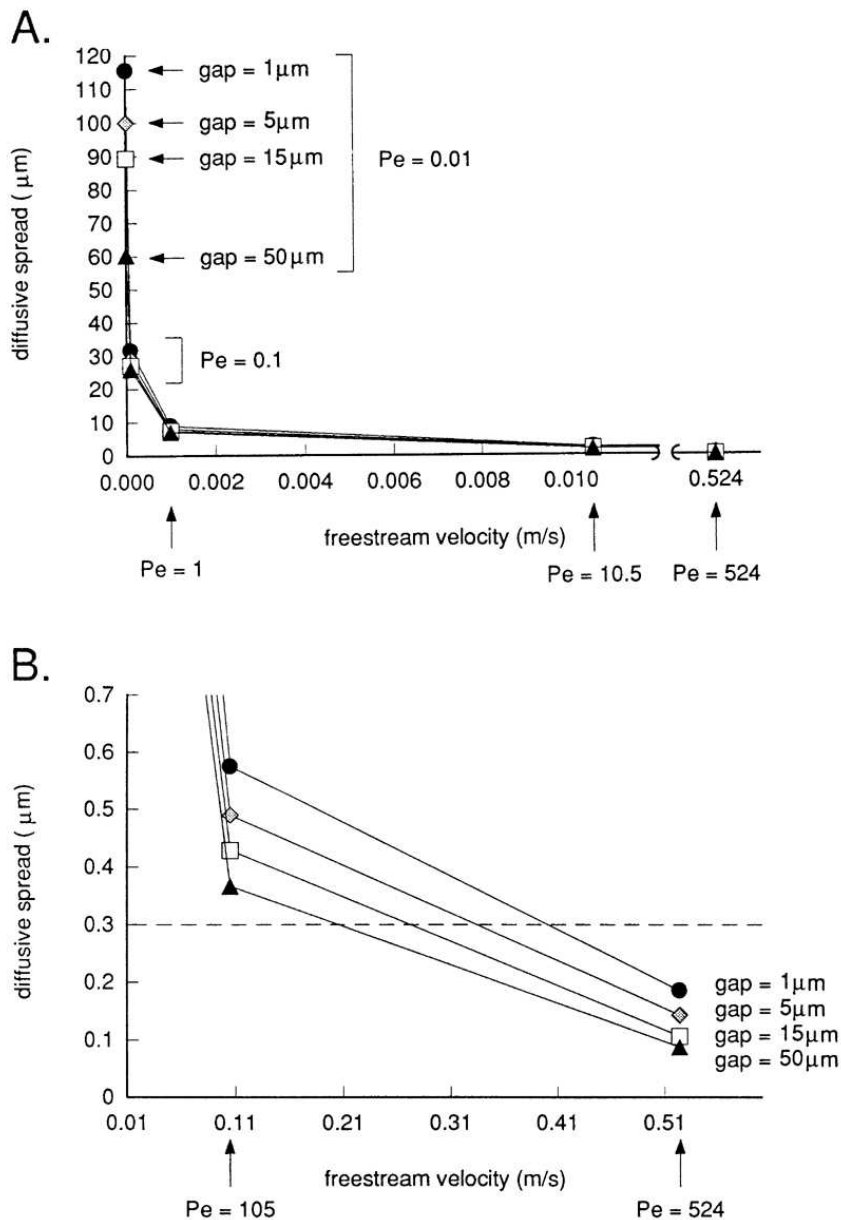
Figure 5 A. Diffusive spread (root-mean-square distance (μm) that molecules in a streamline of water at a distance of 0.3 μm from the surface of a hair could diffuse at right angles to that streamline in the time that it takes for a parcel of water in that streamline to travel the distance of the width of the hair (1 μm)) plotted as a function of freestream velocity (m/s). The greater this r.m.s. distance, the greater the likelihood that molecules arriving in a parcel of water in that streamline might diffuse to the surface of the hair. Péclet numbers (Pé, defined in the text) for the points plotted are indicated with arrows along the velocity axis or with brackets next to the points. All calculations were done for a small molecule having a diffusion, coefficient (D) of 10^{-9} m^2/s in water at room temperature. Each line represents a different width (μm) of gap between neighboring hairs. B. Same as in A, but focusing the higher freestream velocities. The dashed line indicates the distance of the streamline being considered from the surface of the hair.

hair. The Péclet numbers (Pé) shown along the velocity axis in Figure 5 represent the importance of fluid motion relative to molecular diffusion in getting molecules to the surfaces of hairs. Notice that the freestream velocity at which Pé = 1 for hairs 1 μm in diameter is very low: 0.001 m/s. However, since flow through arrays of hairs can be slower than around isolated hairs at the same freestream velocity, the functional Pé's of olfactory hairs may be lower than these estimates suggest, hence the freestream velocities at which Pé = 1 might be faster.

Diffusive spread (S, the root mean square distance that molecules might diffuse from a streamline during the time that a parcel of water in that streamline is "near" a hair) provides another index of the relative importance of diffusion in molecule capture by olfactory hairs. S is very low at freestream velocities above 0.001 m/s (Figure 5, A), and at velocities of 0.01 m/s only a small proportion of the molecules in the streamline 0.3 μm from the hair should have time to diffuse to a hair (Figure 5, B). At very low freestream velocities (low Pé's), narrower gaps between hairs lead to greater S, but at higher Pé's, gap width has little effect on S.

These estimates of Pé and S suggest that if hairy antennae are held still or moved very slowly, they will be good at harvesting via diffusion the molecules in the fluid trapped between the hairs, whereas if they are moved at velocities higher than about 1 mm/s, many of the molecules in the fluid processed by the antenna will "escape". Nonetheless, a greater number of molecules per time can be encountered by an array of hairs exposed to more rapid flow (e.g. Shimeta, 1993), and hence to a greater V/t (see equation 1). Therefore, if a zooplankter swims, produces a scanning current past its body (e.g. Koehl and Strickler, 1981), or flicks its antennae, it can increase its molecule encounter rate. Furthermore, the faster a zooplankter can move fluid relative to its olfactory hairs, the steeper the concentration gradient between "old" water along the hair's surfaces and "new" water containing a different concentration of odorant molecules, and hence the more sensitive to changes in odorant concentration such an antenna might be.

Thus, the first step in "filtering" olfactory signals from the environment can be due to the physical effects on molecule encounter rates caused by the fluid-moving behavior of the animal and by the morphology of its arrays of olfactory hairs, rather than by neural processing.

General Importance of Flow Through Arrays of Hairs

Many organisms from different phyla use appendages bearing arrays of hairs to perform a variety of important biological functions in addition to olfaction, including other mass exchange processes such as suspension-feeding and gas exchange, and momentum-exchange functions such as mechanoreception, swimming, or flying (e.g. Koehl 1992; 1995). Therefore, which morphological and behavioral factors determine the fluid motion through an array of cylinders is an issue of basic biological importance. One general conclusion of our modeling is that such hairy appendages are leaky sieve-like structures if their hairs operate at Re's of 10^{-1} and higher, but are functionally more paddle-like (i.e. little of the fluid that they encounter flows through them) if their hairs operate at Re $\leq 10^{-2}$.

The conclusions of the general analysis presented here can be used to consider other molecule-capturing functions in addition to olfaction, such as gas exchange or capture of nutrient molecules. The rate of molecule encounter by a hair-bearing gill, feeding appendage, or antenna is enhanced if volume flow rate through such a structure is increased, even though the proportion of molecules encountered in each parcel of

water processed is reduced. Hairs that remove certain molecules from the fluid (such as those on gills or feeding appendages) can deplete the fluid near their surfaces of those molecules; the steeper the velocity gradient near the surface of a hair, the steeper the concentration gradient between the undepleted fluid and the hair, and hence the greater the rate of molecule encounter by the hair due to diffusion (e.g. Vogel, 1994; Shimeta and Jumars, 1991). Although olfactory antennae probably do not cause such local depletion of odorants, steeper velocity gradients can lead to increased sensitivity to changes in ambient odorant concentration, as discussed above. This study has shown that increases in freestream velocity increase both V/t and steepness of the velocity gradient near a hair, but that arrays of hairs with narrow gap widths are less sensitive to changes in freestream velocity than are those with more widely-spaced hairs. Furthermore, changes in gap width have bigger effects on diffusive spreading at low freestream velocities than they do in faster flow. In general, for all such hair-bearing appendages, the performance consequences of changes in behavior or morphology depend on the Reynolds number at which their hairs operate.

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