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The Fluid Mechanics of Arthropod Sniffing in Turbulent Odor Plumes

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Abstract

Many arthropods capture odorant molecules from the environment using antennae or antennules bearing arrays of chemosensory hairs. The penetration of odorant-carrying water or air into the spaces between these chemosensory hairs depends on the speed at which they are moved through the surrounding fluid. Therefore, antennule flicking by crustaceans and wing fanning by insects can have a profound impact on the odorant encounter rates of the chemosensory sensilla they bear; flicking and fanning are examples of sniffing. Odors are dispersed in the environment by turbulent wind or water currents. On the scale of an antenna or antennule, an odor plume is not a diffuse cloud but rather is a series of fine filaments of scent swirling in odor-free water. The spatiotemporal pattern of these filaments depends on distance from the odor source. The physical interaction of a hair-bearing arthropod antennule with the surrounding fluid affects the temporal patterns of odor concentration an animal intercepts when it sniffs in a turbulent odor plume.

Key words: antenna, antennule, flick, olfaction, sniff, turbulence

Introduction

Many animals use chemical cues in the water or air around them in ecologically important activities such as locating food, selecting habitats, detecting predators or competitors, and communicating with conspecifics (e.g., Caldwell, 1979, 1982; Cardé, 1984; Hadfield and Scheuer, 1985; Zimmer-Faust, 1991; Berg *et al.*, 1992; Weissburg and Zimmer-Faust, 1994; Atema, 1995; Atema and Voigt, 1995; Koehl, 1996a; Zimmer *et al.*, 1999; Breipthaupt and Atema, 2000; Bushmann and Atema, 2000; Finelli *et al.*, 2000; Nevitt *et al.*, 2000; Weissburg, 2000; Weissburg *et al.*, 2002; Horner *et al.*, 2004). Turbulent wind or water currents in the environment carry odorants from a source to an animal's olfactory organ (e.g., antenna, nose), while small-scale flow near the organ's surface and molecular diffusion transport odorants to the olfactory receptors (Murray, 1977; Koehl 1996a, 2001a; Loudon and Koehl, 2000; Stacey *et al.*, 2002). Thus, to understand the physical mechanisms responsible for the temporal patterns of odorant concentrations arriving at receptors, we must not only understand odorant dispersion in turbulent fluid flow but also how the small-scale fluid dynamics of sniffing filters those patterns on their way to the receptors.

A sniff is a brief increase in air or water flow across an olfactory organ produced by motions of an animal. Such a sudden increase in fluid flow can be created by driving a current of air or water across or into an olfactory organ or by moving the organ through the surrounding fluid. Sniffing can affect the kinetics of stimulus access to the chemosensory receptors in two ways: 1) sniffing may rapidly replace the fluid volume within or along a chemosensory organ, providing the receptors there with a new sample of the odor environment and 2) sniffing may increase the rate at which odorant molecules reach receptors by increasing the fluid velocity along a chemosensory surface (such an increase in velocity reduces the thickness of the layer of slowly moving, stale fluid next to a chemosensory surface, thereby decreasing the distance across which molecules from newly sampled fluid must diffuse) (e.g., Snow, 1973; Schmidt and Ache, 1979; Atema, 1985; Ache, 1991; Gleeson *et al.*, 1993; Loudon and Koehl, 2000).

A basic property of all sensory systems is that the end organ that interfaces with the environment is intermittently exposed to the stimulus (Dethier, 1987). In olfactory systems, such periodic exposure to odorants can offset the adaptation of chemosensory neurons (Ache, 1991). For olfaction, there are two sources of intermittency in the stimulus environment: 1) the intermittent exposure to the stimulus environment due to sniffing (e.g., reviewed by Ache, 1991; Laurent, 1999) and 2) the temporally and spatially fluctuating

structure of turbulent odor plumes in the air or water around an animal (e.g., reviewed by Murlis *et al.*, 1992; Murlis, 1997; Weissburg, 2000; Moore and Crimaldi, 2004). Thus, the first step in understanding the kinetics of olfaction is to decipher how sniffing interacts with intermittent odorant distributions in the environment to shape the signals arriving at the receptors.

The purpose of this paper is to examine the basic fluid dynamics of sniffing by arthropod olfactory antennae and antennules that bear arrays of chemosensory hairs (sensilla, aesthetascs) and to discuss how such sniffing by hair-bearing olfactory organs samples the fine-scale fluctuating structure of turbulent odor plumes in the environment.

Fluid dynamics of molecule capture by hair-bearing olfactory organs

The olfactory organs used by many arthropods to capture odorant molecules from the surrounding water or air are appendages bearing arrays of hair-like chemosensory sensilla (reviewed by Ache, 1982; Zacharuk, 1985; Laverack, 1988). The morphology of such hair arrays differs between species, ranging from simple rows of sensilla to brush-like or feathery structures (Figure 1).

Fluid flow around a hair in an array depends on the relative importance of inertial and viscous forces, as represented by the Reynolds number ($Re = ul/\nu$, where u is velocity, l is hair diameter, and ν is kinematic viscosity of the fluid). Large, rapidly moving bodies operating at high Re experience the messy, turbulent fluid flow dominated by inertia. In contrast, small, slowly moving structures operating at low Re, where viscous forces damp out disturbances to the flow, experience smooth, laminar fluid motion. Kinematic viscosity (ν) is the fluid's dynamic viscosity (μ, the fluid's resistance to being sheared) divided by the fluid's density (ρ). (A fluid is sheared when one layer of fluid moves more rapidly than the layer next to it, i.e., when there is a velocity gradient in the fluid.) Although air is less viscous than water, it is also less dense and has a higher kinematic viscosity (e.g., at 20°C, $\nu_{air} = 15 \times 10^{-6}$ m^2/s and $\nu_{water} = 1 \times 10^{-6}$ m^2/s; Vogel, 1994). Thus, if a hair of a given diameter moves at the same velocity in water and in air, its Re in water is about 15 times bigger than its Re in air.

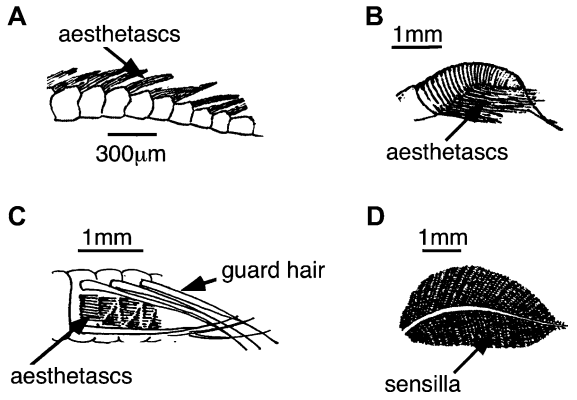

Figure 1 Examples of arthropod olfactory appendages bearing arrays of chemosensory hairs (aesthetascs on the marine crustaceans in **A**–**C**; sensilla on the terrestrial insect in **D**). (A) Section of the aesthetasc-bearing branch of the lateral filament of an antennule of a mantis shrimp (stomatopod), *Gonodactylaceus mutatus*. (B) Lateral filament of the antennule of a blue crab, *Callinectes sapidus*. (C) Section of the lateral filament of the antennule of the spiny lobster *Panulirus argus*. Nonchemosensory guard hairs form an arch over the aesthetascs. (D) Antenna of a male silkworm moth, *Bombyx mori*. The central stalk supports branches, each of which bears sensilla. The crustaceans (A–C) flick the aesthetasc-bearing branches of their antennules through the water, while the moth (D) drives air through its antenna by fanning its wings.

Because the fluid in contact with the surface of a moving object does not slip relative to the object, a velocity gradient develops in the flow around the object (Figure 2A). The lower the Re (i.e., the smaller or slower the object or the greater the kinematic viscosity of the fluid), the thicker this boundary layer of sheared fluid is relative to the size of the object. If the boundary layers around the hairs in an array are thick relative to the gaps between hairs, then little fluid leaks through the array. Our mathematical and physical models of flow between cylinders and through hair arrays on animal appendages (Cheer and Koehl, 1987a,b; Koehl, 1993, 1995, 1996b, 1998, 2000, 2001a,b; Loudon, *et al.*, 1994) revealed that hair arrays undergo a transition between nonleaky, paddle-like behavior (i.e., little fluid flows between adjacent hairs) and leaky, sieve-like behavior (i.e., fluid readily flows between hairs) as Re is increased. The Re at which this transition occurs depends on the spacing of the hairs in the array (Figure 2B). For closely spaced hairs, as on many crustacean antennules and insect antennae, this transition occurs at Re of order 1, where leakiness is very sensitive to velocity.

Some researchers have argued that the diffusion of molecules to olfactory receptors determines the temporal pattern of the onset of neural responses to odorants (e.g., T.V. Getchell and M.L. Getchell, 1977; DeSimone, 1981; Nachbar and Morton, 1981; Moore *et al.*, 1989), whereas others have argued that molecular diffusion does not limit the access of odor molecules to receptors (Boeckh *et al.*, 1965; Futrelle, 1984; Mankin and Mayer, 1984). Mathematical models of an isolated hair show that flow velocity has a small effect on molecule interception rate (Adam and Delbruk, 1968; Murray, 1977), but our models of arrays of hairs showed that changes in velocity can have a profound impact on odorant encounter rates in the Re range in which the leakiness of the array is sensitive to speed (Koehl, 1996a; Loudon and Koehl, 2000; Stacey *et al.*, 2001).

Flicking by crustacean antennules is sniffing

The olfactory organ of most larger crustaceans is the lateral filament of the antennule, which bears chemosensory sensilla called "aesthetascs" (e.g., Atema, 1977, 1995; Gleeson, 1982; Grünert and Ache, 1988; Laverack, 1988; Hallberg *et al.*,

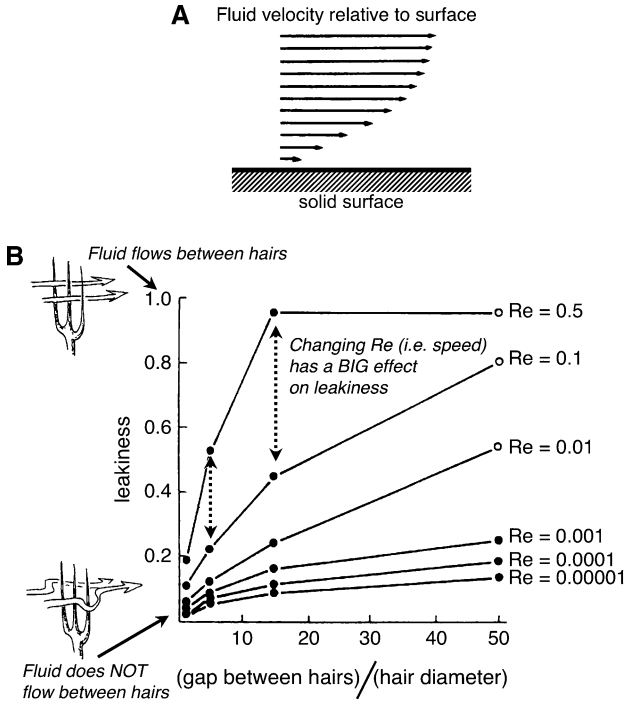

Figure 2 **(A)** Velocity vectors (shown by arrows) of a fluid moving relative to a solid surface. When a fluid (e.g., water or air) flows past a solid surface (e.g., the surface of a hair), the layer of fluid in contact with the surface does not slip relative to the surface. Therefore, a velocity gradient builds up in the fluid between the free-stream flow and the surface. Similarly, when a body moves through a stationary fluid, the layer of fluid in contact with the body's surface does not slip relative to that surface and moves along with the body. A velocity gradient develops in the fluid between the surface of the moving body and the still fluid farther away. The fluid motion relative to the body is in the opposite direction from the direction the body is moving through the fluid. The lower the Reynolds number [Re, equation (1)] of a hair, the thicker the layer of fluid in which this velocity gradient exists relative to the diameter of the hair. **(B)** Leakiness of a row of hairs (leakiness is the ratio of the volume per time of fluid that actually flows through the gap between neighboring hairs and the volume per time that would flow through a space of the same dimensions if the hairs were not there to interfere with the flow) plotted as a function of hair spacing (ratio of the width of the gap between neighboring hairs to the diameter of the hairs). Points on the graph were calculated as described in Cheer and Koehl (1987b). Each line represents a different Re, calculated using hair diameter for l. For closely spaced hairs operating at Re values of order 0.1 to 1, as are the olfactory sensilla and aesthetascs of many arthropods, a change in Re (i.e., a change in the speed of the hair array relative to the surrounding fluid) causes a large change in leakiness. For closely spaced hairs, a change in hair spacing in this Re range can also have a big effect on leakiness.

1992; Atema and Voigt, 1995; Giri and Dunham, 1999; Steullet *et al.*, 2000, 2001; Mead and Weatherby, 2002; Obermeier and Schmitz, 2004; Kamio *et al.*, 2005). Although nonaesthetasc sensilla on antennules or legs of some species can also be involved in olfaction (Giri and Dunham, 1999, 2000; Cate and Derby, 2001; Steullet *et al.*, 2001, 2002; Grasso and Basil, 2002; Keller *et al.*, 2003; Horner *et al.*, 2004), I will focus here on the aesthetasc-bearing lateral branches of the antennules because the fluid mechanics of these organs has been studied.

Many malacostracan crustaceans, such as crabs, lobsters, shrimp, and stomatopods, flick the aesthetasc-bearing lateral branch of the antennule through the water. Such flicking has been described as a mechanism of increasing water penetration into the aesthetasc array, thereby enhancing the access of odors to receptor cells (e.g., Snow, 1973; Schmidt and Ache, 1979; Atema, 1985; Gleeson *et al.*, 1993; Koehl, 1995, 1996). Several lines of evidence are consistent with this idea. Flicking by antennule preparations enhanced the response of lobster olfactory receptor neurons to changes in odorant concentration (Schmidt and Ache, 1979). Pulses of flowing water (to mimic flicking) onto the aesthetascs of lobster antennule preparations increased penetration of tracer molecules into the water between aesthetascs (Moore *et al.*, 1989, 1991).

High-speed kinematic analysis of antennule flicking in water showed that aesthetascs operate in the Re range of the leakiness transition in lobsters (Goldman and Koehl, 2001), shrimp (Mead, 1998), stomatopods (Mead *et al.*, 1999), and crabs (Koehl, 2001a). In all these examples, the flick downstroke or outstroke of the lateral branch of the antennule was much faster than the return stroke, and the aesthetasc array was predicted to be leaky to water flow during the rapid flick but not during the slower return stroke. These predictions were tested by measurement of water velocity fields around the aesthetascs on dynamically scaled physical models of antennules. Such model studies revealed that water does flow through the aesthetasc array during the rapid flick downstroke, but not during the slower return stroke, for spiny lobsters (Koehl, 2001a), stomatopods (Mead and Koehl, 2000), and crabs (Koehl, 2001a).

Because these diverse crustaceans flick their antennules in the Re range at which the leakiness of their hair arrays is sensitive to speed, they are able to take fluid samples into their aesthetasc arrays during the rapid downstroke of a flick when the aesthetasc array is leaky. They then retain that captured water within the hair array during the slower return stroke and subsequent stationary pause of the antennule when the aesthetasc array is not leaky. During the next rapid flick downstroke, that water sample is flushed away and replaced by a new one (Koehl *et al.*, 2001). Therefore, antennule flicking permits these animals to take discrete samples in space and time of their odor environment.

Some species of crabs are intertidal or terrestrial, and thus spent much of their time in air rather than water. Terrestrial robber crabs flick their antennules in air, and their olfactory neurons respond to air-borne odorants (Stensmyr *et al.*, 2005), but whether such flicking occurs in the Re range of the leakiness transition for their aesthetasc arrays cannot be evaluated until the kinematics of their flicking is measured.

Wing fanning is sniffing in insects

When insects flap their wings, pulses of air flow past their bodies as the wings oscillate. This occurs during flight (e.g., Ellington *et al.*, 1996; Birch and Dickinson, 2003) and during

wing fanning by walking insects (Loudon and Koehl, 2000). Measurements of the airflow encountered by the feathery olfactory antennae of male silkworm moths during wing fanning showed that the air speeds produced by the flapping wings oscillated and that the pulses of air movement produced by the beating wings do move between the sensory hairs (sensilla) on the antennae (Loudon and Koehl, 2000). Although wing fanning produces airflow 15 times faster than that experienced by the antennae when the moth walks without fanning, the air speed through the gaps between sensilla is ~560 times faster during fanning because a dramatic increase in the leakiness of the sensilla array occurs at the air velocities produced by fanning. This increase in leakiness leads to an increase in the rate of pheromone interception of about an order of magnitude. Thus, by operating in the Re range at which the transition in leakiness occurs, feathery moth antennae sniff when the animals' wings are beating.

Not only does wing fanning dramatically increase the rate of interception of odorant molecules by the sensilla on moth antennae, but it also enhances the ability of a walking moth to determine the direction of the source of the aroma. Although air velocity through the antennae varies sinusoidally as the wings flap, the air driven through the antennae always moves from front to rear across the animal (Loudon and Koehl, 2000). Therefore, if a wing-fanning moth turns to face different directions, it can draw samples of air from those different directions through its antennae (Ishida *et al.*, 2001). Computer simulations show that this ability to actively sniff air from different directions should enable a moth to find the source of a pheromone signal irrespective of the wind direction (Sakuma, 2002).

Whether insects with other antenna morphologies, and insects in free flight, use the transition in leakiness of their sensilla arrays as a mechanism of sniffing is an area ripe for more research. Some insects flick their antennae when they come in contact with odor plumes (Stensmyr *et al.*, 2005), but whether such flicking results in sniffing is also not yet known.

Physics of turbulent plumes

Odorant molecules are released from a source into the surrounding water or air and are transported across the environment by ambient water currents or wind. Although molecular diffusion does disperse molecules in a fluid via Brownian motion, the time required for molecules to travel through a fluid by diffusion increases as the square of the distance (e.g., Vogel, 1994). Thus, although molecular diffusion is important in dispersing odors over very short distances, flow of the air or water containing odorant molecules is the mechanism by which chemical signals travel large distances. "Advection" is the bulk transport of such fluid-borne materials by the mean air or water flow across a habitat.

Wind and water currents in natural environments are turbulent, so swirling eddies stir odor-laden fluid with the surrounding nonsmelly water or air, thereby dispersing the chemical signal. Such random turbulent mixing has been modeled as a diffusion process, and time-averaged concentrations in turbulent odor plumes show that the plume becomes wider and more dilute with distance from the source (Figure 3A,B) (reviewed in Elkinton and Cardé, 1984; Murlis *et al.*, 1992). Early models of how animals might search for the source of an odor assumed such diffuse plumes (e.g., Bossert and Wilson, 1963). However, arthropods tracking odor plumes to locate the source of the chemical signal move too rapidly to use the time-averaged local concentrations in a plume (e.g., Weissburg and Dusenbery, 2002). To assess the odor environments experienced by such animals, we need to examine the instantaneous concentrations they encounter in a turbulent plume.

Studies of the instantaneous structure of turbulent odor plumes in air are reviewed by Murlis *et al.* (1992) and Murlis (1997) and in water by Weissburg (2000) and Moore and Crimaldi (2004). Parcels of fluid containing high concentrations of odorants released from a source are spread into filaments by shear in the turbulent air or water moving past the source, and these filaments of high-concentration odorant are stirred around in eddies and intermingled with the surrounding odor-free fluid (Figure 3C,D) (e.g., Murlis, 1997; Crimaldi and Koseff, 2001a,b; Crimaldi *et al.*, 2002b; Moore and Crimaldi, 2004). This stirring process greatly increases the area of interface between high-concentration odorant filaments and the clean fluid, and molecular diffusion at these interfaces dilutes and spreads the filaments locally (e.g., Moore and Crimaldi, 2004). Turbulent water currents and wind contain eddies of many sizes, ranging from the scale of millimeters to hundreds of meters. While small and medium-sized eddies stretch and stir the filaments in an odor plume into the surrounding water or air, the larger eddies produce fluctuating changes in current or wind direction that cause the odor plume to meander and undulate (Murlis, 1997). Therefore, a spatially complex and temporally changing three-dimensional distribution of odorant concentrations develops in natural habitats. This distribution of fluid-borne chemical signals is the "odor landscape" in which animals navigate (e.g., Nevitt *et al.*, 1995; Atema, 1996; Moore and Crimaldi, 2004).

Plumes in water versus plumes in air

Molecules spread by molecular diffusion much more rapidly in air than in water. The molecular diffusivity (D, a chemical's propensity to diffuse in a particular fluid) of molecules in water is about 10^{-9} m^2/s but is about 10,000 times greater in air than in water (e.g., Denny, 1993; Vogel, 1994; Moore and Crimaldi, 2004). The Péclet number (Pé = ul/D, where u is the flow velocity) represents the ratio of the time required to displace a molecule a distance (l) by advection (i.e., by fluid flow) to the time required to displace the molecule that distance by molecular diffusion (e.g., Vogel, 1994; Moore and Crimaldi, 2004). The lower the Pé, the greater the rate

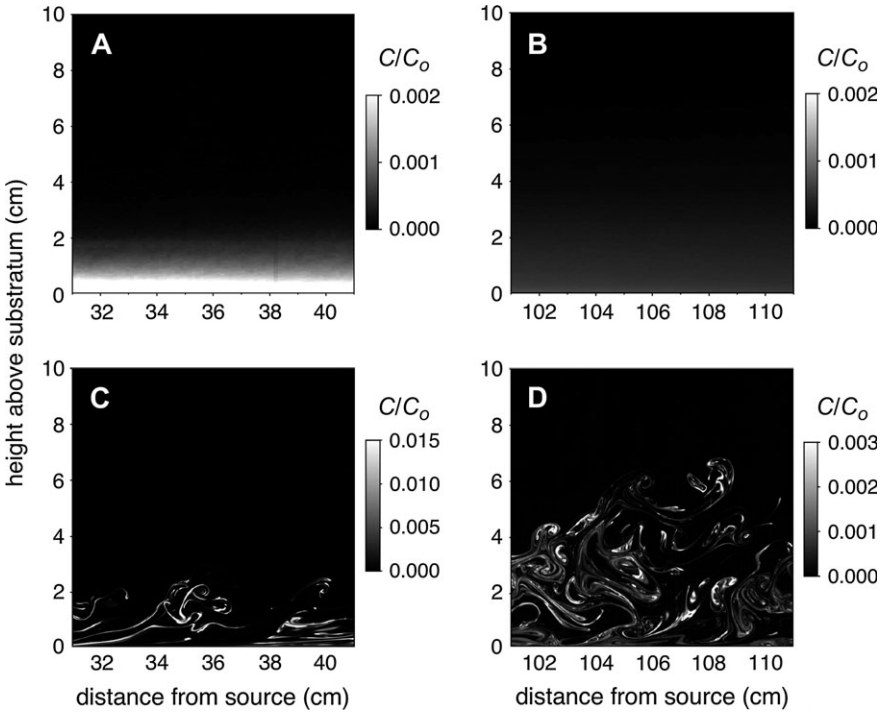

Figure 3 Concentration of dye (Rhodamine 6G, used as an analogue for a dissolved odorant) in turbulent water flow in a flume (a flow tank in which free-stream velocity was 9.84 cm/s) at different distances downstream from a "momentumless" dye source flush with the floor of the flume. A thin vertical slice of water (280 mm thick) along the midline of the dye plume was illuminated by a sheet of laser light; technical details are described by Crimaldi (Crimaldi and Koseff, 2001a,b; Crimaldi *et al.*, 2002b). The lighter the pixel, the higher the concentration (scales differ for each plot; C is concentration and C_o is the concentration of the dye source). Plots **(A)** and **(B)** show time-averaged concentrations (for 8000 video frames shot at three frames/s) and plots **(C)** and **(D)** show instantaneous concentrations in single video frames (shot at 15 frames/s). Plots (A) and (C) show the plume close to the source, while plots (B) and (D) show the plume at a greater distance downstream from the source. Videos of such a plume can be viewed in Crimaldi *et al.* (2002b). (Images provided by J.P. Crimaldi.)

of smoothing of concentration gradients in the fluid by molecular diffusion. Since D values in air are so much greater than in water, Pé values are much lower and the rates at which odor filaments are smeared out by diffusion are much faster in air than in water. The Batchelor scale (the size of the smallest chemical structures that can persist in a turbulent flowing fluid) is thus larger in air than in water (Crimaldi and Koseff, 2001a; Moore and Crimaldi, 2004).

As described above, the kinematic viscosity (ν) of air is greater than that of water. Viscous dissipation damps out velocity fluctuations in a fluid, hence the size of the smallest turbulent eddies that can be sustained (the Kolmogorov scale) in air flowing at a given velocity are bigger than they are in water moving at that speed (Murlis *et al.*, 1992; Denny, 1993; Vogel, 1994; Crimaldi and Koseff, 2001a). For example, the Kolmogorov scale in the boundary layer above the substratum in aquatic habitats is about 1 mm or smaller (Crimaldi and Koseff, 2001a; Moore and Crimaldi, 2004), whereas the Kolmogorov scale in wind is typically about 1 cm (Murlis *et al.*, 1992).

The Schmidt number (Sc = Pé/Re = ν/D) represents the rate at which momentum structures (like eddies) in turbulent flow are dissipated by viscosity to the rate at which chemical structures (like odor filaments) are dissipated by molecular diffusion (Denny, 1993; Crimaldi and Koseff, 2001a; Moore and Crimaldi, 2004). The Sc values in water are high (of order 10^3), hence chemical diffusion is slow compared with momentum dissipation, and the smallest eddies are bigger than the smallest odor filaments. At such high Sc values, the D values of different molecules make little difference to how they are dispersed in the environment. In contrast, the Sc values for turbulent odor plumes in air are about 1000 times smaller than those of plumes in water (Denny, 1993). Therefore, the dominant scales of concentration fluctuations in air are closer to those of the velocity fluctuations, and the D values of different molecules can affect their dispersion.

Although many factors (discussed below) affect the filamentous structure of an odor plume, in general the patches of odorants in air are likely to be the same size as, or larger than, small insect antennae, whereas the patches of odorants in water are likely to be smaller than the large antennules on big crustaceans like adult lobsters and stomatopods.

Chemical signals in a turbulent odor plume are intermittent

Recent studies of turbulent mixing have used a planar laser-induced fluorescence (PLIF) technique in which instantaneous maps of the concentration of a fluorescent dye (an

analogue for an odorant) are visualized in a sheet of laser light and recorded using video (details in O'Riordan *et al.*, 1995; Crimaldi and Koseff, 2001a). PLIF measurements of dye plumes in water currents in laboratory flumes revealed that dissolved substances released from a source and carried in turbulent flow are stirred into complex structures (Crimaldi and Koseff, 2001a,b; Koehl *et al.*, 2001; Webster and Weissburg, 2001; Webster *et al.*, 2001, 2003; Crimaldi *et al.*, 2002b). Those structures are composed of fine dye filaments whose concentration can approach that of the source, surrounded by larger regions of fluid with little or no dye (Figure 3C,D). A turbulent odor plume is actually full of "holes" (i.e., patches of odor-free fluid).

Encounters with chemical signals in such filamentous odor plumes are intermittent (e.g., Moore and Atema, 1991; Finelli *et al.*, 1999; Murlis *et al.*, 2000; Weissburg, 2000). The instantaneous concentrations of various types of tracer molecules have been measured at fixed points downstream from a source in turbulent wind or water currents (reviewed by Murlis *et al.*, 1992; Murlis, 1997; Crimaldi and Koseff, 2001a; Vickers, this volume). Such studies, which have been done in laboratory wind tunnels or water flumes, as well as at terrestrial or aquatic field sites, revealed that the concentration of a chemical signal arriving at a point in a turbulent plume fluctuated. As odor filaments swirling in eddies of various sizes were carried past the measurement point by the ambient flow, brief spikes of high tracer concentration (lasting milliseconds to seconds) were measured. These peaks were separated by longer gaps of no measurable signal (lasting a tenth of a second to minutes). "Intermittency" is the proportion of time that a chemical signal at a point is above some threshold concentration (Murlis, 1997; Crimaldi and Koseff, 2001a,b).

Factors that affect plume structure

A variety of factors can affect the structure of turbulent odor plumes. For example, the faster and more turbulent the ambient wind or water current, the thinner the odor filaments in a plume and the lower their peak concentrations (Moore *et al.*, 1994; Mead *et al.*, 2003). The intermittency of the chemical signal measured at a point in the plume is higher (i.e., the signal is present for a greater proportion of the time), and more odor filaments of shorter duration are encountered per time if the flow is faster and/or more turbulent (Finelli, 2000; Moore and Crimaldi, 2004).

The height of an odor source above the ground can have a profound influence on how chemicals released from it are dispersed (Murlis *et al.*, 1992; Crimaldi and Koseff, 2001a,b; Webster and Weissburg, 2001; Crimaldi *et al.*, 2002b; Moore and Crimaldi, 2004). When air or water flows across a substratum, a boundary layer builds up in the fluid. In the slowly moving fluid right along the bottom, viscosity damps out the turbulent fluctuations in fluid motion, but there is very high shear in the steep velocity gradient just above the substratum. Odorants released from a source on the substratum (see Figure 3C,D) are spread out by shear dispersion along the bottom, and concentrations within the "viscous sublayer" just above the substratum are relatively uniform. Right above this viscous sublayer, the flow velocity increases very steeply with distance above the bottom, and the "turbulence intensity" is high (i.e., the root-mean-square of velocity fluctuations about the mean is high relative to the mean concentration). Turbulent stirring of odor filaments in this region of the boundary layer is significant. At even greater distances above the ground, the velocity gradient becomes less steep as flow speeds approach free-stream velocity, and the turbulence intensity is lower. At heights above the ground that are greater than the thickness of the boundary layer, the structure of the plume is not affected much by the height of the odor source.

The size of an odor source flush with the substratum has little effect on the filament structure of an odor plume, whereas the source size does make a difference when odorants are released at some height above the ground (Murlis *et al.*, 1992; Webster and Weissburg, 2001). The intermittency of plumes from small sources is lower, and the intensity of concentration fluctuations is greater than for larger sources. However, the odor plume produced by a small insect releasing chemical signals while sitting on a larger structure (e.g., a leaf or tree branch) behaves like a plume released by a larger source (Murlis *et al.*, 1992). If odors are actively pumped into the surrounding fluid (i.e., if the source injects momentum into the flow), the structure of the plume can also be altered (Crimaldi and Koseff, 2001a,b; Webster and Weissburg, 2001).

Many shallow coastal marine habitats are subjected to waves as well as water currents. If odorants are released from a source on the substratum exposed to the back-and-forth flow of waves superimposed on a water current, odor filaments are wider and of higher concentration than in an unidirectional current without waves, and the filaments are stirred to greater heights above the bottom. Animals navigating in such wavy flow encounter odor filaments more often than in unidirectional flow, but the concentration gradients at the edges of those filaments are just as steep in waves as in unidirectional currents (Mead *et al.*, 2003).

The topography of a habitat can have a big effect on odor-plume structure. For example, the larger the bumps on the substratum (e.g., cobbles are bigger than sand grains), the greater the turbulence of the overlying flow, the more often the viscous sublayer is locally swept away by eddies, and the more complex the odor landscape (Moore and Grills, 1999; Moore *et al.*, 2000; Moore and Crimaldi, 2004). Vegetation in the habitat also affects the structure of turbulent odor plumes (Murlis *et al.*, 1992, 2000; Murlis, 1997; Finelli *et al.*, 2000; Zollner *et al.*, 2004). For example, terrestrial forests slow the wind and remove the largest and smallest eddies from the turbulent air blowing through them. At a fixed position in a forest, more odor spikes are encountered per time, and these bursts are of longer duration and lower peak

concentration than those encountered over an open field (Murlis *et al.*, 1992). Odor plumes downstream from patch of aquatic vegetation contain more abundant odor filaments of lower concentration, but of shorter duration, than do plumes over unobstructed substratum (Finelli *et al.*, 2004).

Spatial information in the intermittent concentrations in a plume

The structure of a turbulent odor plume varies with distance from the source of the chemical signal (compare Figure 3C and D). A plume becomes wider and taller as it is carried away from the source, whereas the intermittency of a plume decreases with distance from the source (Murlis, 1997; Zollner *et al.*, 2004). For example, a chemical signal in turbulent wind was present 40% of the time at a position 2.5 m downstream from the source but only 10% of the time at a spot 20 m downstream (Murlis *et al.*, 1992). Furthermore, the durations of bursts of odor and of interburst periods tend to be longer at greater distances from the source (Murlis, 1997; Webster and Weissburg, 2001; Zollner *et al.*, 2004). For instance, at a position 20 m downstream from a source in wind, bursts of chemical signal lasted twice as long, and interburst periods lasted seven times longer than at a position only 2.5 m from the source (Murlis *et al.*, 1992). The concentration of the chemical signal in filaments is, on average, lower farther from the source; although some odor spikes of very high concentration do occur far from the source, they are encountered less frequently than when they are closer to the source (Murlis *et al.*, 1992, 2000; Murlis, 1997; Webster and Weissburg, 2001). The quantity of odorant molecules in each burst (the dose) also decreases with distance from the source (Murlis *et al.*, 1992; Zollner *et al.*, 2004), as does the intensity of concentration fluctuations (i.e., the root-mean-square of concentration fluctuations about the mean concentration, normalized to the mean concentration) (Murlis *et al.*, 1992; Crimaldi and Koseff, 2001a). The concentration gradients at the edges of odor filaments are steeper near to the source, before they are blurred by molecular diffusion. Therefore, the rate of increase in odor concentration at the start of an odor burst is greater near to the source than far from it (Murlis *et al.*, 1992).

The structure of an odor plume also varies with distance from the midline of the plume. Intermittency (percentage of time exposed to odor) and the intensity of concentration fluctuations are both higher in the center of a plume than along its edges (compare the top edge to the middle of the plume in Figure 3D) (Murlis *et al.*, 1992; Murlis, 1997; Crimaldi and Koseff, 2001a,b; Crimaldi *et al.*, 2002b). Although fewer odor spikes occur per time at the edges of a plume, the concentrations of those spikes are as high as in the middle of the plume (Murlis *et al.*, 1992; Murlis, 1997). On larger spatial and longer temporal scales, turbulent plumes meander from side to side. A plume tends to spend more time at one side or the other of its meander than it does moving back and forth between these positions, hence encounters with the plume are more likely at meander edges than at the center of the space across which the plume drifts (Murlis, 1997).

Thus, although odor plumes in turbulent wind or water currents are made up of complex, ever-changing patterns of filaments of odor-laden fluid swirling around in unscented fluid, there are measurable differences in those filament patterns at different positions in a plume. Can an animal use the patterns of odor filaments it encounters as it moves around its environment to ascertain its position relative to the source of a chemical signal?

Sniffing in turbulent odor plumes

Plume-tracking behavior by insects and crustaceans

A number of investigators have suggested that animals searching for the source of an odor might get directional information from the differences between the temporal structure of odorant concentrations that occur far from versus close to an odor source or at the edge of a plume versus its centerline (e.g., Moore and Atema, 1988; Murlis *et al.*, 1992; Finelli *et al.*, 1999; Justus *et al.*, 2002; Wolf *et al.*, 2004). The olfactory organs of an animal must be able to sample the temporal structure in a plume if the animal is to use that information while navigating through the environment.

Many studies of how arthropods behave in odor plumes have been conducted to work out the search algorithms they use to find the source of a chemical signal. Investigations of insects flying (e.g., Murlis *et al.*, 1992; Mafra-Neto and Cardé, 1994; Murlis, 1997; Vickers, 2000; Vickers *et al.*, 2001; Justus *et al.*, 2002; Willis, 2005) or walking (e.g., Willis and Baker, 1987; Kanzaki *et al.*, 1992; Willis, 2005) in turbulent odor plumes in air have been undertaken. Likewise, many investigators have documented the movements of benthic crustaceans walking in turbulent odor plumes in water (reviewed in Grasso *et al.*, 2000; Weissburg, 2000; Kozlowski *et al.*, 2001; Grasso and Basil, 2002; Kraus-Eppley and Moore, 2002; Weissburg and Dusenbery, 2002; Wolf *et al.*, 2004). The observation that plume-tracking success can be affected by the level of turbulence in the flow (e.g., Weissburg and Zimmer-Faust, 1993; Mafra-Neto and Cardé, 1994; Vickers and Baker, 1994; Moore and Grills, 1999) is consistent with the hypothesis that these arthropods can use information in the filamentous structure of a plume to determine their position relative to an odor source. Other evidence that the temporal pattern of odorant encounters can provide information to an animal during plume tracking has been revealed by experiments in which on–off pulses of odor were released from a source. Such studies showed that source-finding success can depend on the temporal scale of pulses of odorants (e.g., Kanzaki *et al.*, 1992; Kozlowski *et al.*, 2001, 2003; Keller and Weissburg, 2004).

In plume-tracking studies like those mentioned above, the fine-scale instantaneous concentrations of the chemical

signal actually intercepted by the olfactory organs (e.g., antennae or antennules) of the animals were not measured while the animals were searching for the odor source. Therefore, the ability of such studies to reveal the search algorithms the animals were using is limited. Fortunately, recent technical advances now enable investigators to simultaneously record the instantaneous signals intercepted by arthropod antennules/antennae and the behaviors executed by the animals while searching for an odor source. Vickers (this volume) reviews such work for insects, so I will focus here on odor interception by the flicking antennules of large benthic crustaceans in turbulent odor plumes in water.

Seeing the chemical concentrations that a flicking antennule samples

Because the Schmidt number (see above) in water is so high, dye molecules are dispersed in a turbulent plume in the same way as odorant molecules. Therefore, we can release solutions of fluorescent dye plus odorants from a source and can use the brightness of the dye to measure the local concentrations of odorants in the water.

When an antennule flicks, it sweeps through the water and samples only a thin slice of the odor plume. Therefore, in order to assess the instantaneous dye concentrations (and hence odorant concentrations) encountered by a flicking antennule, dye brightness should only be measured in that slice of water through which the antennule sweeps. This can be accomplished by illuminating the plane in a dye plume in which an antennule sweeps with a sheet of laser light about the thickness of the width of the antennule (Figure 4) (Koehl *et al.*, 2001; Mead, 2002; Mead *et al.*, 2003). By using the PLIF technique described above, we can measure the instantaneous dye concentrations intercepted by the aesthetasc array on the antennule, and we can determine how those concentrations change over time (Figure 5) (Koehl *et al.*, 2001).

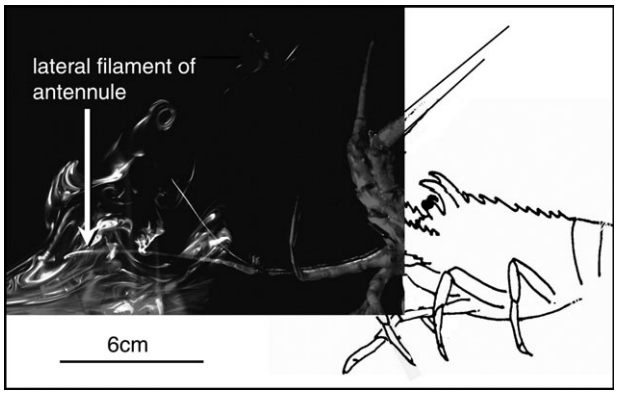

Figure 4 Frame of a video (shot at 250 frames/s) of a mechanical lobster (fabricated from the shed exoskeleton of a *Panulirus argus*) flicking a fresh lateral filament of a *P. argus* antennule in a plume of dye (Rhodamine 6G, an analogue for a dissolved odorant) in turbulent water flow in a flume (free-stream velocity = 10 cm/s). Technical details are described by Koehl *et al.* (2001). The antennule, which was 1 m downstream from the source on the substratum (see Figure 3), was programed to flick using the kinematics measured for *P. argus* antennules (Goldman and Koehl, 2001). The dye plume was illuminated by a sheet of laser light (280 mm thick); the lighter the pixel, the higher the dye concentration. Water flow is from left to right.

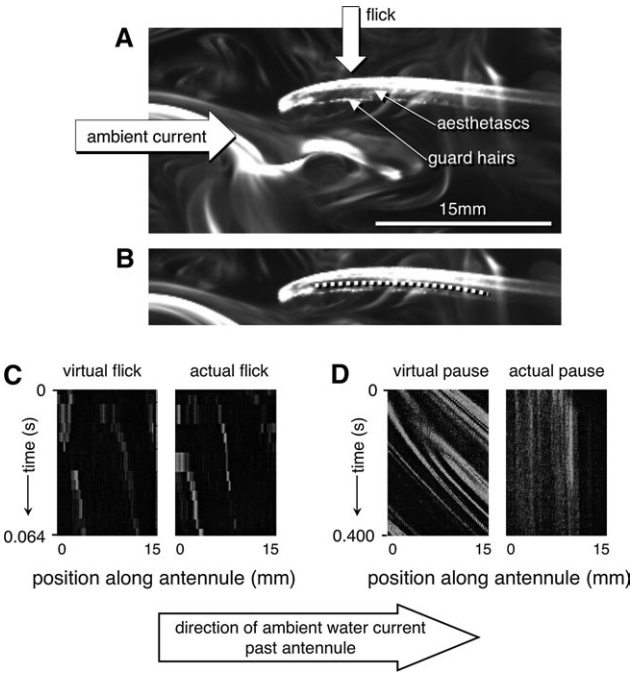

Figure 5 Dye capture by the aesthetasc array on the lateral filament of the antennule of a *Panulirus argus*. The experimental setup is described in Figure 4, and technical details are described by Koehl *et al.* (2001). The lighter the pixels, the higher the concentration of the dye, an analogue for dissolved odorant. **(A)** Frame of a video (250 frames/s) of the antennule during the rapid downstroke part of a flick when water can penetrate into the spaces between the aesthetascs. Filaments of dye can be seen within the hair array. **(B)** Position of the transect through the aesthetasc array along which dye concentration was sampled for each frame of the video. **(C)** Dye available to be captured (virtual flick) and dye within the aesthetac array (actual flick) measured during the flick downstroke. The virtual flick shows the dye that would be encountered by the antennule if it did not interfere with the flow during the flick; details of how it is measured are given by Koehl *et al.* (2001). Time is plotted along the vertical axis, with the start of the downstroke at the top. Position along the antennule is plotted on the horizontal axis and corresponds to the transect shown in (B). The pattern of light and dark along a horizontal strip at the top of each graph shows the concentrations of dye along the antennule in the first video frame, the pattern of light and dark along the next horizontal strip down shows the concentrations of dye along the antennule in the second video frame, and so on. The light stripes (dye filaments intercepted by the antennule) appear as diagonal lines on these plots because they are being carried downstream by the ambient current (left to right) during the course of the flick downstroke. The pattern of dye moving through the aesthetasc array (actual flick) is very similar to the pattern of dye available in the odor plume (virtual flick) during the flick downstroke, when water and dye flow into the spaces between aesthetascs. **(D)** Dye available to be captured (virtual pause) and dye within the aesthetasc array (actual pause) during the stationary pause of the antennule between flicks, when water does not flow into the spaces between the aesthetascs. The vertical stripes in the plot for the actual pause indicate that the pattern of dye within the hair array does not change with time (i.e., the pattern of dye filaments captured during the previous flick is retained in the trapped water within the aesthetasc array), even though dye filaments are flowing past the antennule (indicated by the diagonal stripes on the plot for the virtual pause).

We used such a PLIF approach to reveal how the hydrodynamics of flicking antennules physically alters the spatiotemporal patterns of concentration that they capture in a turbulent odor plume (Figures 4 and 5) (Koehl *et al.*, 2001). When the spiny lobster, *Panulirus argus*, flicked its antennule, water and the fine filaments of dye (i.e., odorant) it carried flowed through the spaces between aesthetascs during the rapid downstroke. Thus, spatially fine-scale, temporally high-frequency patterns of concentration moved through this array of chemosensory hairs (Figure 5C). (Similarly, an analysis of the fluid dynamics of a feathery moth antenna ventilated by wing beating also indicated that the duration of odorant pulses was not altered as air passed through the gaps between chemosensory hairs on the antenna; Loudon and Davis, 2005.) For a lobster antennule pointing upstream in a water current, the spatial pattern of concentration within the aesthetasc array was blurred a bit by flow along the length of the antennule during the downstroke. The spatial pattern of concentration peaks and valleys that happened to be in the aesthetasc array at the very end of the downstroke was then retained in the water trapped among the aesthetascs during the slower return stroke and stationary pause, even though the ambient patterns of odorant concentration around the antennule were changing (Figure 5D). That pattern of concentrations trapped between the chemosensory hairs on the antennule was not shed until the next flick, when a new sample of water flowed into the aesthetasc array. Therefore, each time an antennule flicks, it takes a discrete sample in space and time of the odor plume.

Because benthic crustaceans like lobsters, crabs, and stomatopods sniff by flicking their antennules, they provide excellent systems for studying search algorithms that can be used to find the source of an odor in a turbulent environment. These animals take discrete odor samples during the rapid, leaky outstroke phase of their antennule flicks. The PLIF technique described above enables us to measure the instantaneous odorant concentrations that they capture with each sniff. Therefore, plume-tracking studies can now be done in which the time course of odorant capture by each antennule can be matched with the sequences of behaviors used by the animal as it searches for the source of an aroma (Mead *et al.*, 2003).

Sweeping an antennule through a plume affects odor filament encounters

When an antennule flicks through a region of an odor plume, it samples a bigger area of the plume than it would encounter if it were stationary, and it moves into and out of odor filaments more rapidly than if it were static. By using a virtual antennule (see Figure 5C) to sweep through the changing concentration field in a slice of a turbulent dye plume illuminated by a sheet of laser light, we could measure the effects of flicking on encounters with filaments in the plume (Crimaldi *et al.*, 2002a). This analysis showed that an antennule (with the dimensions and kinematics of a *P. argus* antennule) was about seven times more likely to encounter odor filaments when it flicked than when it was stationary. Flicking not only increased the probability of encountering odor filaments but also altered the frequency content of the concentration field that the antennule intercepted. In addition, a flicking antennule encountered odor bursts with steep onset slopes (i.e., with high rates of increase in concentration of the signal as a filament encounters the antennule) more often than did a stationary antennule.

Flicking through an odor filament affects the kinetics of odorant arrival at aesthetasc surfaces

When odor filaments are carried into the array of aesthetascs on an antennule, molecular diffusion disperses them across the short distances in the water between the aesthetascs. We modeled the flux of molecules to the surfaces of the aesthetascs of stomatopod antennules of various morphologies when they flicked through odorant filaments (Stacey *et al.*, 2002). By using measured water velocity vector fields between the aesthetascs of stomatopod antennules (Mead and Koehl, 2000), we calculated the advection of odorant filaments through the aesthetasc array. The size and concentration profile of the filaments in our calculations were based on measured dye filaments in real odor plumes (Koehl *et al.*, 2001). As the filaments were carried through the array, odorant molecules dispersed locally via molecular diffusion, and some encountered the surfaces of the aesthetascs.

We used this advection–diffusion model to calculate the flux of molecules (number of molecules arriving per area per time) to the surface of an aesthetasc when a moving antennule encountered an odorant filament. If an antennule with odor-free water trapped between its aesthetascs was executing a slow return stroke when it encountered an odor filament, there was little flow of the water carrying the filament into the spaces between the aesthetascs and a very low flux of odorant molecules to aesthetasc surfaces. In contrast, if an antennule with odor-free water between its aesthetascs encountered a filament during the rapid, leaky outstroke of a flick, the peak instantaneous flux of odorant molecules to the aesthetasc surfaces was 10- to 80-fold greater (depending on antennule morphology) than the flux during the nonleaky return stroke. Furthermore, the steepness of the onset slope (i.e., the rate of change of odorant flux to an aesthetasc that occurred when the antennule encountered an odorant filament) was also increased by similar factors during the rapid, leaky outstroke of the flick.

Our studies of crustacean antennules have shown that flicking enables antennules to take discrete water samples in space and time and that the fine-scale odor-filament structure in those samples can be captured in the array of aesthetascs. However, although we have predicted the kinetics of the flux of odorant molecules to the surfaces of the chemosensory hairs when an antennule flicks through odor filaments, we do not yet know whether the rapid temporal fluctuations

in odorant concentration encountered by the aesthetascs during the leaky flick downstroke are resolved by the receptor neurons or the first synaptic relay in the olfactory pathway. Furthermore, we do not yet know if or how the olfactory pathway processes the fine-scale spatial patterns of odorant concentrations encountered along the length of the antennule. The positions of the patches of odorant along the antennule change during the leaky flick downstroke (Figure 5C) but remain static in the water trapped within the aesthetasc array during the return stroke and interflick interval (Figure 5D). If the olfactory pathway can resolve fine spatial patterns along the antennule, when during the flick/interflick cycle does it do so? Thus, although crustacean antennules physically can capture the fine-scale spatial and temporal concentration information in a turbulent odor plume, whether the animals use that information to help them navigate is still a mystery.

Conclusions

The intermittent spatiotemporal distribution of odorant concentrations in the turbulent water current or wind in an animal's environment contains information about the position of the animal relative to the source of the smell. The fluid dynamics of sniffing by the hair-bearing olfactory organs of many arthropods alters the temporal pattern of odorant concentrations arriving at olfactory receptors in predictable ways. Therefore, the physical process of capturing odorant molecules from the surrounding fluid is the first step in filtering the temporal information in the odor environment, before neural processing.

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