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On the usefulness of bilateral comparison to tracking turbulent chemical odor plumes

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Abstract

This article reports on the usefulness of bilateral comparison of chemosensory information to an animal or agent tracking an odor to its source. Instantaneous concentration fields of a chemical plume diffusing in a fully developed, turbulent, open channel flow are measured using planar laser-induced fluorescence. The plume is released isokinetically 25 mm above the smooth bed ($z^+ = 90$), thus transport is mainly due to advection and ambient turbulence. A spatial cross-correlation function in the spanwise direction gives a strong indication of the relative position of the centerline and distance from the source. The relative direction of the plume centerline can be estimated from the instantaneous concentration, provided the sensors are separated by a distance larger than the spanwise integral length scale of the concentration field.

Many aquatic and terrestrial animals rely on sensory cues to track turbulent odor plumes in order to locate food and mates (Vickers 2000; Zimmer and Butman 2000). Very long time records would be required to accurately determine traditional statistical measures of odor concentration, such as time-averaged concentration and variance (Elkinton et al. 1984; Moore and Atema 1991; Murlis et al. 1992). But it has been observed that animals, such as blue crabs, do not wait long enough at a location to accurately assess these time-averaged quantities and their small spatial variations. Thus, these animals must be using instantaneous observations of the odor plume to make tracking decisions.

The instantaneous spatial and temporal structure of a turbulent odor plume is complex and depends on transport within the flow. Measurements of chemical plumes released into turbulent boundary layers in the laboratory (Fackrell and Robins 1982; Bara et al. 1992) and field (Murlis and Jones 1981; Jones 1983; Murlis 1986; Hanna and Insley 1989) show highly intermittent concentration time records. Time-averaged properties, such as the mean and variance of concentration, are typically calculated from the time records and compared to models based on turbulent diffusion. Although these data and models may be useful for predicting time-averaged distributions, they provide no information about instantaneous quantities that may be useful to an animal tracking the plume.

There is evidence that rapidly moving foragers are not using sequential sampling to acquire orientation cues (Webster and Weissburg 2001); thus, our attention now turns to the ‘‘information content’’ in the instantaneous spatial distribution of odor concentration. Little evidence is available about the nature of this information content. It should be pointed out, however, that benthic crustaceans are rarely successful in locating the odor source in the absence of mean flow and turbulent transport (Weissburg and Zimmer-Faust 1994). Thus, measurements of the fine-scale spatial distribution of a chemical tracer are needed to evaluate the usefulness of spatial sampling.

In this study, tracer concentration fields of a plume diffusing in a turbulent open channel flow were measured using the planar laser-induced fluorescence (PLIF) technique. With the rapid development of modern lasers, digital cameras, and computer acquisition systems, long sequences of high-resolution concentration fields can now be obtained and stored. Information on the instantaneous concentration fields and spatial correlations that were previously unattainable can be readily obtained. The objective of this article is to report on the value of a sensory cue, namely bilateral comparison, available to animals such as blue crabs in a turbulent odor plume.

Methods

Fully developed, uniform, open channel flow was established in a tilting flume 1.07 m wide and 24.4 m long with rectangular cross-section and smooth bed. The average velocity in the flume was 50 mm s^{-1}, the flow depth H was 200 mm, and the water temperature was 20°C. The flow was uniform with a depth varying by less than 0.3 mm for at least 12 m approaching the measurement location. The wall shear velocity ($u* = \sqrt{\tau_0/\rho} = 3.55$ mm s^{-1}) was calculated by fitting a logarithmic curve to the mean velocity profile measured with laser Doppler velocimetry. The turbulent length scales ranged from the Kolmogorov scale, $\eta \approx (\nu^3/\epsilon)^{1/4} = 0.7$ mm, to the integral scale, $l \approx 100$ mm (estimated as $0.5H$), where ν is the kinematic viscosity of the fluid, $\epsilon \sim u'^3/l$ is the turbulent energy dissipation rate, and u' is the standard deviation of the velocity fluctuations. The integral time scale was 2.0 s, whereas the Kolmogorov time scale was 0.5 s. The scale for molecular diffusion of the chemical tracer is the Batchelor length scale calculated as $L_B = (\nu D^2/\epsilon)$, where D is the molecular diffusion coefficient. The Batchelor length and time scales were 0.02 mm and 0.0004 s.

The experimental configuration is shown in Fig. 1 of Webster and Weissburg (2001). The plume source consisted of a brass nozzle with a 4.7-mm internal diameter and a brass fairing attached to minimize the wake perturbation. The nozzle was located 25 mm ($0.125H$, $z^+ = 90$) above the bed,

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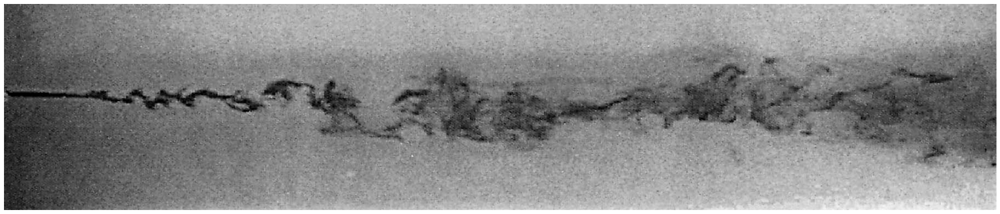

Fig. 1. Chemical plume released isokinetically into fully developed turbulent 200-mm-deep open channel flow. The perspective is from above the flume, and the flow is from left to right. The release height is 25 mm (0.125H) above the bed.

which was in the logarithmic layer of the turbulent boundary layer. The effluent velocity matched the mean channel flow velocity, thus creating an isokinetic release.

The planar laser-induced fluorescence (PLIF) technique was used to record long time histories of instantaneous planar concentration fields. A small amount of fluorescent dye, Rhodamine 6G, was mixed with the effluent such that dye concentrations in the plume were extremely small (<100 μg L^{-1}). Laser light causes the dye to fluoresce, and a digital CCD camera captured the emitted light. The light intensity emitted by the dye is directly proportional to the dye concentration and laser intensity (Ferrier et al. 1993). Thus, the planar concentration field can be determined from the instantaneous images of the plume and an in situ calibration of the system. The calibration procedure and discussion of measurement uncertainty is given in Webster et al. (2001). Measurements were performed at four distances downstream, such that the fields overlapped to form a continuous data set up to 12 channel depths (2.5 m) downstream. The dye concentration in the effluent was increased with downstream sampling distance in order to exploit the full dynamic range of the camera at each measurement location.

A scanning mirror swept an approximately 1-mm-diameter argon-ion laser beam (wavelength = 514 nm, power = 2 watts) through the flow to illuminate the fluorescent dye. The resulting laser sheet was parallel to the bed and in the same horizontal plane as the source nozzle.

A Kodak MegaPlus ES 1.0 camera (eight-bit, with 1,018 vertical and 1,008 horizontal pixels) viewed the plume from above, and a thin Plexiglas sheet was placed at the water surface to eliminate optical distortion due to disturbances on the free surface. The capture rate was 10 frames s^{-1}. A Fujinon 12.5 mm focal length lens was used to capture a field of view of about 1 m square. The spatial resolution was therefore about 1 mm, slightly larger than the Kolmogorov scale. The peak values of the concentration measurements depend on the sample size; measuring the true peak values requires resolving the smallest concentration scale, the Batchelor scale. Since the sample size was much larger than the Batchelor length scale, the true local peak concentration values are larger than those measured here.

The images were stored directly on a hard drive array in real time, a process referred to as a real-time-to-disk (RTD). For each measurement region, 6,000 images were captured, which produced a time record of 10 min. This time period is significantly longer than the longest time scale of the flow.

Results and discussion

Consider the photograph of a dye plume shown in Fig. 1. Even a cursory inspection of the photograph suggests that the time-averaged value at each point would be a very poor measure of the tracer concentration there. The photograph suggests that an observer or searcher in the plume would experience intermittent high and low levels of concentration, whereas the time-averaged concentration would be much lower than the intermittent peak values. This can be seen in the instantaneous concentration field shown in Fig. 2. This is a three-dimensional landscape where the measurement plane consists of the streamwise, x, and the spanwise, y, directions, and the elevation is the local instantaneous concentration level normalized by the source concentration, C_0. The flow is from upper right to lower left (i.e., in the positive x direction) with the nozzle at the coordinate origin. Concentration measurements near the nozzle, $x/H < 0.6$, are not shown because the peak values are beyond the linear range of the calibration and are not reliable.

The instantaneous concentration field consists of sporadically located patches of high local values separated by steep concentration gradients. Although the dye advects downstream, turbulent fluctuations stir and spread the patches. Meanwhile, molecular diffusion acts at the Bachelor scale to reduce the peak concentration levels. The plume, therefore, expands its volume and becomes more dilute with distance from the source. The peak concentration values decrease dramatically with distance from the source.

Animals such as blue crabs have chemosensors on their appendages, which are separated horizontally. Previous investigators have hypothesized that animals may be using bilateral comparison of these chemosensors to orient toward the source location (e.g., Reeder and Ache 1980; Atema 1996; Hanna et al. 1999). Zimmer-Faust et al. (1995) suggested that an animal with sensors spanning the plume edge would be able to orient toward the plume centerline. Weissburg (2000) refined this idea by defining the spatial integration factor (SIF) as the dimensionless ratio of the sensor spacing to the plume width and suggested that a large SIF allows the detection of a plume edge. The data set collected in this study allows an examination of the usefulness of such bilateral comparisons of chemosensory signals.

Time records of concentration presented in Fig. 3 demonstrate that the concentration peaks are larger and more frequent near the plume centerline. These time records were

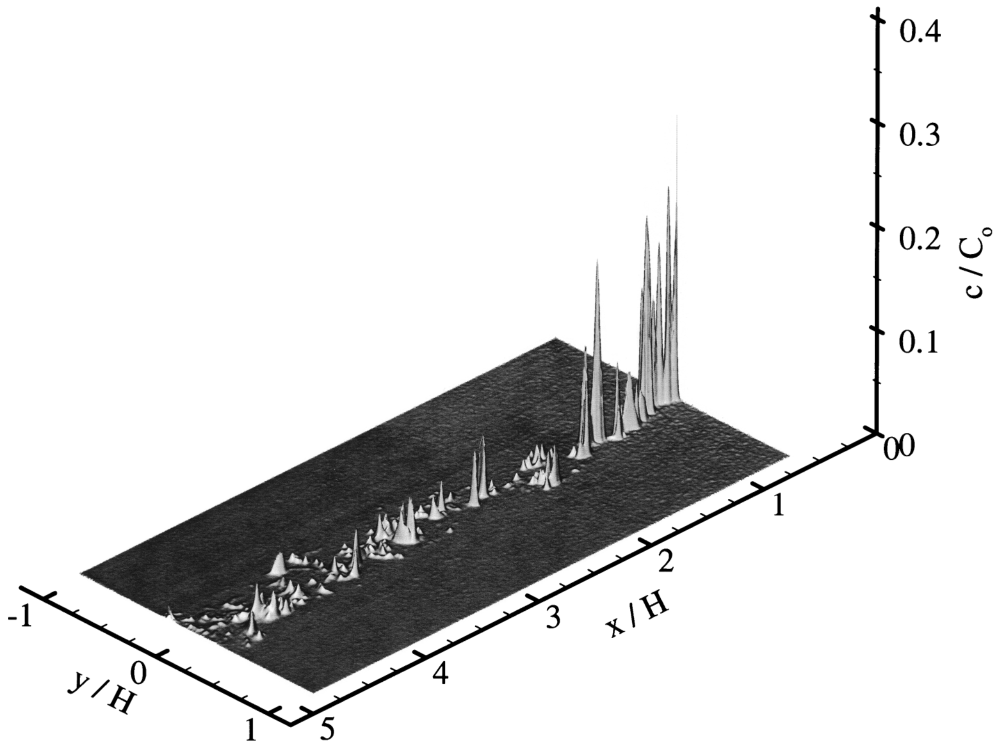

Fig. 2. Instantaneous concentration field. The plume source is at the coordinate origin.

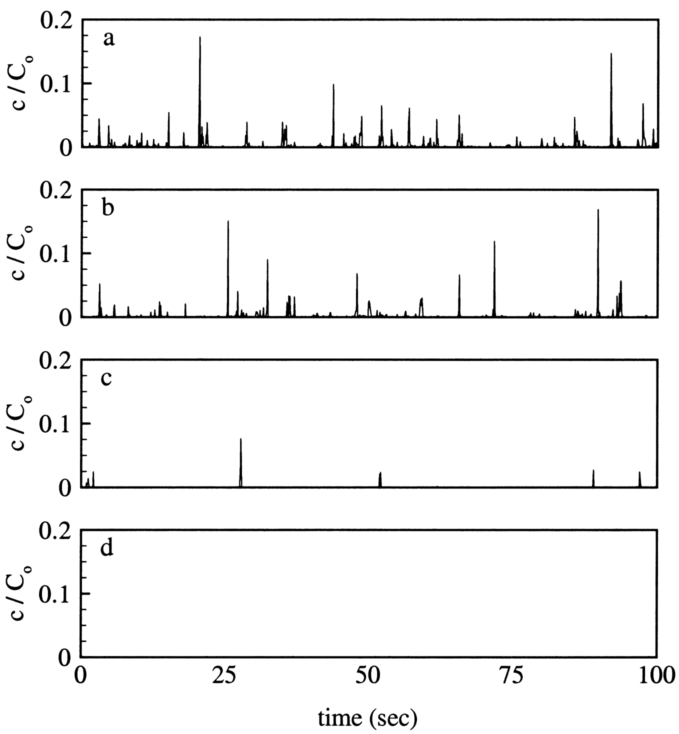

Fig. 3. Simultaneous time series of instantaneous concentration at (a) centerline, (b) 20 mm (0.1H), (c) 50 mm (0.25H), and (d) 100 mm (0.5H) laterally away from the centerline.

collected at a distance of 2.5H downstream from the source. The time record at 20 mm from the centerline appears to be similar to the centerline record with respect to peak magnitude and burst frequency, whereas the records at 50 mm and 100 mm are obviously different. This would enable a blue crab, with appendage sensors separated in the spanwise direction by roughly 100 mm, to compare the time series and get a clear indication of its the relative position to the plume centerline.

This variation is quantified in Fig. 4, which shows the spatial correlation between the instantaneous centerline concentration, c_0, and the instantaneous concentration at distance y from the centerline, c_y.

$$\overline{c_p c_q} = \frac{1}{T}\int_0^T c(y = p, t) \times c(y = q, t)\, dt \qquad (1)$$

The correlation is identically one at the centerline and decreases rapidly with increased spacing because the dimensions of dye filaments are smaller than the sensor spacing. The area under the correlation curve increases as the plume grows downstream. This can be quantified by defining an integral spanwise length scale, L, calculated from the area under the correlation curve. As shown in Fig. 5, this integral length scale increases with distance from the source. One could speculate that a searcher with sensors separated by a distance larger than the integral length scale, L, could better assess the instantaneous gradients and therefore identify the plume centerline more easily.

The correlation function shown in Fig. 4 compares absolute instantaneous values rather than instantaneous deviations from the mean (i.e., the fluctuating values). From a

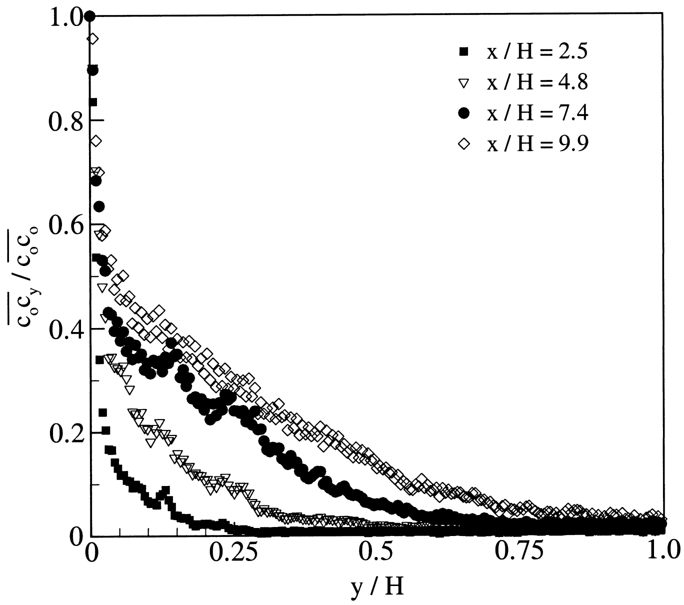

Fig. 4. Spanwise spatial correlation of absolute concentration at four locations.

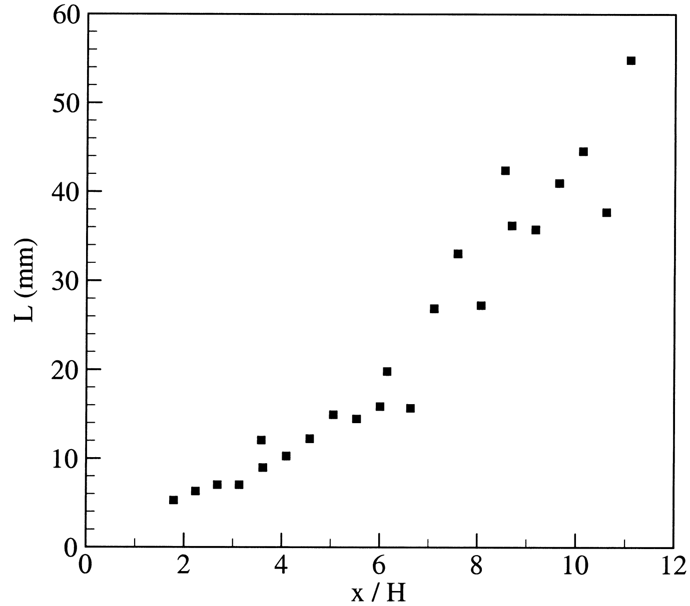

Fig. 5. Variation of spanwise integral length scale with distance from the source.

tracking perspective, this is important because an observer in the field cannot know the local time-averaged value a priori but, rather, measures absolute instantaneous values. Even assuming adaptation or organism memory, the local time-averaged concentration cannot be readily assessed because statistical convergence is limited by the physics of the intermittent concentration time record (Webster and Weissburg 2001). In addition, there is evidence that comparing the instantaneous concentration provides a clearer indication of the relative centerline position. The spatial correlation between concentration fluctuation at the centerline, c_0', and at any distance y off the centerline, c_y', lacks the clear systematic variation in the streamwise direction shown in Fig. 4 for the spatial correlation of instantaneous concentration.

Although the streamwise variation of the spanwise spatial correlation in Fig. 4 is dramatic, it is unlikely that animals are calculating or directly exploiting this variation. In fact, calculating the correlation function requires time integration in the same fashion as calculating time-averaged values or the standard deviation. Because the concentration record is very intermittent, accurately determining any time-integrated quantity requires a long time record in order to include a significant number of rare concentration burst events. For the plume discussed here, it takes $>$200 s for the time-averaged concentration to converge to a well-resolved value and even longer for higher order statistics (Webster and Weissburg 2001).

Nevertheless, the variation in the spatial correlation suggests that a bilateral comparison could be useful. Indeed, even a simple bilateral comparison provides useful information to a strategy of assessing the relative position of the plume centerline and heading upstream. This mode essentially adds bilateral comparison to the odor-gated rheotaxis response suggested by Zimmer-Faust et al. (1995) and Finelli et al. (1999, 2000) based on controlled field observations. The instantaneous concentration at $y = 4$ mm and 20 mm (the latter shown in Fig. 3) is greater than the centerline value 33 and 29% of the time, respectively. For spanwise separations that are significantly larger than the integral length scale, the percentage of time when the concentration is greater away from the centerline is much smaller. For instance at $y = 50$ mm and 100 mm (both shown in Fig. 3), the concentration is greater than that at the centerline 12 and 8% of the time, respectively. Thus, by separating the sensors by a distance greater than the integral length scale, the probability of determining the relative position of the centerline of the plume by simple comparison of the instantaneous concentration magnitude is much greater. This notion is consistent with the suggestion of Weissburg (2000) that an animal with a large SIF can sample broadly across the plume and hence detect an edge.

To generalize this idea, Fig. 6 shows the spanwise correlation with sensor spacing equal to a multiple of *L*. The abscissa corresponds to the location of the inner sensor and is nondimensionalized by the standard deviation, σ, of the Gaussian shape of the time-averaged concentration spanwise profile. The collapse of the data onto a single trend indicates that the scaling is correct: the sensor spacing scales with *L*, and the sensor location scales with the plume width.

From a tracking perspective, there are two important observations from Fig. 6. First, the relative magnitudes of the correlation for spacing of 4*L* and *L* confirm the advantage of relatively large sensor spacing. As discussed above, with larger sensor spacing, an animal or agent can determine with reasonable reliability the direction of the plume centerline from instantaneous concentration measurements. With a sensor spacing of 4*L*, the correlation is low throughout the plume, thus providing the necessary sensor contrast to reasonably determine the direction of the plume centerline with a single sample. Second, there is an advantage to being able to adjusting the sensor spacing. A tracking agent who adjusts

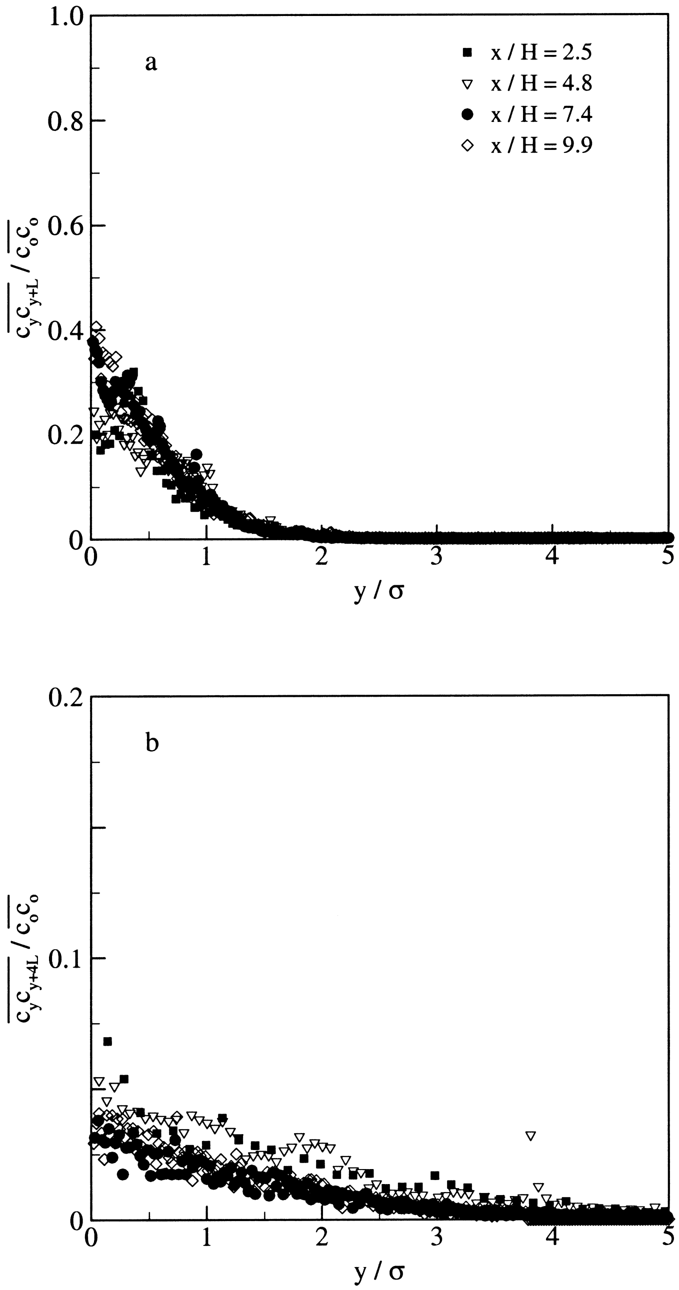

Fig. 6. Spanwise spatial correlation as a function of lateral distance from the axis. Correlation spacing is (a) L and (b) $4L$.

the spacing could continually have the ideal spacing for the local plume width, which is a multiple of L, as demonstrated by the self-similarity of the correlation curves. Because L is increasing with distance from the source, the ability to adjust the sensor spacing or having an array of sensors would eliminate the need to move in and out of the plume to deduce the spanwise variability of the plume.

It is important to conclude with some comments about these results in relation to animal behavior. Animals demonstrate a wide range of behaviors (e.g., Mafra-Neto and Cardé 1994; Atema 1996; Vickers 2000; Weissburg 2000) depending on chemical composition, concentration, and fluid transport (Zimmer and Butman 2000). The results here suggest that a spatial assessment of the field rather than a temporal analysis may be beneficial. In particular, for a macroscopic animal tracking a turbulent odor plume, a bilateral comparison can yield useful information, provided the sensor spacing is relatively large compared to the plume (as quantified by the parameter L). To what extent or how well a particular animal uses this information is an open question that must be answered through behavior trails. Although a number of aquatic animal studies have been reported in recent years (e.g., Moore and Atema 1991; Weissburg and Zimmer-Faust 1994; Breithaupt et al. 1999; Finelli et al. 2000), the use of bilateral comparison has not been definitively shown in those trials.

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