A Multidisciplinary Study of Spatial and Temporal Scales Containing Information in Turbulent Chemical Plume Tracking


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Abstract. This report describes the results of a multidisciplinary study of turbulent chemical plume tracking of blue crabs and autonomous agents. The study consists of a coordinated investigation of animal behavior, fluid mechanics, strategy simulations, and chemical sensing. The objective is to provide a comprehensive understanding of chemical plume tracking in a single biological system and to prescribe strategies that are effective for autonomous agents. The consensus of the study is that spatial variation in the plume, measured by sampling at multiple locations simultaneously, yields information that is useful for plume tracking. Behavioral investigations reveal that blue crabs demonstrate the ability to detect the chemical plume and use lateral movements to avoid losing contact with the odor. Blue crabs move rapidly towards the source, strongly suggesting that temporal comparisons of odor properties are not employed during navigation. Analysis of the concentration fields reveals that a spatial correlation between spanwise-separated sensors indicates the relative direction of the plume centerline over short time periods provided the sensor spacing is scaled appropriately relative to the plume. Similarly, simulations of tracking strategies reveal an optimal separation for the sensors at a distance roughly equal to the plume width; both smaller and larger sensor spans degrade tracking performance. The simulations further reveal an optimal sensor size above which the fine details of the concentration distribution are obscured and below which there is insufficient contact with the odor to enable effective navigation. Finally, analysis of the chemical signal shows that the frequency-dependent correlation function between two (or more) sensors indicates the relative position of the source.

1. Introduction

Many aquatic and terrestrial animals use fluid-borne chemical signals to mediate behaviors. Insects and crustaceans, in particular, are known for their ability to follow chemical plumes to sources that routinely are tens to hundreds, and even thousands, of body lengths away [1, 2]. Although these animals operate largely in turbulent environments where chemical signal dynamics are complex, they are still

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able to operate efficiently by mechanisms that are just beginning to be discerned. The ability to track distant sources using information in turbulent chemical plumes is of great practical, as well as academic, interest. Man-made analogues of the chemical-sensing systems employed by animals would allow us to locate sources of dangerous chemicals leaking into the environment, improve detection of hazards such as unexploded ordinance (mines) that may be remotely sensed using their chemical signatures, or analyze complex turbulent flows in nature by analyzing the dynamics of their odor fields in situ.

Investigation of chemically mediated orientation presents a unique challenge because turbulent flows are chaotic, unpredictable, and ill-suited to analytical description. These qualities present a number of difficulties that have severely limited the ability to understand chemical tracking. First, it is impossible, except in a qualitative sense or statistical sense, to predict the temporal sequence of signal intensity experienced by sensors located in a turbulent plume, and it is extremely difficult to determine both chemical signal dynamics and animal response simultaneously. This handicap is significant, since hypotheses on signal structures that contain information used by animals in turbulent plumes depend on establishing the response of animals to known variations in signal properties. Second, similar limitations occur with modeling approaches because the spatial and temporal evolution of turbulent odor fields at biologically relevant scales (μm to mm and ms to s) cannot be reproduced by even the most advanced computational techniques [3]. Here too, it is difficult to determine the relationship between signal input and corresponding output of the (model) organism. Thus, simulations of chemically mediated guidance have been restricted to laminar or diffusive flows where temporal and spatial properties of odor fields vary smoothly and can be accurately predicted [4, 5]. Lastly, identifying the necessary properties of artificial sensors requires sufficient knowledge of the nature of chemical signals in turbulent flows to enable testing of man-made sensors in a realistic environment.

These considerations suggest that understanding chemical sensing in turbulent plumes is best accomplished by a thorough study of chemical signal dynamics in well-defined flows, followed by evaluation of animal behavior, the performance of simulated searching, and sensor properties in similar fluid and chemical signal environments. This approach requires a carefully coordinated multidisciplinary effort. We describe such an approach in this paper, and how the interaction among fluid dynamists, chemists, and biologists, has proven particularly valuable. Our goal is to understand chemically mediated guidance in the blue crab (Callinectes sapidus), and to use this understanding to determine the properties required of artificial sensing systems that will operate in similar environments. We focus on the following questions:

- What are the basic animal strategies and aspects of organismal performance?
• What are the basic features of the chemical signal environment, and which properties contain useful information for chemosensory guidance that are consistent with behavioral observations?

• How can this process, which is not amenable to analytical approaches, be simulated? Can simple strategies inspired by behavioral and fluid physical observations produce behavior consistent with animal movements in turbulent plumes?

• How can tools be developed to test chemical sensors in stimulus environments similar to that produced in turbulent plumes, and does the signal extracted by arrays of such sensors provide strategies for orientation?

We attempted to answer these questions by using behavioral trials to examine how animals respond complex turbulent plumes. Subsequently, we used quantitative visualization of plumes to search for likely sources of information used by agents with similar spatial and temporal sampling abilities as our experimental animals. Simulation approaches, and artificial chemical sensor arrays were then developed based on our knowledge of chemical signal and animal properties, and employed to test various ideas on how information may be extracted from turbulent chemical plumes.

2. The Multidisciplinary Framework

Marine crustaceans are extremely proficient at locating odor sources in turbulent plumes, and provide excellent model systems for the study of chemically mediated guidance. Crabs, crayfish and lobsters rely on chemical sensing to detect food, mates, and dwelling sites as well as to mediate social communication [6–8]. For many of these tasks, the fluid environment exhibits a profound effect on the efficiency with which these creatures locate chemical sources [9–11]. This modulation suggests that a combined analysis of signal structure and resulting behavior in differing conditions will provide clues as to those features of turbulent plumes that animals use to acquire information.

Our investigation starts with an analysis of the behavior of a common marine crustacean, the blue crab (Callinectes sapidus). This animal is well known for its ability to find food and mates using chemosensation [6, 9]. It lives in habitats where water currents are relatively steady, largely unidirectional, and flow over substrates composed of small-diameter (i.e., one to several mm) sediments that are reasonably devoid of large-scale topography [12]. This simplifies the creation and analysis of the appropriate flow environments relative to areas with topographical complexity (e.g., coral reefs, sea grass beds, many river bottoms) or wave-driven water movement. Fully developed equilibrium boundary layers are the most common, although certainly not the only flow conditions, experienced by a foraging crab.

These animals have multiple chemosensor-bearing appendages. Chemosensory neurons are present on the claws, legs and the second pair of antennae (antennules)
[6, 13]. The legs are particularly interesting because they represent an extended array of sensors that potentially sample across a spatial field extending greater than 100 mm. The antennules, which are very prominent in lobsters, are small in blue crabs and separated by roughly 10–20 mm.

The behavioral investigations were designed to provide basic information on the movement patterns and search capabilities in a well-defined flow in which detailed fluid physical measurements were taken. The successful linkage of behavioral strategies to chemical signal structure requires that both investigations take place in the same fluid mechanical context, so the flow conditions used for behavioral and fluids studies were carefully matched. Visualization of chemical signal dynamics was used to quantify various odor field properties. Time-averaged quantities, such as concentration mean and variance, have been usually used to characterize such plumes, but recent work has suggested that they are of little value to a fast-moving animal tracking such a plume [10, 14]. Consequently, analysis of signal structure was geared towards understanding the instantaneous properties such as local concentration gradients and spatial variation, that appear to be more useful to an extremely mobile, crab-sized creature.

We developed simulation approaches to information processing to test particular hypothesis of how animals or artificial systems can use sensory stimuli. These hypotheses stemmed from our observations of animal performance and signal structure, both of which emphasized the importance of spatial sampling. The virtue of simulations is that they use explicitly defined sensory information, processing algorithms, and motor responses. They therefore act as empirical validation that particular signal parameters (e.g., spatial properties, temporal comparisons) can indeed convey useful information. The concentration measurements provided the essential data on which to base simulations of strategies for tracking a turbulent plume to its source. Blue crab behavioral studies furnished basic input parameters (e.g., movement speed) and established levels of search efficiency and locomotory performance by which the success of the model strategy was evaluated.

The model was intended as an idealization to identify methods for extracting useful information, and to confirm general ideas of the appropriate scales for sensor arrays. It was not meant to duplicate exact conditions such as sensor configurations found on an actual searcher, or to interact with the flow. Particulars such as flow perturbations and sensor overlap would be unique to the specific size, morphology, and movement rate of the searcher. Given that there is so little information available on basic strategies by which a chemosensory array might extract information from a complex turbulent plume, a general modeling framework, however idealized, yields important insights and suggests general principles that may be pursued with more physically realistic investigations. The prime focus of the simulation component was the relationship between the spatial scale of both the sensors and the sensory array, and tracking performance.

Further analysis of the ways in which arrays can extract information utilized a group of artificial sensors coupled to a fluid control system. This device, the Bench-
top Plume, subjected multiple chemical sensors to fluctuating signals crudely similar to those present in a turbulent stream. By precisely controlling the stimulus presentation time across members of the array, as well as stimulus concentrations and rise times, the Bench-top Plume allows for rapid and inexpensive verification of new concepts in chemical sensing.

It is important to realize the distinction between biologically-inspired engineering solutions versus solutions that attempt to exactly replicate the mechanisms used by animals. Airplanes take advantage of principles of wing lift inspired by an examination of bird flight, but they do not slavishly duplicate avian propulsion. In the context of chemical plume tracking, strict mimicry of animal designs is not feasible since we lack sufficient information about what animals actually do. Yet, we may be able to identify properties that seem crucial to the success of organisms and attempt to incorporate them into man-made designs. The obvious utility of spatially separated sensors suggests that methods to extract information from sensor arrays should be explored. A varying chemical signal can be decomposed into mean and fluctuating components, similar to decompositions used to describe turbulence. A strategy could be based on information acquired from the fluctuating portion of the signal, in particular whether fluctuations at two sensors are correlated in time. A similar approach has been suggested by Laurent for gaseous plume tracing [15]. The question is whether the magnitude and frequency components of the correlation function provide useful information. Sensing arrays have been used in order to minimize the undesirable effect of chemical interference, but here we hypothesize a more direct benefit; that is, arrays can use signals fluctuating in the spatial-temporal domain to mediate chemosensory guidance. Experiments with the Bench-top Plume assessed the possibility of encoding fluctuating chemical information in a turbulent stream, and whether such information can be retrieved by an engineered sensory system.

3. Experimental Methods

3.1. Flow Environment

We characterized blue crab search behavior in a recirculating flume (10 m long × 0.75 m wide) with controlled fluid flow and boundary layer conditions. The flume bed was lined with fine sand to provide a natural substrate on which blue crabs could move (grain size = 0.894 ± 0.0124 mm, mean diameter ± SD, n = 37), and was free of obvious ripples or other surface features. The experimental section was placed more than seven meters downstream from the flume entrance to provide ample distance for the boundary layer to become established. Water velocity was controlled using a variable-speed pump and the discharge was monitored using an inline meter. Average flow velocity was maintained at 49.0 ± 0.8 mm s⁻¹ (mean ± SD) with a water depth of 230 ± 3.5 mm (mean ± SD) controlled by a vertical tailgate.
Velocity measurements (LDV) indicated that an equilibrium boundary layer exists in the trial region of the flume. The friction velocity, \( u^* = 3.10 \text{ mm s}^{-1} \), was within the range reported for natural blue crab habitats [9, 10, 12]. Previous investigations with these animals indicated that the resulting roughness Reynolds number provides a level of turbulence in which crabs exhibit near-optimal performance [8, 9]; under increasingly turbulent conditions their ability to locate odor sources decreased, whereas they had virtually no ability to orient in the absence of flow [9].

Fluid dynamics measurements took place in fully developed, uniform open channel flow established in a 1.07 m wide, 24.4 m long tilting flume with a rectangular cross-section and smooth bed. This flume provided more precise control over the flow conditions, but was not designed for use with seawater, preventing its use in behavioral trials. Average velocity in the flume was 50 mm s\(^{-1}\) and the flow depth, \( h \), was 200 mm. Flow was uniform in depth to within 0.3 mm for a distance of at least 12 m upstream of the measurement location. The turbulent boundary layer over the bed had a friction velocity, \( u^* \), equal to 3.55 mm s\(^{-1}\).

The plume source for both fluid physical and behavioral studies consisted of a brass 4.7 mm diameter nozzle with a brass fairing attached to minimize the wake perturbation. The effluent velocity matched the channel flow velocity thus creating an iso-kinetic source. For the data presented here, the nozzle was located 25 mm above the floor of the flume.

3.2. Behavioral Trials

For all behavioral experiments, blue crabs were moved carefully to the flume and placed in a Plexiglas box (272 mm long, 195 mm wide, 165 mm high) with a plastic grate (100 mm\(^2\) grid) forming front and rear panels. This design enabled the flow to pass freely through the box while keeping the crab in a known starting position. The upstream edge of the box was 1.5 m downstream of the odor source, and the box was centered on the plume midline. Blue crabs were placed in the box for 15 min prior to the introduction of the odor to provide time for acclimation to flume conditions. The stimulus source was water conditioned with exudates from fresh shrimp, collected by soaking 7 g of shrimp flesh for 30 min in 1 l of seawater taken from the flume.

To track the position of subjects in the flume, we placed two red-light-emitting diodes (LED) on the carapace of each blue crab before each experiment. The behavior of the animal was video-recorded in near darkness using a low-light-sensitive CCD camera mounted approximately 2 m above the working section of the flume. LEDs with different intensities were used so that the blue crab's body orientation could be easily determined.

The left and right LEDs on the carapace of the blue crabs were tracked digitally using Motion Analysis™ software. The centroid of each lighted area was calculated at each frame, generating a 60 Hz time-series of x-y pixel values for each
LED. These x and y pixel locations were smoothed over three consecutive frames using a moving average algorithm, and every 15th frame extracted to produce a 4 Hz time series. A typical track lasted approximately 35 s (see results), and the 60 Hz data set thus contained approximately 2100 points for each centroid. The time series pixel data were then converted to actual distances using a calibration function. An additional camera mounted on the side of the flume allowed us to examine movements of the animal in the vertical direction, as well as affording a closer view of the appendage movements.

3.3. CHEMICAL SIGNAL STRUCTURE

Long time-histories of instantaneous concentration fields were obtained by planar laser-induced fluorescence (PLIF). A small amount of fluorescent dye, Rhodamine 6G, was mixed with the source effluent such that the plume contains extremely low dye concentrations, of the order of 10 $\mu$g l$^{-1}$. An Argon-ion laser beam was swept with a scanning mirror in the same plane as the plume source to create a horizontal light sheet (Figure 1). The laser sheet caused the dye to fluoresce, and a digital CCD camera (1008 $\times$ 1018 pixels) captured the emitted light over a 1 $\times$ 1 m region. This arrangement yielded a spatial resolution of roughly 1 mm, slightly larger than the Kolmogorov scale (0.7 mm) and much larger than the Batchelor scale (0.02 mm), which correspond to the scales below which velocity and concentration variation is negligible. Although the true peak values therefore were not resolved, the resolution was similar that of aquatic decapod chemosensors [16], making the measurements relevant to the current context.

Instantaneous concentration fields could be determined from the instantaneous plume images because the emitted light intensity is directly proportional to the dye concentration and laser intensity. Measurements were performed at several distances with overlapping fields to obtain a continuous data set up to 12 channel depths (2.5 m) downstream. The source dye concentration was increased with increasing downstream distance of each field to compensate for the plume dilution. In addition, the horizontal sweep rate was varied so that the light intensity increased downstream in the image in order to take full advantage of the dynamic range of the camera. The image capture rate was 10 frames s$^{-1}$ and 6,000 sequential images were collected at each downstream location. The resulting 10-min sequence was sufficient for statistical convergence of the concentration field.

The system was calibrated by filling the flume with known, uniform dye concentrations and obtaining images of emitted light intensity. The dye was injected at controlled flow rates from a diffuser extending the width of the flume near the head box. Turbulent jets exiting the diffuser holes caused rapid initial mixing of the dye and further mixing occurred as the dye advected down the channel, resulting in a nearly uniform concentration distribution at the measurement region. Eighty images were captured for each of six concentration levels, ranging from 0 to 50 $\mu$g l$^{-1}$. To remove any remaining non-uniformities, the 80 images were
averaged to produce a single calibration image for each concentration level. Calibration images were corrected for laser attenuation due to light absorption by the dye by following the procedure described in Ferrier et al. [17]. A calibration slope and intercept at each of the 1008 × 1018 pixel locations were calculated using a linear least-squares fit. This calibration procedure accounts for laser sheet non-uniformity, lens vignette, and pixel response variability [18]. The $R^2$ values were greater than 0.995 for all calibration fits.

Three-dimensional LIF fields were obtained by employing a lower resolution (512 × 512 pixels) camera at a higher frame rate (100 frames s$^{-1}$). Emitted light was imaged in rapid succession in twenty parallel horizontal laser sweeps. The planes were combined to form a nearly instantaneous, three-dimensional dataset of concentration.

3.4. COMPUTER SIMULATION OF SEARCH BEHAVIOR

The basic simulation software has been described previously [19]. A major element of this software was reasonable representation of noise in both sensory inputs and motor outputs. Care was also taken that the searcher did not use information about
its position. The only directional reference was to flow direction, which reflects observations that many animals use this cue as a pointer for the upstream direction [8]. Flow direction was a new type of information that was added to the purely chemical tracking mechanism of the previous algorithm.

Concentration fields from our PLIF measurements were used to represent the stimulus field experienced by blue crabs in a turbulent plume, with an appropriate spatial resolution (approximately 1 mm²) to simulate their behavior. With the frame rate of 10 Hz, and velocity of 50 mm s⁻¹, parcels of fluid travel 5 pixels on average between frames, which produces an unrealistic jumping of stimulus parcels at successive time steps. For example, a chemical parcel 1 mm in diameter would appear in pixels spaced 5 mm apart in two successive frames, but never in the intervening pixels. This is problematic, since most sensors output a continuous record of concentration integrated over some time interval (which we assume in the range 0.02–0.2 s). Fortunately, mean flow advection dominates the scalar transport and a linear interpolation between frames smoothed the flow without distorting it. The simulation had a time step of 0.02 s (5 interpolated steps between concentration fields), so that on average the flow moved only one pixel (1 mm) between steps. Each run (with 1 to 100 searchers) was started at a randomly-chosen frame in the long sequence. The record of 6,000 frames was treated as an endless loop, which produced a rare temporal discontinuity when going from frame 6,000 to frame 1.

All studies here were confined to a plane, and all spatial characteristics of the sensory array were circular and characterized simply by a radius. We studied a strategy in which an array of three sensors (evenly distributed around a circle) provided an indication of chemical gradient direction and another sensory system was assumed to provide information on flow direction. The basic model had three chemical sensors centered at equal distances from the center of the searcher and a sensor indicating flow direction. When a chemical signal is detected, the searcher is commanded to move in a direction between the up-chemical and upstream directions. If no signal is detected the searcher does not move.

Each chemical sensor reported the average value of all pixels within a defined radius of integration. Integration over time was not extended beyond the step time of 0.02 s.

To simulate the conditions in which blue crabs were tested, virtual searchers started 1.44 m downstream of the source, roughly equivalent to the starting distance in the behavioral trials. The searcher did not move unless chemical stimulation reached a threshold level, which corresponded to 0.003 of the initial source concentration, C₀. The searcher's speed of locomotion was limited to 156 mm s⁻¹, which corresponded to the 90th percentile of the velocity shown by crabs in the behavioral trials (see results, Figure 4).

Noise in the chemical sensors was incorporated in a manner similar to that employed in previous simulations [19], with most parameters multiplied by a factor close to unity. A newly chosen factor was determined for each time step as e^x, where x was a number randomly selected from a normal distribution with a mean.
of 0 and a standard deviation of 0.01 of a revolution (3.6 degrees). This noise level was found to give good fit to experimental data for cells moving in smooth chemical gradients [19]. Determination of flow direction also was modified by adding noise and an individual bias. Noise was yearly chosen at each time step as a value randomly drawn from a normal distribution with a mean of 0 and standard deviation of 0.01 of a revolution. The bias was constant for each individual over a given run but different for different individuals, and was drawn from the same function that generated the noise factor. With the given geometry and this degree of bias, a searcher always commanded to move upstream has a 40% chance of contacting the source.

In this study, the searcher moved only if stimulated and then at maximum speed. This is consistent with the rapid locomotion of crabs when stimulated in behavioral trials, although the use of a step function to control velocity is a simplification. Thus the direction of locomotion was the primary behavior controlled by chemical stimulation. The commanded direction was based on two directions stipulated by the chemical gradient and flow. A vector pointing in the direction of higher chemical stimulation (C) was determined as equal to the vector from the geometric center to the center of mass, where each sensor represents a mass at its location with a magnitude proportional to the degree of chemical signal intensity. A vector of identical magnitude pointing in the upstream direction (except for noise in the flow direction) is also generated (F). The commanded direction of movement, D is determined by a weighted sum of these two vectors:

\[ D = wF + (1 - w)C. \]  \hspace{1cm} (1)

Many simulations indicated that performance was high with any weighting value, w, in the range 0.5–0.9 (Dusenberry et al., unpub.), and a value of 0.7 was chosen for these studies (i.e., the flow vector was weighted by 0.7 whereas the chemical gradient vector was weighted by 0.3). The use of a spatial sensing mechanism, combined with a general response to flow, captures the essential elements of the navigational strategy suggested by behavioral and fluid physical data.

We were primarily interested in strategies for using chemical signals to move to the vicinity of the source, and in these simulations each searcher was stopped when it reached the streamwise (longitudinal) position of the source, since it would not get any closer with continued simulation. The simulations reported here were run for a maximum of 10,000 time steps corresponding to 200 s.

Initial experiments indicated that two lengths influence search success: searcher radius (the size of the sensor array) and integration radius (the size of the area over which an individual sensor integrates the chemical signal). Searching was simulated for various combinations of these two parameters.

Performance was measured by two parameters: time to reach the streamwise position of the source and distance of the closest approach to the source, within the 10,000 time steps simulated. Observation indicated that searchers not reaching the
Figure 2. Block schematic of the Bench-top Plume used to study two-frequency modulation. F1 and F2 represent frequencies introduced by solenoid valves, L1 and L2 represent lengths of the delay elements, D1 and D2 represent dispersion elements with two different dispersion values, and S1 and S2 represent flow-through amperometric sensors.

Streamwise position of the source within this time were likely to take much longer to reach it, if ever.

3.5. ARTIFICIAL CHEMICAL SENSING STUDIES

A bench-top fluidic system (Figure 2, the Bench-top Plume) was constructed to emulate a sensing array placed in the flowing stream [20]. The sensor array consisted of eight amperometric electrodes. This type of chemical sensor was selected for the speed and linearity of its response. Initial studies were done on only a pair of electrodes positioned in two fluidic channels. Each channel consisted of a solenoid valve that controlled the delivery of pulsed chemical marker, a delay line emulating the distance between the source of the marker and the sensor, a dispersion element crudely mimicking flow turbulence, a flow-through cell housing the sensor, and a flow meter. This system is capable of simulating the rapid odor bursts that are characteristic of turbulent odor plumes.

The focus of our research has been on the correlation analysis of the fluctuating signal, performed in the frequency domain. The methodology of this approach has been described in detail in previous papers [21, 22]. The important point to
realize is that the source of a chemical plume has a unique frequency generated by periodically actuating the solenoid valve. The navigational task is then to locate the source of such frequency in the presence of other, non-correlated frequencies. Coherence is the frequency dependent correlation coefficient. It is the ratio of the square of the cross-power spectrum to the product of the auto-power spectra from the two channels.

\[ \alpha^2(\omega) = \frac{[X_{A,B}(\omega)]^2}{[X_{A,A}(\omega)][X_{B,B}(\omega)]}. \]  

(2)

The coherence is unity for two completely correlated signals in sensors A and B and zero for two completely non-correlated signals, and is defined for the entire frequency range.

4. Results and Discussion

4.1. Behavioral Trials

Blue crabs displayed an impressive ability to locate the odor source. Of the 14 trials, 11 (79%) resulted in successful source location, with animals displaying rapid and efficient search paths en route to the nozzle. Total travel times were approximately 34 ± 6.3 s (mean ± standard error), with an average speed of 8.8 ± 0.45 cm s\(^{-1}\). In the absence of odor, animals moved considerably slower, with an average walking speed of 4.8 ± 0.72 cm s\(^{-1}\). Thus, the ability to navigate in these turbulent plumes does not seem to require elaborate sampling schemes that restrict locomotion. A typical search path is shown in Figure 3. Animals moved at relatively high velocities; even at the beginning of the search phase crabs moved at speeds of greater than 5 cm s\(^{-1}\). Progress towards the source was both rapid and sustained (Figure 4), and animals spent very little time stationary, suggesting they continued to derive appropriate orientation cues from the plume. Rapid location of chemical sources has been noted in other investigations of crustacean olfactory search behavior as well [8–11].

Search paths displayed by the animals were fairly direct. Cross-stream tacking maneuvers, when they occurred, were generally seen as animals exited the holding box and were traveling through plume regions 1.5–1.0 m from the source. The net-to-gross displacement ratio (NGDR), which is the ratio of the shortest distance between the path origin and destination to the total travel distance, was 0.65 ± 0.06. Animals not exposed to odor moved much more directly upstream, and showed a NGDR of 0.94 ± 0.03, suggesting that the ability to navigate in these plumes requires some directional changes in response to the local distribution of odor. Interestingly, lateral movements of the animal were associated with decreases in movement speed. Animals moving from the centerline of the plume slowed down sharply, whereas they sped up as they moved back into the plume. This suggests that as animals lose contact with the plume by moving beyond its edge, they momentarily slow down and perform a course correction that allows them to recontact the plume and to resume their rapid upstream movement. Blue crabs in
natural environments also tend to immediately move towards the plume centerline when they straddle the plume edge [23].

The side camera observations suggested that animals use information from a number of different elevations within the plume. The height of the animal influences the sector sampled by the chemosensory appendages, particularly those on the antennules. We determined the percentage of time that animals spent in a normal body posture compared to instances when animals either lowered their abdomen close to the substrate or extended their walking legs to elevate above their normal height during locomotion (Figure 5). There was a great deal of variation in sampling height both among animals and within the path of an individual. Although animals spent most of their time in a normal body posture, they periodically appeared to sample close to the substrate and in the upper regions of the plume.

4.2. CHEMICAL SIGNAL STRUCTURE

The analysis of signal structure indicated that for these plumes, sequential sampling of odor intensity is unlikely to guide behavior, whereas spatial comparisons provide useful information. The filamentous nature of the plume is evident in the ‘concentration landscape’, which consists of very high instantaneous peaks or bursts separated from other peaks by areas with very low, or zero, concentration levels (Figure 6). As a result, local concentration gradients can be very steep. Peak
concentrations in the bursts decrease rapidly with distance from the source due to the combined action of turbulent stirring and molecular diffusion at the Batchelor scale.

The mean concentration field, in contrast to the instantaneous field, varies smoothly in space (Figure 7). The ratio of the peak concentration to the mean is about an order of magnitude (and would be even higher if the sample size were smaller). It should be realized that the mean concentration field is a product of the averaging process; it never actually exists. Long sampling times are needed to obtain statistically stable averages due to the highly intermittent nature of the fluctuating signal. Webster and Weissburg [14] report that for this plume, statistical convergence requires sampling intervals longer than 200 s. Accurate assessment of time-averaged properties at a single location in plumes would require sampling times orders of magnitude longer than the average duration of the entire blue crab search path (see also [1, 8, 14]). Concentration bursts, rather than the time-averaged properties, seem the most likely signal features enabling animals to orient rapidly in turbulent plumes.

The length and time scales of the flow relative to those of animal behavior, may help to determine how the bursts provide information. For instance, the Kolmogorov and Batchelor length scales are 0.7 mm and 0.02 mm, respectively, for this flow and the corresponding Batchelor time scale is 0.4 ms. This suggests that certain instantaneous properties of the fluctuations may be unavailable to a for-
Figure 5. Time budgets for body posture of foraging animals. The figure shows the proportion of time each animal spends in each of the three different body postures. Low is defined as when the abdomen is less than 0.5 cm from the substrate, normal is the animal’s body posture during normal locomotion, where the top of the carapace is approximately 5.0 cm above the substrate, high is defined as when the animal extends its legs to elevate the top of the carapace. The trials were ordered based on increasing time in the low position.

In a similar plume, because most aquatic animal sensors cannot sample rapidly enough to accurately characterize the concentration slopes in individual bursts. Information on the temporal sampling abilities of crustaceans is scarce, but most lobster antennary chemosensory neurons fail to resolve odor pulses presented at rates exceeding 4–5 Hz, and require 50–100 ms to code the peak intensity of an odor burst [24, 25]. Although adaptation processes may produce neural responses that are capable of resolving pulse properties on shorter time scales, whether this actually occurs is unknown. Present evidence thus suggests that response rates of crustacean chemosensors, as they are currently understood, are too slow to characterize the onset or offset slopes, and may possibly result in an inability to even detect bursts of short-duration. These and other considerations have led to a hypothesis that simple temporal characteristics of odor field properties are unlikely
Figure 6. Instantaneous concentration distribution in a plane along the centerline for the turbulent plume created as described in this study. The instantaneous concentration is normalized by the source concentration, \( C_0 \) and the \( x,y \) axes are normalized by the water depth, \( d \).

Figure 7. Time averaged concentration distribution in a plane along the centerline for the turbulent plume created as described in this study. The average concentration is normalized by the source concentration, \( C_0 \) and the \( x,y \) axes are normalized by the water depth, \( H \).
Figure 8. 3-Dimensional PLIF visualization of the turbulent plume. The intensity (chemical concentration) increases from white to black.

to provide information on biologically realistic time scales [1, 14]. Rapid upstream progress of animals in our behavioral trials may result from a generalized upstream response to odor detection, a mechanism similar to that employed by insects in turbulent airborne plumes (see also [1, 2, 8–10]).

The behavioral observations (Figure 5) suggest that animals can, and probably do, compare information obtained at different heights, requiring us eventually to acquire and analyze the odor plume in three, rather than two, dimensions. Our initial forays into examining this little-known aspect of plume structure suggest considerable changes in vertical distribution of odorants as the plume evolves downstream (Figure 8). Near the source the plume is confined to regions near the same vertical plane as the nozzle elevation, whereas farther downstream the vertical spread has increased dramatically. The sudden absence of odor high in the boundary layer observed by an animal moving upstream may indicate close proximity to the source, and may be the cause of the postural changes displayed by the animal during navigation. Generally, the vertical plume distribution is a strong function of release location and geometry. For instance, sources may be relatively flush to the bed (e.g., a buried clam or small piece of carrion) or may be larger objects such as other crabs. We are just beginning to appreciate the consequences of three-dimensional information, and the necessity for extending planar measurements to volumes.

The lateral movements displayed by crabs at the edge of the odor field (Figure 3) leads to the hypothesis that spatial information on the odor distribution may play a role in allowing animals to maintain their position relative to the center line of the plume. Webster et al. [26] found that spatial correlations of the instantaneous concentration field provides information useful to animals trying to remain in the
Figure 9. Time series of instantaneous concentrations at the centerline and at a point 5 cm off of the centerline, and a distance 50 cm downstream from the source. Positive values refer to the concentration at the centerline, negative values at 5 cm from the centerline.

The correlation tends to zero at the plume edges, but is large over a significant fraction of the plume width (Figure 10). Thus, if the sensor spacing is large compared to the integral length scale of these correlation curves, then the sensors will have sufficient contrast to steer the animal towards the centerline of the plume.
Figure 10. Across-stream cross-correlation coefficients of instantaneous concentration at the centerline and various distances from the centerline, for four downstream distances. The correlation function is defined by Equation (3) and the position of the sensor, $y$, is non-dimensionalized by the water depth, $H$.

The integral length scale corresponds to the length over which perfect correlation would have the same area as the correlation function curve, thus:

$$L = \int_{0}^{\infty} \left( \frac{c_x c_y}{c_x c_y} \right) dy.$$  \hspace{1cm} (4)

Physically, the spanwise integral length scale provides a measure of the size and spatial homogeneity of the plume and hence provides a relative comparison for the sensor spacing [26]. This analysis of spatial signal structure is consistent with the tendency of the crabs to slow down and turn back towards the plume centerline. As the animal moves away from the core of the plume, stimulation of sensors becomes less correlated, and animals must pause momentarily in order to acquire the appropriate sensory feedback and relocate the plume center.

Since the plume is widening as it moves downstream, adjustable sensor spacing or an array of sensors appears advantageous. A similar conclusion was drawn by Grasso et al. [29–31] based on a series of robot behavioral trials. In these trials, performance of robots increased with sensor spacing or where the plume was less dispersed, which suggests that useful steering information can be extracted provided the sensor spacing is wide compared to the plume. Expansion of the plume,
as well as the meander, may account for the behavioral observations that show
greater lateral movements farther from the source.

4.3. COMPUTER SIMULATION OF BEHAVIOR

Simulations of animal behavior suggested that a simple strategy of moving up
stream in response to odor presence, combined with simultaneous spatial compar-
isons produces behavior similar to that seen in real animals. It is clear that there is
an optimal size for good performance of virtual searchers that use this algorithm,
and that performance can be very good with little variation between individuals
(Table I). Although it is difficult to define precisely the width of the plume, the
optimal array span is similar to the plume’s expanse in the region where across
stream tacks are the most frequent. A reasonable approximation of plume width can
be obtained from the cross-correlation analysis (Figure 10); between 50–100 cm
downstream of the source, the cross-correlation falls to approximately 5% at a
length scale equal to that of the optimal array size of 32 mm. The decreasing per-
formance at array spans larger than the plume width suggests that greater accuracy
when approaching close to the source can be achieved by a smaller array. Although
the array size in our simulation was fixed, animals have movable appendages and
sensors spaced at different distances that may allow them to achieve an optimal
array size at different lengths from the plume source.

Time to the streamwise position of the source depends primarily on the inte-
gration radius of the sensors, with larger sensors reducing the time. This occurs
because smaller sensors are less likely to detect a burst in the instantaneous plume.
Larger sensors detect a chemical signal with higher probability and weaker depen-
dence on where the searcher happens to be. Animals generally have a large number
of small sensors on each sensory appendage, although the extent to which these
outputs are combined, or remain independent, is unknown. The primary sensory
hairs in lobsters (the aesthetascs) are on the order of 1,000 μm in length and
10 μm in diameter. Each appendage has approximately 400,000 of these sensors
[32]. Such an arrangement may be the optimal balance between having sensors
small enough not to disrupt the odor field as it passes through it, combined with
the redundancy necessary to provide a high likelihood of detecting the signal.

Spatial accuracy (closest approach to the source) depended primarily on the
size of the sensor array, with best accuracy obtained by arrays of about 10–32 mm
radius. The optimal array therefore spanned a distance similar to the plume width.
These results are expected based on our analysis of signal structure, which showed
that the cross-correlation of chemical signal intensity is small for a sensor sepa-
ration that is large compared to the local plume width (Figure 10). Sensor spans
significantly larger than the plume width result in a lack of specificity because large
arrays fail to provide precise information on the location of the plume edge. Accu-

cy declined for radii smaller than 10 mm because the searcher easily lost contact
with the plume, and failed to move upstream. Thus, the first case corresponds to a
Table I. Searching performance with variations in sensor and array sizes.

<table>
<thead>
<tr>
<th>Sensor integration radius (mm)</th>
<th>1</th>
<th>3</th>
<th>10</th>
<th>32</th>
<th>100</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>(6640, &gt;10k)</td>
<td>(3702, &gt;10k)</td>
<td>(4325, &gt;10k)</td>
<td>(7256, 8788, &gt;10k)</td>
<td>(665, 751, &gt;10k)</td>
</tr>
<tr>
<td></td>
<td>[2.3, 603, 1178]</td>
<td>[2.2, 881, 1190]</td>
<td>[1.9, 825, 1146]</td>
<td>[2.8, 14, 1124]</td>
<td>[16, 78, 867]</td>
</tr>
<tr>
<td>3</td>
<td>(3174, &gt;10k)</td>
<td>(1438, 2657, &gt;10k)</td>
<td>(1064, 2324, &gt;10k)</td>
<td>(1636, 1782, 1873)</td>
<td>(532, 546, 564)</td>
</tr>
<tr>
<td></td>
<td>[1.7, 469, 633]</td>
<td>[1.3, 2.3, 741]</td>
<td>[1.8, 3.3, 768]</td>
<td>[1.4, 4.5, 8.9]</td>
<td>[5.0, 26, 50]</td>
</tr>
<tr>
<td>Sensor array radius (mm)</td>
<td>10</td>
<td>(2312, 2546, 4930)</td>
<td>(933, 1160, &gt;10k)</td>
<td>(680, 740, 826)</td>
<td>(604, 620, 633)</td>
</tr>
<tr>
<td></td>
<td>[1.3, 3.1, 5.3]</td>
<td>[1.2, 3.1, 486]</td>
<td>[1.0, 2.3, 3.3]</td>
<td>[1.6, 4.1, 7.9]</td>
<td>[2.3, 8.2, 21]</td>
</tr>
<tr>
<td>32 (mm)</td>
<td>(3060, 3660, 4174)</td>
<td>(1499, 1730, 2145)</td>
<td>(616, 785, 952)</td>
<td>(498, 500, 502)</td>
<td>(493, 495, 496)</td>
</tr>
<tr>
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<td>[1.6, 4.5, 11]</td>
<td>[1.6, 4.5, 9.7]</td>
<td>[1.3, 4.5, 9.9]</td>
<td>[1.4, 4.2, 7.9]</td>
<td>[2.7, 10, 22]</td>
</tr>
<tr>
<td>100 (mm)</td>
<td>(7014, 8246, &gt;10k)</td>
<td>(3379, 4107, 6738)</td>
<td>(1235, 1994, 3908)</td>
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<td>(491, 494, 497)</td>
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<tr>
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<td>[2.3, 10, 34]</td>
<td>[3.4, 14, 37]</td>
<td>[5.7, 20, 39]</td>
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<tr>
<td>316 (mm)</td>
<td>(&gt;10k)</td>
<td>(&gt;10k)</td>
<td>(&gt;10k)</td>
<td>(6490, 6516, 9856)</td>
<td>(1600, 3004, 8726)</td>
</tr>
<tr>
<td></td>
<td>[626, 856, 1037]</td>
<td>[72, 224, 655]</td>
<td>[8.8, 32, 72]</td>
<td>[8.3, 34, 85]</td>
<td>[9.3, 44, 125]</td>
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<tr>
<td>1000 (mm)</td>
<td>(&gt;10k)</td>
<td>(&gt;10k)</td>
<td>(&gt;10k)</td>
<td>(8770, &gt;10k)</td>
<td>(3758, 9526, &gt;10k)</td>
</tr>
<tr>
<td></td>
<td>[1297, 1380, 1440]</td>
<td>[1195, 1333, 1440]</td>
<td>[962, 1041, 1440]</td>
<td>[28, 920, 1440]</td>
<td>[18, 174, 1440]</td>
</tr>
</tbody>
</table>

For each combination of array radius and integration radius, the results are presented as 10, 50, 90th percentiles of distance from the source in [ ] and time to reach the streamwise position of the source in ( ). Distance is measured in the pixels, with a spacing of 1.0417 mm pixel⁻¹. 1440 pixels corresponds to 1,500 mm. The simulation was run for 10,000 time steps (200 s) with 100 individual searches for each combination of parameters. Time is measured in simulation time steps of 0.02 s. The bounded cell shows the parameter set that results in the most efficient guidance behavior.
searcher with poor spatial resolution whereas in the latter case a searcher does not have a large enough spatial expanse to even detect the plume edge. Spatial accuracy also declines if the integration radii increase much beyond the array radius. In this case, the integration areas of different sensors overlap, reducing the signal contrast that otherwise provides gradient information.

There is some conflict between optimizing for time and accuracy. However, the simulations demonstrate that optimal searchers can reliably come much closer to the source than the size of their array radius in nearly the minimum time of 480 steps (9.6 s). Although simulations cannot prove what mechanisms animals actually employ, this simple algorithm using kinematic data taken from real animals and realistic plume data produced behavior strikingly similar to that of live crabs. This result suggests that the signal parameters hypothesized to carry information based on our behavioral and fluid dynamics investigations are at least sufficient to account for animal tracking, and consistent with our observations.

Two other parameters related to spatial and temporal scales were explored. Temporal integration was modeled as a sum of previous levels of stimulation with an exponential decay of weighting into the past: $R(t+1) = R(t) + A[S(t+1) - R(t)]$, where $R(t)$ is the sensor output (after adaptation or temporal integration) at time $t$, $S(t)$ is the spatially integrated signal from the sensor before temporal integration, and $A$ is the integration rate. The results presented in Table I were for $A = 1$, where there is no temporal integration. Increasing temporal integration ($A = 0.3$ and 0.1) caused no clear change in the results, but spatial accuracy might have been degraded somewhat. Reducing the walking speed from 156 to 50 mm s$^{-1}$ caused no change except increasing the time to reach the source by 3-fold. Thus, these other parameters do not seem to play an important role in this model.

4.4. ARTIFICIAL CHEMICAL SENSING

Results using the Bench-top Plume indicate that arrays also may be used to extract information from the fluctuating signal component (Figure 11). At the stimulus frequency of 1 Hz the coherence function was maximized. The presence of higher harmonics in all coherence spectra results from the fact that the excitation signal is periodic but not sinusoidal. We find that longer dispersion tubes increase the ratio of coherence of the fundamental frequency relative to the higher harmonics [21]. This suggests that distance to the source in a turbulent plume may be estimated based on the coherence function. Additionally, one of the most interesting observations was that coherence frequency is independent of flow velocity [21]. A strategy for encoding chemical concentration that does not have to take into the account flow velocity of the medium has a major advantage.

Fluctuating signals modulated at two different frequencies can be easily detected and analyzed. The details of these investigations can be found in references [21, 22]. A brief example (Figure 12), shows the coherence spectrum corresponding to the two-frequency (2.0 and 2.7 Hz) modulation of the chemical concentra-
Figure 11. Information in the modulated signal of the Bench-top Plume. (A) The time series for the two channel flow modulation experiment. Modulation frequency was 1 Hz, and flow rate was 0.6 ml/min; (B) auto power spectrum densities for both channels calculated from the time series given in (A); (C) coherence between the two channels in the frequency domain for the given time series.

tion. Again, the base frequency and higher harmonics are present in the coherence spectra. The ability to discriminate among frequencies could be of potential use by an animal or robot attempting to discriminate between odor sources of different sizes, which would create plumes that meander or shed vortices at different frequencies [33].

Using information from the fluctuating signal component is advantageous for other practical reasons. The long-term recognition of steady state, averaged signals (the constant signal component) is inherently difficult because it assumes that the sensing system has stable performance parameters, namely the baseline and the sensitivity. That is usually not the case, and in reality, sensors require periodic calibration that compensates for drift and changes in sensitivity. Reliable information acquisition using the steady state signals is not possible in situations where frequent calibration of the sensors is not feasible. However, the fluctuating component is less dependent on stable baselines and sensitivity of individual sensors since it is measured as the covariance in the sensor response, and may present an alternative
Figure 12. Coherence spectrum obtained with simultaneous two-frequency modulation. The first frequency was $F_1 = 2.0$ Hz and the second was $F_2 = 2.7$ Hz.

Figure 13. Schematic of the array of virtual sensors that was used to extract information on the odor fields preserved in the PLIF data set. The sensor spacing was set at 1 cm.

for coding chemical signals in environments where sensors are expected to perform over long time periods with little opportunity for adjustment.

Along with the bench top experiments, eight virtual sensors were placed in the PLIF concentration fields to determine if an array provides unique and useful information. The sensor array (Figure 13) was intended to crudely represent the array of appendages that a blue crab possesses. The sensor output is assumed to equal the instantaneous concentration at the corresponding pixel location. The objective
was to assess whether the array provides information, such as the flow direction, that cannot be obtained by a single chemical sensor.

When the array of eight sensors is immersed in the plume (PLIF concentration fields), it is exposed to intermittent stimuli [34]. Figure 14 shows a sequence of response patterns of the sensor array placed 50 cm downstream from the source. The darker pixels represent higher concentration, and the interval between the successive patterns was 0.2 s. It can be seen from Figure 14A–C that a dye filament successively passes sensors 6, 7, and 8. This signal sequence obviously corresponds to the flow moving from left to right. Thus, a searcher can quickly determine the flow direction from a simple comparison among the sensor elements, whereas the
time lag between sensor responses can be used to compute flow speed. Given that flow information appears critical for the success of both real and simulated agents, the ability to extract flow information from the patterns of sensor response could be an additional advantage of arrays.

A difficult challenge to a fully autonomous search is how to declare the source location and terminate the search. Devising rules for the source declaration has proven to be much more challenging than constructing algorithms for navigation to the source. For instance, the source location is difficult to obtain from the steady-state part of the signal when the initial source concentration is not known a priori. The sensor array may provide a simple solution to the source declaration dilemma. Distinctive response patterns were observed when the array straddles the source location, (Figure 15A–C). From the responses of the sensors 2 and 3, the flow can be determined to be from left to right. However, the sensors 1, 4, and 6 at the upstream edge of the array do not show any response. Considering the fact that the plume always trails in the downstream direction, one can declare from this response pattern that the source is located within the array.

5. Synthesis and Conclusions

The purpose of addressing the chemical plume tracking problem with a multidisciplinary team was to build synergy between the various components of the study. Chemical plume tracking in turbulent environments is extremely difficult to understand and yet blue crabs and other animals perform at a high rate of success under varying conditions. Combined expertise in the areas of crustacean behavior, fluid dynamics, sensory ecology, and chemical sensing is needed to fully understand this process. We found that coordinated animal and fluid physical studies are particularly useful for hypothesis generation and testing, as is sharing rigorous physical measurements of odor field structure for use in simulation or computational approaches.

The fine details of the spatial and temporal variation of the concentration distribution appear to be beyond the sampling ability of aquatic crustacean chemosensors. In addition, because of the signal intermittency the convergence time for any time-averaged quantity is far longer than the total search period observed in the behavioral trials. Thus, temporal sampling of the fine details of the turbulent field with a single sensor appears to have limited utility.

The main consensus of the current study was that spatial sampling and comparison in the plume yields rapid, useful information. We know from the behavioral studies that blue crabs are highly successful at rapidly locating a chemical source once they acquire the odor. They possess chemosensors at multiple locations on their bodies, which may serve as redundancy, but may also serve as a sensory array. During foraging, they appeared to identify the edge of the plume and turn toward the plume center and therefore reliably remain in contact with the odor. The most
readily available information to mediate this action is a simple comparison between the left and right appendage chemo sensors (i.e., a bilateral comparison).

A spatial correlation between spanwise-separated sensors reveals the relative direction of the plume centerline very rapidly. Analysis of the concentration fields shows that a sufficiently wide separation is required to be effective and that the separation distance should be measured relative to the length scale of the lateral correlation function. This length scale increased as the plume evolved downstream, indicating that adjustable sensor spacing is advantageous. The strategy simulations using arrays of fixed width further documented the usefulness of spatial sampling by revealing an optimal sensor spacing, for which search was both rapid and robust.
Virtual searchers performed quite well relative to that of blue crabs under similar conditions, suggesting that even a fixed array may be quite effective in gathering information requisite for plume navigation. The chemical sensor analysis provided additional support through use of the coherence function between a pair of sensors, which revealed the relative position of the plume source. An array of sensors also identified the local flow direction and resulted in a simple mechanism for declaring the source location.

Although our results suggest important connections between plume characteristics, tracking performance, and methods to extract information from turbulent plumes, it is important to realize that these findings depend greatly on both ambient flow and plume source characteristics. We have studied a single case of a small plume released iso-kinetically into ambient flow. In these stimulus conditions, its is primarily the turbulence of the ambient fluid that determines the resulting character of the plume. Plumes that create their own turbulent structures by interacting significantly with the ambient (i.e. jets) will have a radically different character even when released into similar flow conditions as used in this study, and mechanisms that we have identified as being useful may fail in these other environments. For instance, Grasso et al. [31] observe that a robotic lobster mimic starting far from the source failed to find it using simple bilateral comparisons, even when the sensor span was quite large, although both our plume data and computer simulations suggest this is a robust guidance mechanism. One important difference between this study that of Grasso and colleagues is that their robot tracked a plume created by a jet source. In these conditions, shear at the boundary of the jet will rapidly and effectively homogenize the plume, such that large bilateral contrasts between even widely spaced sensors may be rare (e.g., [14]). Resolution of viable mechanisms for extracting information from chemical signals embedded in turbulent plumes will require studies that simultaneously assess behavior, tracking mechanisms, and plume signal characteristics in a variety of fluid flow environments and plume configurations.

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References