Lobsters extract information from complex signals in turbulent odor plumes and it guides them to mates or food sources. To test hypotheses about this guidance information, we have developed a robot as a physical model of a lobster. Here we present the results of experiments designed to test the efficacy of amplitude information—a single component of a complex signal—in guidance. The robot used a bilateral pair of conductivity sensors (sensor surface spacing = 5–7 cm, 5 cm separating two 1-cm wide sensors) to sense a salt plume simulating an odor plume.

The experiments were performed in a fresh-water flume with a mean flow rate of 0.6 cm/s. A 0.76 M NaCl solution (containing crystal violet for visualization and ethanol to adjust buoyancy) was injected parallel to the flow from a 2 mm diameter nozzle into the flume at a rate of 250 ml/min. The resulting plume had two distinct regions: a proximal cone originating at the source, and a distal patch field downstream from the jet. The proximal jet is the region where the velocity of the jet exceeds the mean flow in the flume. The distal patch field corresponds to plume positions downstream from the proximal cone where the mean flow is the major source of plume velocity (relative to the floor).

Two robot control algorithms were tested:
1. The robot turns toward the side with the higher salt conductance signal or goes forward if the difference between the right and left sensor signals drop below 9 μS.
2. As in #1, with the added feature that the robot goes backward if the conductances of both sensors drop below a threshold of 7 μS.

The robot was placed in the center of the flume, 90 cm downstream from the plume source, and was started in two orientations for each algorithm: pointed upstream directly into the oncoming plume, and pointed 45 degrees to the right of the plume axis. Each of the four conditions (2 orientations and 2 algorithms) was replicated 10 times. The robot’s trajectory was recorded by a video camera. Data from a single run using algorithm #1 are presented in Figure 1.

As the robot moved through the patch field, its behavior was characterized by sequences of abrupt, brief turns that occurred at irregular intervals. When it entered the proximal jet, the robot moved with more regular side-to-side oscillations: a characteristic series of alternating smooth left and right turns (often of greater magnitude than those seen in the distal patch field). Once inside the proximal jet the robot often found its way to the source (50% algorithm #1 and 72% algorithm #2).

The starting orientation had a substantial effect on the success of the algorithms. Algorithm #2 with the robot pointing into the plume had a higher rate of direct “hits” onto the source than algorithm #1 with the same orientation (66% vs 33%). We attribute the greater failure rate of algorithm #1 to the fact that when both sensors happen to exit the plume, algorithm #1 moves the robot in a straight line away from the point of exit. The

Figure 1. (A) Right and left conductance measurements during an experimental run (algorithm #1, robot start pointed up the central plume axis). Left sensor data were inverted for visualization purposes. (B) Conductance difference (right-left) and turning rate. Vertical scale is in μs for conductance difference and in deg/s for turning rate. Turning events follow sensor signal differences by 0.6 s. (C) Robot trajectory during the same run as Figure 1a, b. Points are robot positions at 1-s intervals. The dotted lines denote the plume at the end of the experiment and show the region where the proximal cone makes the transition into the distal patch field.
back-up behavior of algorithm #2 corrects for plume exit. Orienting the robot at 45 degrees reduced the probability of the robot finding the cone and thus reduced the probability of the robot finding the source (algorithm #1: 33% vs 0%; algorithm #2: 66% vs 10%).

These experiments show that simple bilateral amplitude comparisons generally suffice to guide a robot within the proximal jet of a chemical plume. Lobsters may use such an algorithm for guidance in the proximal cone. This simplest algorithm fails in the distal patch field where the structure of the chemical signal is less regular. Lobsters show different behavioral strategies at different distances from the source of an odor. Consequently, additional algorithms will be required for successful guidance of the robot from greater distances toward the proximal cone. This gradual build-up of algorithm complexity, coupled with lobster behavior analysis, is expected to lead to a general understanding of guidance principles in odor plumes.

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**Effects of Varying Plume Turbulence on Temporal Concentration Signals Available to Orienting Lobsters**

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Lobsters locate odor sources in turbulent plumes (1, 2). Based on the speed and accuracy with which lobsters orient to such odor sources, Moore, Scholz, and Atema (2) argued that these animals are guided by temporal features of the odor concentration profile arriving at their chemoreceptors as a series of concentration peaks. Physical investigations (3, 4, 5) of the temporal odor signal identified a number of peak parameters as candidate guidance cues. These physical studies and the behavioral ones were both conducted using axisymmetrical jet plumes generated in a single turbulent regime (defined by mean flow through the plume and jet injection rate). Here we extend the physical investigations to include multiple turbulent regimes. Specifically we aim to address the question: Do the candidate peak parameter gradients identified by Moore and Atema (5) retain their guidance potential for the lobster in plumes generated with different source injection rates?

To facilitate these initial measurements, we created saline plumes (source 0.76 M NaCl) containing dye and ethanol for neutral buoyancy in a fresh-water flume (366 × 90 × 36 cm, mean flow 0.7 cm/s). Conductivity measurements enabled us to estimate salt concentration at 40 Hz or about 10 times the signal frequency resolution of lobster chemoreceptor cells (6). The electrochemical methods used in the previous studies (5) were limited to 10 Hz. This allowed us to record the signal amplitude while minimizing temporal distortions due to signal masquerading in the bandwidth of lobster chemoreceptor cells (6). Our interest here is in turbulent (inertial) dispersal where flow dominates molecular transport. Ethanol is not measured and salt, as well as dopamine which was used in some of our earlier studies, are useful tracers for turbulent mixing processes. The use of salt plumes also complements our studies with a robot that orients with conductivity sensors. Although salt and ethanol diffuse differently than food odors at the molecular scale, we observed no visual differences in plume structure between odor plumes and ethanol-salt plumes. Thus, this study provides a reasonable physical model of a food odor plume in a way that informs future behavioral and robot orientation studies.

We estimated the salt plume concentration time-course (from measured conductivity) at five distances along the flume midline from the source (0, 25, 50, 75, and 100 cm). To produce different plumes we varied the rate of source injection (0.5 ml/min), (40 ml/min), (80 ml/min), (120 ml/min) and (160 ml/min). Each injection was delivered continuously through a 2.2-mm inner diameter glass tube located at the flume midline 9 cm from the flume floor. Conductivity measurements were taken with a pair of silver-tipped electrodes placed 9 cm from the flume floor (approximate lobster antennule height). The electrodes had a 1-mm spatial separation (scale of a lobster sensillum). Thus, we sampled a horizontal line through each plume at an elevation and spatial scale that matched that of the lobster lateral antennule receptors.

We converted the conductivity profiles to concentration (moles/liter). In agreement with earlier studies, the temporal profiles that we examined were so patchy that accurate estimates of the concentration gradient would require greater than 30 s of sampling. We therefore turned to an analysis of the temporal parameters of the patches themselves. Patches in the spatial domain are seen as peaks in the concentration profile. Peaks were defined (5) as the profile region between the time the concentration exceeded the background by 0.75 mM and the time the concentration fell below 30% of the maximum concentration of the peak. We examined five peak parameters: peak height (PH, maximum concentration), rise-time (PR, time from the beginning of a peak to its maximum), peak slope (PS, ratio of peak height to rise-time), peak duration (PD, time from peak start to end), and interpeak interval (IPI, time between consecutive peak maxima).

We used a two-way ANOVA to analyze the effects of distance and injection rate on each of the five peak parameters. These analyses indicated significant effects of injection rate and distance on all five peak parameters ($P < 0.001$ all analyses). These results are consistent with earlier studies (5). They also revealed significant interactions of distance and injection rate on all five peak parameters ($P < 0.001$ all analyses.)