

Chemical Plume Tracking Behavior in Animals and Mobile Robots

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ABSTRACT: *The most important and challenging feat of navigation for many animals is locating important resources by tracking fluid-borne chemicals. As molecules of a source dissolve into flowing air or water they form a patchy turbulent plume which results in the intermittent stimulation required by many odor tracking animals. Most animals need two pieces of information to track a plume: (1) the presence of odor, and (2) the direction of the flow. In most cases, steering into the flow and moving upstream while in contact with odor should lead the tracker to the odor's source. How plume trackers sample for odor information and what rules they use to generate the behavior we observe have been addressed using computer simulations or mobile robots as models of the biological trackers. These approaches also result in the development of control algorithms for autonomous man-made plume tracking systems.*

INTRODUCTION

A plume is a distribution of chemicals resulting from the interaction of flowing fluid (air or water) with a source of volatile chemicals, and it has a discontinuous patchy structure (Figure 1) [1–4]. In general, plume tracking animals *require* this patchy structure to respond [5–8]. Because the intermittent structure of odor plumes is caused by turbulence and not diffusion, there is no concentration gradient to use to steer toward the source [2, 9]. Thus, in most known cases, animals tracking odor plumes in flowing fluids *use the flow direction to steer toward the source*, not olfactory cues [10–14]. The chemical cues in the plume modulate the animals' orientation to flow. Thus, any successful odor tracking organism must be able to detect the direction and magnitude of wind or water flow and the type and amount of the chemicals in the plume. The method of locomotion to a large extent determines how any organism extracts flow information from the environment.

FLOW SENSING WHILE WALKING OR FLYING

If the tracker knows the flow direction, in most cases it knows the direction to the source. In many natural environments wind passing across a fixed odor source will carry the molecules in a straight line downwind [15, 16]. Thus, if you detect odor you should orient into the wind and move directly upwind. If the wind direction shifts, simply re-orient to the new wind direction and continue this

strategy [15]. However, in forested or wooded environments, low wind speeds often combine with rapidly shifting wind directions, causing this relationship to break down thus making odor-guided navigation nearly impossible [17, 18].

A flying or swimming animal orienting and navigating toward an odor source must determine the direction of the flow bearing the odor molecules indirectly. Since it is suspended in the dynamically moving fluid bearing the odor plume it observes the wind direction as the difference between the heading it is attempting to fly and the heading that it actually generates. A flying animal determines the wind direction and steers accordingly by measuring how it is being driven off course by the wind using visual cues [7]. Biological flight and flight control, at their foundation, require visual information for stabilization and steering (see papers by H. Krapp in this journal). Although flying moths and other flying odor trackers use their visual systems to stabilize their flight, steer with respect to the wind and control speed over the ground, they typically use drag-induced deflection of their antenna to detect their airspeed, or how fast they are moving through the air [19, 20]. Thus speed and steering control during odor-guided navigation results from an integration of visual and mechanosensory derived information. In the only experiment on steering and swimming speed control during odor tracking, it was demonstrated that a visual-flow-derived mechanism similar to that used by flying insects was used by male rainbow trout orienting

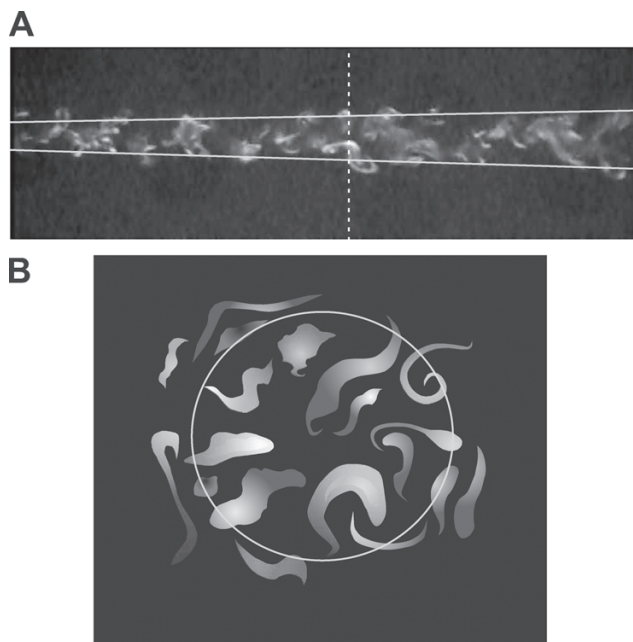


Fig. 1—Turbulent structure of odor plume from (A) experimenter's (overhead) view and (B) tracker's point of view (looking upstream toward source). Grey lines depict time-averaged edge. (B) cross section at dotted line in (A) (from [21]).

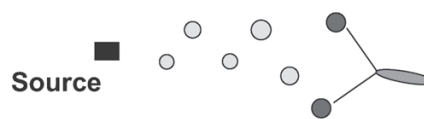
to females in streams [22]. Whether in air or water, we expect there to be many such similarities amongst animals tracking odors in fluid media.

Animals orienting and navigating toward an odor source while walking can directly determine the direction of the flow by measuring the deflection of wind sensitive hairs on their bodies. Because a walking plume tracker is in constant contact with the ground it has a fixed reference frame with which to compare the perceived flow direction. In contrast to animals flying or swimming into the flow to track odors, walking animals have been shown to be relatively insensitive to visual flow, and do not seem to use it for walking speed control [23, 24] or for determining distance traveled [25]. However, walking insects are sensitive to rotational visual flow [24] and walking cockroaches have been shown to learn the spatial relationship of visible objects in their environment and use this information to navigate in controlled laboratory arenas [26]. Thus, even though walking odor trackers probably do not use visual flow information to determine wind direction and control their steering like flyers do, they still integrate multiple types of sensory information to acquire wind direction and control their steering and walking speed.

SPATIAL VERSUS TEMPORAL SAMPLING IN PLUME TRACKING

Historically, the concept of spatial or temporal sampling has been used to explain how organisms track odors through a concentration gradient to a

Spatial



Temporal

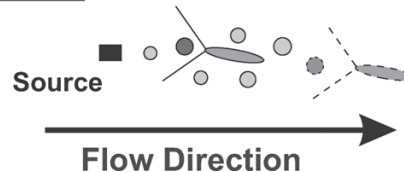


Fig. 2—Schematic diagram of spatial and temporal plume trackers.

source [27–29]. In gradient orientation, steering according to simultaneous bilateral comparisons is known as tropotaxis, whereas steering according to sequential samples is called klinotaxis. Klinotactic orientation is typically associated with the animal actively moving its sensors or its body through the environment. Since odor plumes are not the smooth concentration gradients required for tropo- or klinotactic mechanisms to orient toward the source, one can consider chemo-orienting plume trackers as using spatial and temporal sampling to maintain contact with the segment of the odor plume in their immediate vicinity (Figure 1B) [13, 30]. Chemical information acquired by temporal or spatial sampling contributes to source location in three ways: 1) activating and maintaining upstream orientation to flow, 2) activating or modulating internally-stored steering behavior that is not directed by the plume (triggered by *temporal sampling*), and 3) directing steering responses that maintain contact with the plume (triggered by *spatial sampling*). Some have proposed that 2 and 3 may both operate in some plume-tracking animals [31, 32].

The basic rules underlying spatial and temporal sampling are simple (Figure 2). An animal using spatial sampling to steer toward an attractive plume turns toward the sensor detecting the highest concentration. Continuous forward progress results if both sensors receive equal non-zero stimuli, and if no odor is detected by either sensor a pre-programmed search may result. A tracker using temporal sampling compares sequential samples as it moves through the environment. If the second sample is the same or higher concentration, forward progress continues; if lower, the animal steers to return to the previous position or executes a pre-programmed search behavior. Unlike the spatial strategy, a temporal strategy requires some form of memory to operate. This could be as simple as sensory adaptation and disadaptation.

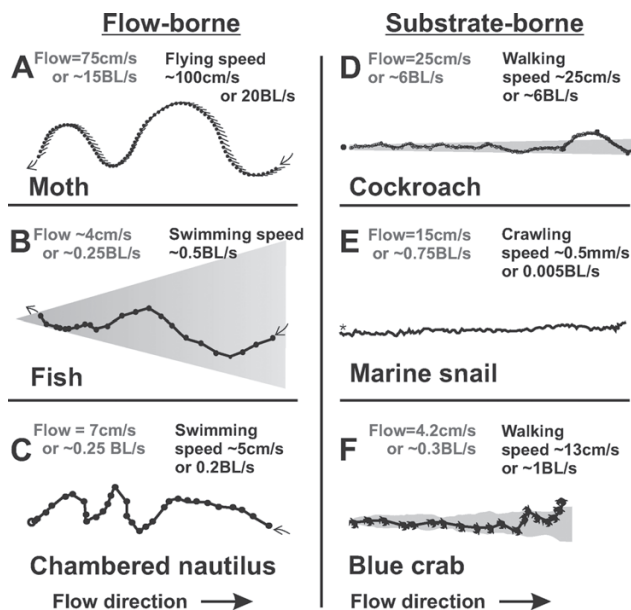


Fig. 3—Paths of flow-borne and substrate-borne plume trackers. (A) male moth tracking female pheromone [12], (B) Antarctic fish tracking a water-borne plume of prey extract [33], (C) Nautilus tracking a water-borne plume of prey extract [34], (D) male cockroach tracking female pheromone [14], (E) predatory marine snail tracking prey odor [35], (F) path of a blue crab tracking prey odor [36]. In all images the fluid flows from left to right. Shading = time-averaged plume, BL/s = body lengths/second.

Steering maneuvers in the tracks of swimming or flying odor trackers are thought to result from internally-stored turns that are activated, but not directed, by concentration differences, while those of walking odor trackers are thought to be directed by spatial comparisons [11, 13, 37]. In fact, the paths of substrate-borne and flow-borne plume trackers appear to be very different (Figure 3). Flow-borne tracks typically have fewer turns/track, and have larger lateral excursions relative to walking tracks, whereas the turns in walking tracks occur near the edges of the plume rather than being centered on the plume's midline (Figure 3), especially far downstream of the source. The speed of encountering the plume of flow-borne and substrate-borne trackers overlaps broadly; flow-borne trackers vary across two orders of magnitude (approximately 35–0.45 body lengths/s) and substrate-borne-trackers across one order of magnitude (approximately 12–0.75 body lengths/s) (Figure 3).

What are the bases of the differences observed in Figure 3? Answering this question requires disentangling the complex interaction of the tracker's speed, mode of locomotion, sensors, and the olfactory environment. Because walking (approximately 6 body lengths/sec) and wind speed near a substrate (approximately 6 body lengths/sec) are both slow, a male cockroach will encounter odor filaments at low frequency. The animal may be able to use its long antennae to make spatial comparisons and steer back into the plume upon detecting the large con-

centration drop at the lateral margins of the plume [14]. In contrast, a flying male moth is typically moving through the air much faster (20–30 body lengths/s) and the wind bearing the plume is also typically moving faster (approximately 15–30 body lengths/sec). By the time the flying moths detect and process the odor (*M. sexta* approximately 10Hz; [38]) and alter their steering (*M. sexta* approximately 500 ms; [39]), the section of plume that they are responding to may be almost a meter behind them. Thus, a temporal sampling strategy may be the *only* one available to flying plume trackers.

Since the majority of odor-tracking animals have bilateral odor sensors, both spatial and temporal strategies could be operating, either synergistically or independently [28, 29]. However, careful experiments to resolve these questions have rarely been pursued [40–44]. These approaches have recently shown that both rats [45] and humans [46] can discriminate both temporal and spatial concentration differences. One study has even shown that humans can follow a trail of chocolate scent laid on the ground [46], and that subjects had a lower performance when spatial information is experimentally removed.

EFFECTS OF BEHAVIORAL CONTEXT ON PLUME TRACKING BEHAVIOR

The control circuits underlying walking or flying could automatically switch an animal's odor sampling strategy to match its mode of locomotion. Alternatively, as mentioned above, the higher speed of flow-borne relative to substrate-borne locomotion may result in a higher rate of encounters with plume filaments, and thus *require* different sampling strategies. We are not aware of any published experiments designed to discriminate between these two alternative explanations.

Insects are the ideal animal in which to test these ideas, since most both walk and fly. However, only a few studies have challenged flying plume trackers to track pheromone while walking [47, 48], and none were designed to determine if the change in locomotion affected the odor sampling behavior. Our pilot experiments challenging *M. sexta* males to track pheromone plumes while walking have shown tracks that look very different from those generated during flying plume tracking behavior (Figure 4). These tracks are generally oriented due upwind with very few turns and an obvious lack of the zigzag turns that characterize plume tracking in flight.

EFFECTS OF THE OLFATORY ENVIRONMENT ON PLUME TRACKING BEHAVIOR

Environmental turbulence shapes odor plume structure, which then dramatically affects the

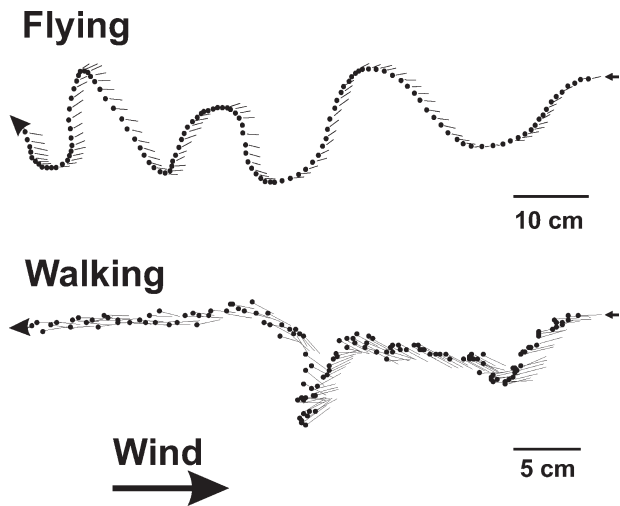


Fig. 4—Tracks of *M. sexta* males flying and walking upwind in pheromone plumes. Moth positions are demoted by black dots marked each 1/30sec. Lines attached to dots are the longitudinal axis of the body. Note lack of stereotyped “zigzagging” in walking moth. Wind speed is 1m/s for both flying and walking moths.

behavior of walking and flying plume trackers [13, 49–55]. Recent collaborations of behavioral biologists and engineers studying fluid dynamics have begun to clarify these important effects [1–3, 53, 56–59]. From this and previous work, we know that odor tracking insects extract information on the concentration of the filaments of the plume [60, 61], the blend of chemicals in the plume [62–65], and the timing of encounters with structures in the plume [5, 7, 8, 66–69].

Recent studies of the behavioral responses of *P. americana* males as they tracked pheromone plumes of different dimensions and turbulence show that these variables affect the behavior of this putative spatial tracker ([14]; Figure 5). Several important points are illustrated in Figure 5. First, without the time-averaged plume envelope, the track in the “point source” plume treatment (Figure 5A) could be interpreted as a walking version of a zigzagging moth track (Figure 4) (thought to use a temporal strategy), as opposed to that of a spatial tracker following a pheromone clean-air edge. This emphasizes that *similarity in performance may not necessarily result from a similar mechanism*. Second, the straightest track is the response to the non-turbulent “ribbon” plume that is narrow enough to allow the animals’ antennae to span its full width. Third, the animal in the wide plume does not track from edge to edge, but walks upwind. Alternatively, this spatial tracker could be using a temporal strategy but few turns are triggered because it encounters, or detects, few odor on-offs in the wide plume. Fourth, animals tracking the most turbulent plume generated

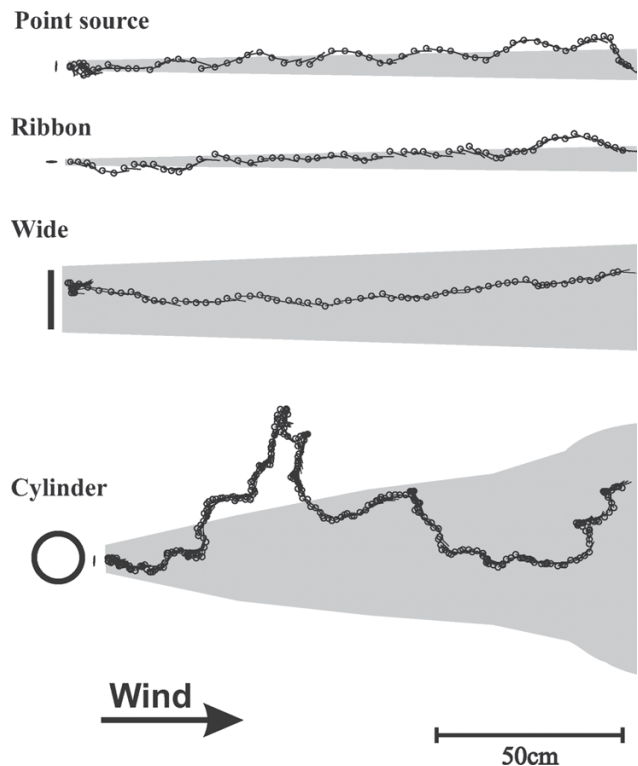


Fig. 5—Walking tracks of *P. americana* males walking upwind in pheromone plumes of different structures. Time-averaged plume in gray.

much more tortuous tracks, sometimes apparently turning downwind away from the source (Figure 5). The large diameter of the cylinder (approximately 7.6 cm) resulted in the generation of large eddies being shed relatively infrequently. Thus, it is possible that the cockroaches were experiencing a decreased frequency of odor encounters and/or the size of the eddies were interpreted as a shifting wind direction, causing them to continuously re-orient to the wind as they tracked.

MODELING CHEMICAL PLUME TRACKING BEHAVIOR

Most simulation and modeling studies aimed at understanding chemo-orientation have focused on responses to diffusion gradients, not tracking a turbulent chemical plume [27, 70]. This is due to the difficulty in simulating the complexity of a turbulent plume. The few plume tracking simulation studies that have been published [71–73] tested biological hypotheses using model trackers based on behavioral and anatomical measurements of specific organisms. An important limitation of this work is that the plumes were typically fixed in space, not dynamically changing and moving downwind like real plumes. Notable exceptions are studies using a dynamic plume video [73] and a realistic dynamic plume model [74].

Our studies of model spatial or temporal trackers responding to simplified time-averaged smoke plumes showed that 90–100% of the spatial trackers located the source, while only 20% of the temporal trackers did, similar to a random walk model. The model plumes in this study were an array of elements whose concentrations were randomly picked from a normal distribution with its peak at the longitudinal midline and concentrations decreasing with distance downwind of the source. The model trackers could move one of three ways: (1) straight ahead, (2) right, or (3) left. *Spatial agents* turned towards the sensor of higher concentration. If the concentrations at both sensors were equal, the agent moved straight forward. Note that, in clean air, inputs to the sensors were also equal. *Temporal agents* turned randomly to the right or left when concentration, summed across both sensors, decreased. If the concentration stayed the same or increased, the agent moved straight forward. Agents were “released” at starting locations inside the downwind end of the plume. They moved forward according to their strategy until they reach the source or “upwind” edge of the wind tunnel.

When our simple spatial and temporal trackers were challenged with more realistic turbulent model plumes their ability to locate the source decreased (35% and 2.6% respectively), but recovered when challenged with time-averaged plumes (100% and 8% respectively). Neither strategy’s success was affected by tripling the sensors’ lengths if the sensors were directed straight ahead. However, when the antennae were oriented 45° to either side of midline, performance of the spatial strategy improved to nearly 100% in single plumes. Varying antennal posture had no effect on success of the temporal agent. They appeared to perform a random walk while encountering plumes. This suggests that a temporal agent that reverses its direction on concentration decrease rather than turning randomly could be more successful. In the above experiments, each strategy was run with 99 starting locations in each of the 100 single plumes and in the “time-average” plume.

Chemical plume tracking has been easier to model using mobile robots because the artificial agents track real turbulent plumes, not simulations [75–78]. Much of this work has aimed to fabricate odor tracking robots for commercial use [77, 79–82]. However, others have modeled their robots after biological plume trackers to test biological hypotheses [75, 76, 83]. Using existing biological knowledge, these mobile robots model the dimensions and performance of known animals, and experimental results are used to inform the design and interpretation of subsequent behavioral or neurophysiological studies of the biological track-

ers. Results from these robotic experiments [75, 76] have caused reexamination of our previous understanding of odor tracking. For example, robot experiments suggest that efficient plume tracking in lobsters may require flow information because robots using chemo-orientation perform poorly [76]. Another study of a robot that alone can track like a flying moth suggested that resetting an internal turning response aligned the tracker with the plume centerline [75].

Recently we have begun to use computer simulation models and mobile robots to test hypotheses generated by our behavioral experiments. Initial simulation studies were aimed at testing long-standing hypotheses about the control rules underlying the plume tracking behavior of flying moths [71]. The simulations’ control algorithms were constructed from those posed in published biological papers and the variables and parameters of the models were set by values measured from moths tracking plumes in laboratory wind tunnels [71, 72]. The results of these simulation experiments were enlightening and caused a continuing reexamination of the biological hypotheses. In this case, as in the case of any simulation study aimed at elucidating an existing biological system, the requirement to express verbal descriptions and hypotheses as mathematical expressions revealed how much was really unknown about the biological system.

Our robots are challenged to track plumes in the same wind tunnels used for insect odor tracking experiments or those built to resemble them [78, 84]. Our previous simulation experiments and all robot studies are quantified using the same methods we use in our insect plume tracking experiments [32, 38, 85]. Thus we can make direct comparisons between animal and robot plume tracking behaviors. Our first robot experiments were performed with a small wheeled robot with custom fabricated plume and wind detecting systems (Figure 6). This robot was approximately the same size as the wingspan of the large moth that we study (approximately 5 cm diam.) and was challenged to track plumes in the same laboratory environment used in our insect navigation studies. We used ionized air as a model of a chemical plume because the ion generator makes a plume similar in structure to a chemical plume [1] and the detectors have a temporal response similar to the insects’ odor detectors. Even though the control algorithms used by the robot to perform the plume tracking task were much simpler than those suspected to underlie animal navigation, the robot performed well in a simplified laboratory environment. Our initial algorithms demonstrated a clear trade-off between the speed of plume tracking behavior and the probability of locating the source. Some settings resulted in fast plume tracking but

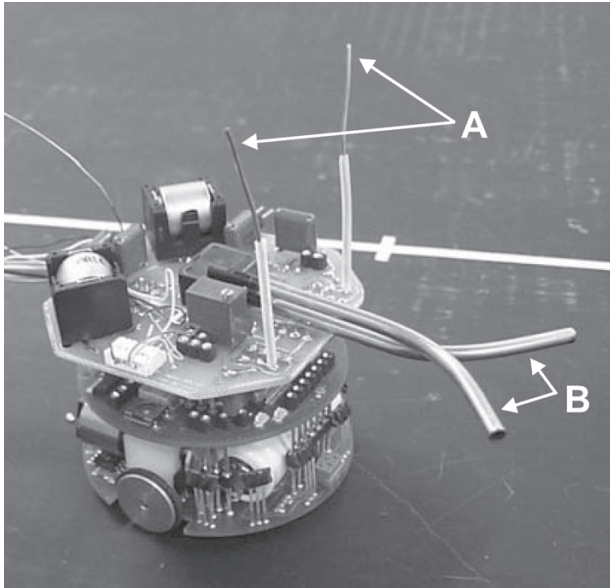


Fig. 6—A commercially-available khepera robot with a custom designed and fabricated sensor turret mounted on top. (A) Bilaterally-symmetrical ion detectors used as plume detectors. (B) Paired inputs to a MEMS differential pressure transducer which served as the wind direction sensor.

low success at locating the source, while others resulted in very slow plume tracking leading to nearly 100% success at locating the odor source. Another algorithm had its turning and steering settings modulated by the local odor concentration in a manner similar to that observed from insects; it achieved rapid plume tracking and was highly successful at locating the source.

Our most recent robot has been constructed to move in a way that will simulate a flying moth tracking a plume through a laboratory wind tunnel [84]. It is comprised of a Cartesian robotic positioning system mounted in the downwind cross-section of a wind tunnel built to the same dimensions as the tunnel used in the insect navigation research. The sensors are mounted on the positioning system which provides movement in altitude and lateral position, and a conveyor belt controls the position of the plume source (ionized air as with the smaller wheeled robot) (Figure 7). This robot has been named “Robomoth” because it is meant to simulate moth control algorithms and flight trajectories. Eventually Robomoth will have a suite of sensors similar to the moth including: visual system, wind detecting systems, and odor detection system. Currently the only sensors functioning are the ion detecting antennae making up the olfactory system. However, even with a simplified sensor suite Robomoth can be a useful tool, and has already generated useful data that has led us to reconsider some of our ideas about insect flight orientation. These realizations have and will continue to lead to insect odor tracking experiments aimed at

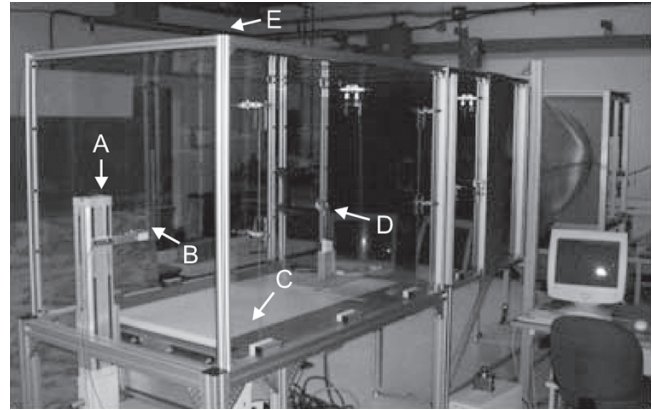


Fig. 7—A custom fabricated robotic system for testing biological control algorithms for navigating odor plumes in wind (AKA Robomoth). (A) Vertical translator controlling the altitude of the “flight” trajectory for the robotic positioning system (horizontal translator is not visible). (B) Sensor platform of Robomoth. (C) Conveyor belt controlling the “upwind/downwind” movement of the “flight” trajectory. (D) Ion source mounted on the conveyor belt which is moved closer to the sensor platform as Robomoth “flies” upwind. (E) Open throat-open loop wind tunnel that provides the wind for Robomoth. (Note the fan and smoothing box to the right in this image.) From [84].

understanding the biological system. It is through this reiterative biology-to-robot-to-biology cycle that we aim to make rapid progress toward understanding how biological systems successfully achieve the complex task of navigating through a complex environment to locate an odor source. Of course we expect that an additional outcome of this research cycle will be an autopilot for an autonomous odor tracking flying vehicle.

SUMMARY

To summarize this brief introduction to odor-guided navigation in insects and mobile robots:

1. Successful navigation of odor plumes to their sources requires information on the magnitude and direction of the wind as well as the odor.
2. During plume tracking in flight, information on wind speed and direction is acquired via the visual system.
3. During plume tracking while walking, wind information may be provided exclusively via mechanosensory structures.
4. In both flying and walking plume tracking, the structure of the odor plume modulates tracking behavior.

Furthermore, the integration of multiple approaches including the use of robots to test hypothetical biological tracking algorithms has led to significant progress in the understanding of odor-guided navigation. To date our focus has been on the use of the required odor and wind sensors, however, navigation through any real environment

will require the integration of multiple additional sensors to serve additional tasks such as obstacle avoidance. Future research will focus on iterative cycles of biology-to-robot-to-biology experimentation and increasing the complexity of the environment and the complexity of the sensory information available to our robotic odor trackers.

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