Integration of flow and odor orientation enable plume tracking behavior in walking cockroaches.

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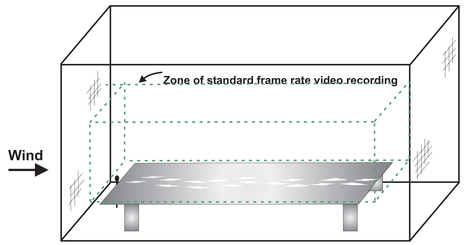
INTRODUCTION

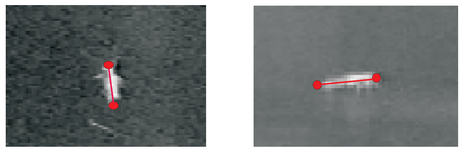
Animals tracking odor plumes to locate important resources are activated to track by the presence of odor, and typically steer their path toward the source using directional cues provided by the flowing air, or water, bearing the odor. To study how these two crucial sensory inputs interact to support this behavior, we challenged virgin male cockroaches, *Periplaneta americana*, to track plumes of airborne female sex-attractant pheromone. We video-recorded and analyzed their responses as the odor plume and wind were experimentally manipulated during plume tracking behavior.

To determine whether a memory of a previously experienced wind direction could provide the directional information necessary to locate an odor source, we challenged males to track plumes in an arena with no wind to provide directional cues after pre-exposing them to: 1) wind plus pheromone, 2) wind only, and 3) neither wind **nor** pheromone. The males' responses to these treatments were compared to males tracking a pheromone plume in continuous wind.

Controlling wind speed and odor presentation enables study of multi-sensory control of navigation.

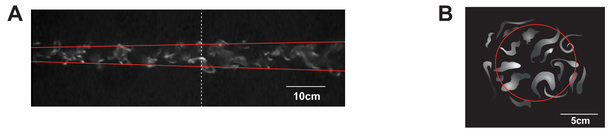


The roaches tracked pheromone plumes on a raised aluminum floor in a wind tunnel with a 25 cm/s wind speed. In this diagram wind flows from left to right with the pheromone source positioned at the upwind end. The intermittent pheromone plume is depicted as irregular white patches.



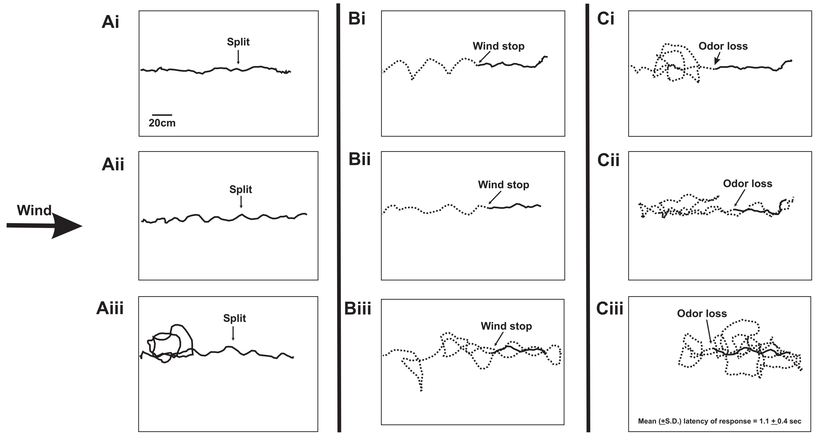
The position of the roach's body was digitized using Motus motion analysis software (Vicon Peak) to measure the movements of the body and path trajectories. We used this data to calculate our desired angles and measurements.

Smoke visualizations show that the experimenters' and odor-trackers' perspectives are quite different.



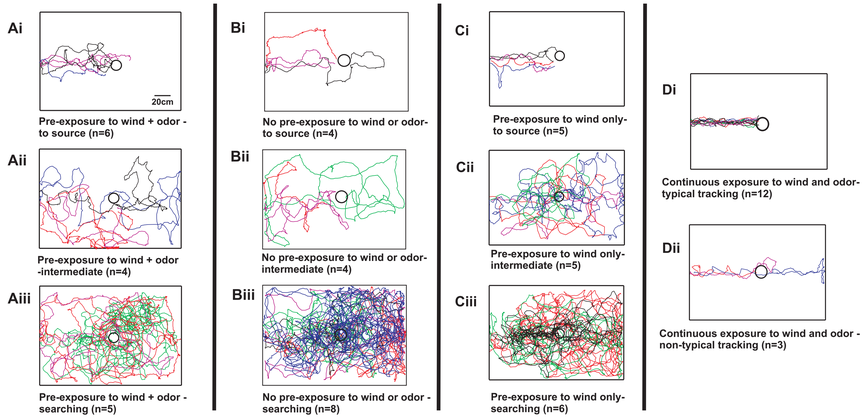
(A) A single field from a video recording of a $TiCl_4$ smoke plume in a laboratory wind tunnel viewed from above. The time averaged plume boundaries are represented by red lines running from the upwind to the downwind side of the image (i.e., from left to right). (B) A schematic approximation illustrating the "tracker's eye view" of the smoke plume visualization depicted in (A). The red circle represents an extension of the time-averaged plume boundaries in (A) onto this cross section.

Cockroaches react differently to the cessation of wind vs. the cessation of odor.



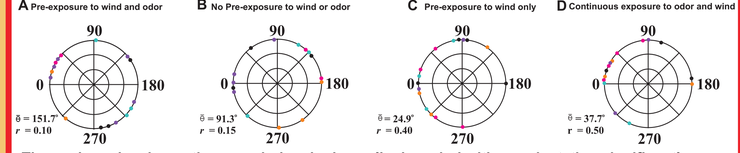
Examples of a typical track (Aii, Bii & Cii) together with the simple (Ai, Bi & Ci) and complex (Aiii, Biii & Ciii) extreme responses of cockroaches tracking a pheromone plume upwind during continuous odor and wind (column A), and response to loss of wind (column B) and odor (column C). In columns B and C the solid line depicts behavior when wind and odor are present, and the dotted line depicts behavior after the loss of wind (B) or odor (C). The point of wind (B) or odor (C) loss is indicated by an arrow. In column A the arrow delineates a length of track corresponding to the average pre-wind stop and pre odor loss tracks. This was to facilitate statistical comparison to wind stop and odor loss treatments.

Pre-exposure to different combinations of wind and odor does not support rapid plume tracking and source location.



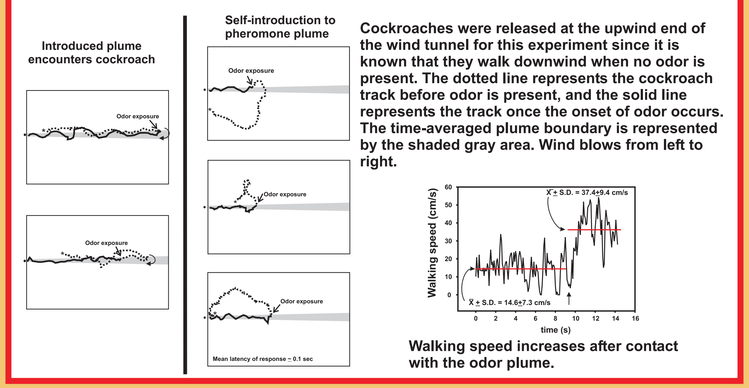
Odor tracks of each cockroach pre-exposed to different combinations of wind and odor as seen from above. The rectangle represents the experimental arena with the odor source located on the center of the left (upwind) side. The release cage is shown as a black circle in the center of the arena. Wind blows from left to right. Each color represents different individuals on different experimental days. Please note that in all cases the cockroaches eventually locate the odor source.

Walking direction is random except when exposed to continuous odor and wind.



The cockroaches in continuous wind and odor walked upwind with an orientation significantly different from random. In this figure 0° is due upwind. Each dot represents an individual roach's take off direction on different experimental days (represented by different colors). Theta represents the mean take off direction and *r* is a measure of variance around Theta.

Onset of odor causes cockroaches to reverse their orientation to wind and increase walking speed.



Cockroaches were released at the upwind end of the wind tunnel for this experiment since it is known that they walk downwind when no odor is present. The dotted line represents the cockroach track before odor is present, and the solid line represents the track once the onset of odor occurs. The time-averaged plume boundary is represented by the shaded gray area. Wind blows from left to right.

Walking speed increases after contact with the odor plume.

Summary

- Continuous exposure to wind and odor is required for rapid source location. When the wind is stopped during plume tracking, cockroaches continue to track the plume by maintaining contact with the plume and continuing to walk in the pre-wind stop direction. Loss of odor during tracking triggers looping turns with variable orientation to the wind that can be interpreted as a local search.
- Pre-exposure to combinations of wind and odor caused the cockroaches to search longer for the odor source, but all eventually located it. Take off direction of these cockroaches was not significantly different from random, except when the cockroaches were continuously exposed to wind and odor.
- Encountering an attractive odor while walking in odor-free wind causes cockroaches to reverse their walking direction and increase their speed.

Future Directions

- Are turning directions always determined by spatial comparisons between the two antennae?
- How are the orientation to wind and odor integrated to result in a controlled behavioral response?

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