

Crossmodal Visual Input for Odor Tracking during Fly Flight

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Summary

Flies generate robust and high-performance olfactory and visual behaviors. Adult fruit flies can distinguish small differences in odor concentration across antennae separated by less than 1 mm [1], and a single olfactory sensory neuron is sufficient for near-normal gradient tracking in larvae [2]. During flight a male housefly chasing a female executes a corrective turn within 40 ms after a course deviation by its target [3]. The challenges imposed by flying apparently benefit from the tight integration of unimodal sensory cues. Crossmodal interactions reduce the discrimination threshold for unimodal memory retrieval by enhancing stimulus salience [4], and dynamic crossmodal processing is required for odor search during free flight because animals fail to locate an odor source in the absence of rich visual feedback [5]. The visual requirements for odor localization are unknown. We tethered a hungry fly in a magnetic field, allowing it to yaw freely, presented odor plumes, and examined how visual cues influence odor tracking. We show that flies are unable to use a small-field object or landmark to assist plume tracking, whereas odor activates wide-field optomotor course control to enable accurate orientation toward an attractive food odor.

Results and Discussion

We investigated the motor control of active plume tracking by adapting a magnetic tether system [6] into a “virtual plume simulator” in which a fly is free to steer into and out of a spatially discrete plume of vinegar odor while simultaneously receiving visual feedback from a stationary wraparound electronic display (Figure 1A). Flight behavior on the magnetic tether, like in free flight, is characterized by segments of straight flight interspersed with transient “spikes” in angular velocity called “body saccades” for their functional analogy with our own gaze-stabilizing eye movements [7–9]. Within a visual arena composed of equally spaced, high-contrast vertical stripes, a pattern that generates strong, spatially homogeneous optic-flow signals when the animal rotates on its pivot, we periodically switched the vinegar plume between 0° and 180° positions in the circular arena and tracked the fly’s heading. Under these conditions, the animal periodically encounters the plume by steering into it. Upon plume contact, identified by the animal’s heading with respect to the odor port, the interval between saccades increases, whereas subsequently deviating from the plume results in a return of the typical saccadic rhythm (Figure 1B). Thus by presenting only the water vapor control, flies iterate saccades with little

apparent preferred orientation, resulting in an even distribution of heading within the arena (Figure 1C, left). By contrast, encountering an odor plume results in stabilized flight heading directed toward the plume at either side of the arena (Figure 1C). These results confirm that the two odor plumes were the most attractive features of the arena, that both locations could reliably and reversibly elicit stable odor tracking, and that the plume itself is narrow, as reflected by the 18° width of the heading histograms at half-maximum (Figure 1C).

When compared to the high-contrast panorama in the absence of an odor plume, the visually uniform arena itself elicits smaller angle saccades, with shorter intervals between them (Figures 1D and 1E). In an odor plume, these two responses would work against one another for stable tracking; smaller amplitude saccades would keep the animal close to the plume, but shorter saccade intervals (increased rate) would not. Upon encountering the odor plume within the high-contrast visual panorama, flies show decreased saccade amplitude and increased intersaccade interval (ISI) in comparison to the same flight trajectories oriented outside the plume. These two responses combine to facilitate plume tracking because saccades that would move the fly out of the plume are fewer and smaller. Under uniform featureless visual conditions, there are no such changes in saccade frequency or amplitude upon plume contact, indicating a crossmodal influence on saccade motor commands (Figures 1D and 1E). Furthermore, only within the high-contrast visual treatment are saccade amplitude and ISI outside the attractive odor plume lower than during the no-odor experiment. It would appear, therefore, that like the casting dynamics of free flight [10], saccade amplitude and ISI are influenced both by plume acquisition and subsequent plume loss but in a visual-context-dependent manner. It seems reasonable to postulate that visual feedback provides a directional cue that enables a fly to correct a deviation from the plume during a saccade.

Once initiated, saccade dynamics are coordinated entirely by mechanosensory feedback [11], whereas flying straight and avoiding collisions require well-studied optomotor equilibrium reflexes [12]. Here, we show that saccades in the odor plume are fewer and smaller, but not altogether absent. Is the visually dependent quantitative reduction in saccade rate and amplitude fully sufficient to enable stable plume tracking, or do odor cues activate optomotor responses in order to stabilize flight heading between saccades? There is no a priori reason to suspect the latter, particularly because a walking fruit fly is capable of orienting toward a static concentration gradient delivered across the antennae in the absence of visual cues [1]. Yet, for accurate odor tracking during free flight, *Drosophila* require visual feedback from the lateral panorama [5].

To address this issue, we measured the accuracy of plume tracking for animals exposed to a sequence of different visual conditions. Taking advantage of a well-known and powerful object-orientation reflex in which flies actively fixate a high-contrast, vertical stripe within their forward field of view [13, 14], we slowly oscillated a narrow stripe to visually “drag” flies into the odor plume at the 180° arena position before instantly replacing the stripe with a stationary visual panorama.

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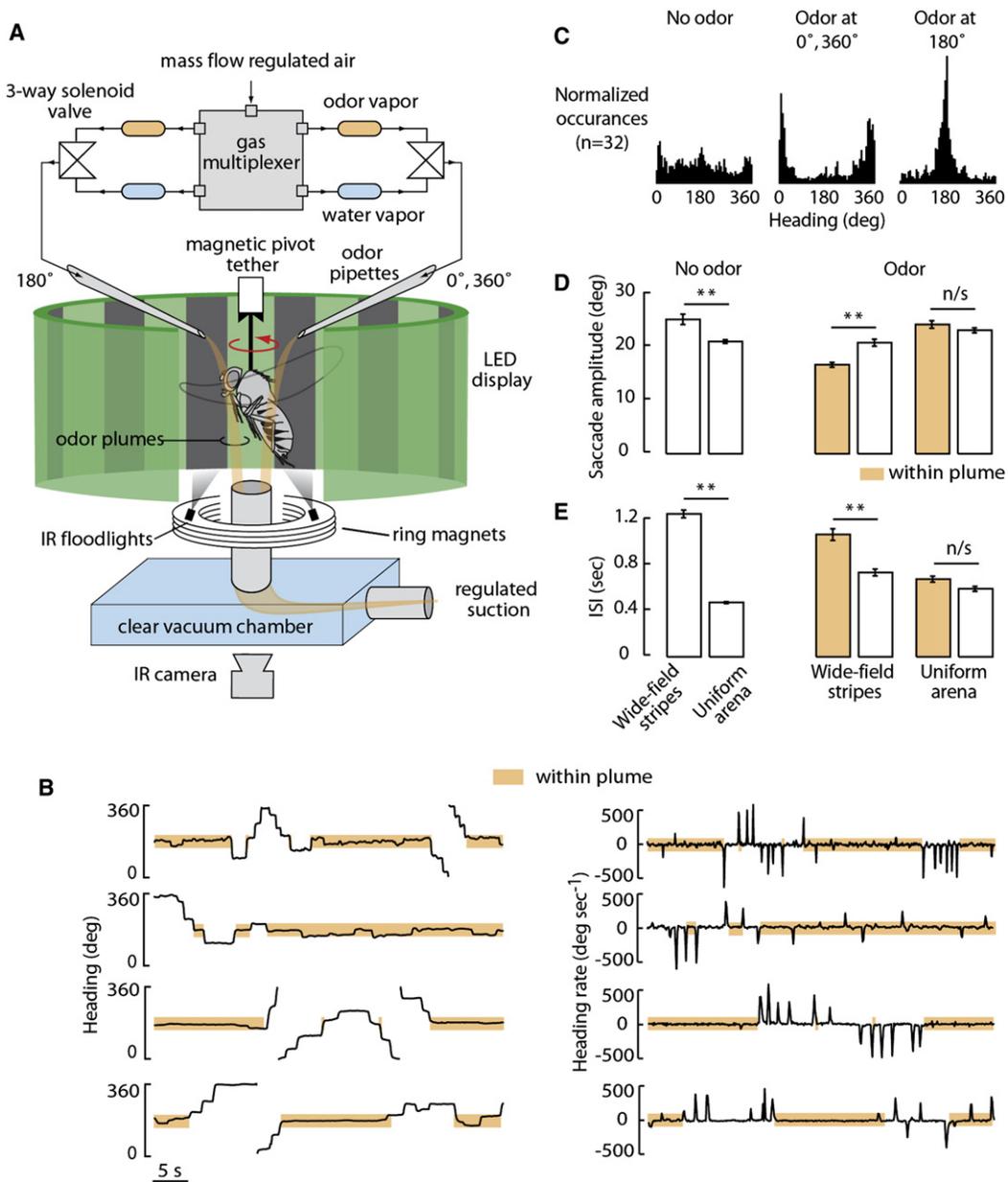


Figure 1. Magnetic Tether Flight Arena and Active Odor Plume Tracking

(A) A fly glued to a steel pin is suspended on a magnetic pivot, free to yaw. Visual stimuli are displayed on a computer-controlled, circular LED array. Air is diverted through solenoid valves, bubbled through reservoirs of water and apple cider vinegar, and delivered in narrow, laminar plumes drawn downward into a vacuum chamber. The fly's body is illuminated with infrared light and is tracked with infrared video.

(B) Left: Shown are four exemplar flight trajectories illustrating variation in heading within the circular arena. In each trace, vinegar odor was continuously emanating from the 180° position and water vapor from the 360° position. Right: for the same heading trajectories, the rate of change of heading reveals transients representing varying-amplitude body saccades. Orange shading indicates segments in which the fly was oriented directly into the odor plume defined by the $\pm 20^\circ$ fraction of the arena surrounding the plume location.

(C) Distribution of heading for flies flown in each of three odor treatments for 30 s shows that flies track attractive odor stimuli at both sides of the arena. The visual stimulus consisted of a high-contrast, evenly striped panorama. Bin width is 6° , $n = 32$ flies.

(D and E) In (D), graphs illustrate the mean saccade amplitudes for experiments in which the flies received only the water vapor control (no odor) and for experiments in which the vinegar vapor was presented at 180° and water vapor at 0°. (E) Graphs show mean intersaccade interval (ISI). For (D) and (E), $n = 39$ flies, error bars represent SEM; Paired t test, $**p < 0.01$. Saccades were programmatically identified by fluctuations in angular velocity greater than 1 SD from the mean, a lower threshold than has been used in other studies [9, 11].

Therefore, for each experimental treatment, animals started from the same heading within either the water or vinegar plume and were subsequently exposed to either a high-contrast pattern of evenly spaced stripes or a featureless grayscale panorama of identical mean luminance, which provides light

levels necessary to sustain active flight but provides minimal visual motion cues. To quantify the accuracy of plume tracking for each flight trajectory, we derived the cumulative deviation from the odor plume by subtracting 180 from the heading values, taking the absolute value and integrating it over time.

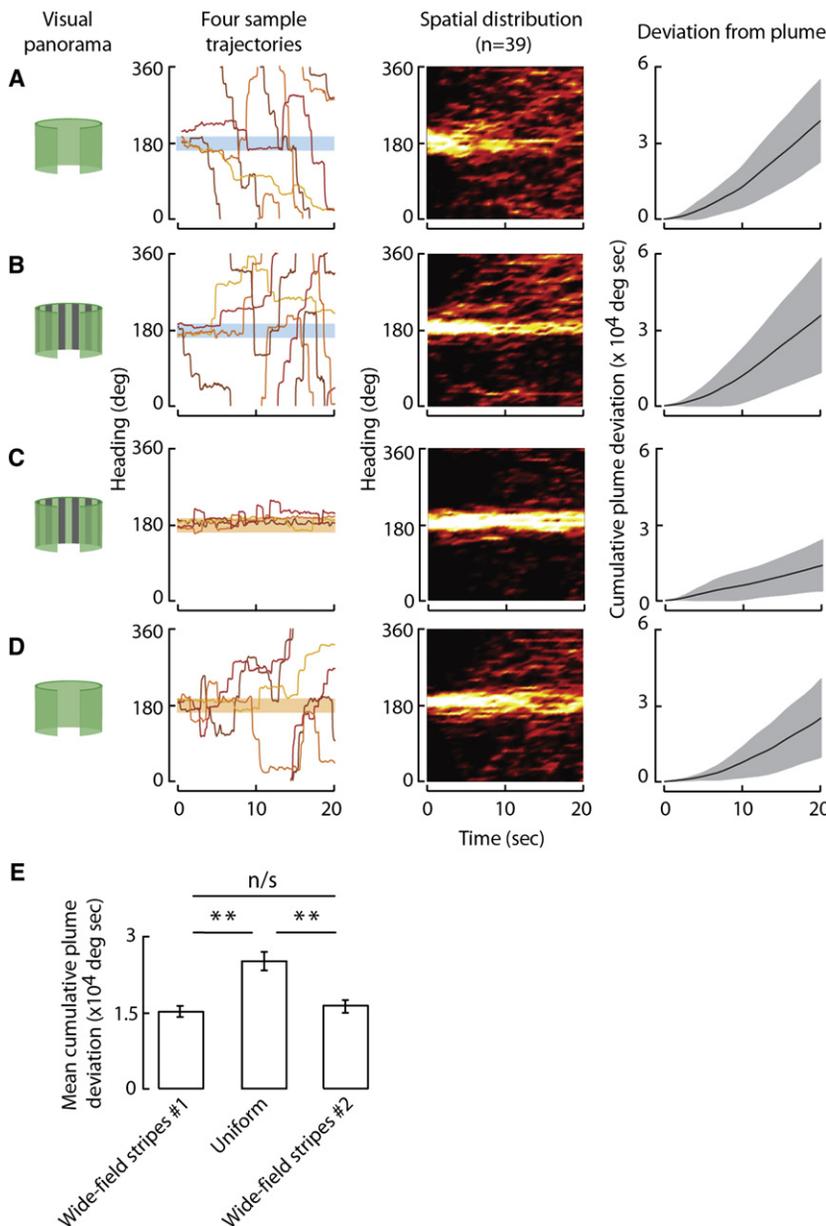


Figure 2. Influence of Wide-Field Panoramic Visual Feedback on Active Odor-Plume Tracking

Each fly was drawn into the plume (vinegar or water vapor control) with an oscillating vertical stripe, and then the visual scene was instantaneously switched to either a wide-field, high-contrast striped pattern or a uniform grayscale pattern of equal mean luminance. Each column indicates (1) the visual stimulus, (2) four sample trajectories colored for visual distinction, (3) mean trajectory distribution with the relative probability indicated with pseudo-color, (4) a measure of how well flies track the odor plume—the mean cumulative deviation from the 180° plume position (i.e., line integral of the absolute value of heading minus 180) such that smaller values indicate better plume tracking. The mean and SD are represented by the black line and gray envelope, respectively. Each fly was presented once, and only once, with all stimulus conditions that included (A) uniform visual background and water vapor plume (indicated with blue shading), (B) high-contrast visual background and water vapor plume (indicated with orange shading), (C) high-contrast visual background and odor plume (indicated with blue shading), and (D) uniform visual background and odor plume. (E) To “rescue” the effect of diminished visual feedback, flies were sequentially flown for 20 s in the high-contrast stripe treatment, the uniform treatment, and a second high-contrast treatment while the vinegar plume was present continuously. $n = 39$ flies; Paired t test, $**p < 0.01$; Error bars represent SEM.

The resultant cumulative time series has units of degree seconds and represents the flies’ ability to stabilize the plume such that low values represent accurate plume tracking, and high values correspond to orientation “error”—turning away from the plume into other regions of the arena. Note that cumulative deviation generally cannot remain at zero because flies continuously make fine-scale, back-and-forth adjustments to their heading, which results in an ever increasing cumulative deviation from the 180° arena position. Therefore, by design, mean cumulative plume deviation is a conservative estimate of a fly’s ability to actively track a plume.

For the water vapor plume set against the uniform grayscale visual panorama, flies executed the usual rhythm of saccades and thus deviated from the plume within a few seconds after the start of the trial (Figure 2A). Switching the visual panorama to high-contrast stripes did not significantly change flies’ cumulative plume deviation (Figure 2B). Predictably, for the water vapor plume and both visual treatments, flies oriented randomly throughout the arena. However, upon activating

the odor plume against the high-contrast stripe background, the same animals remained tightly centered within the plume for the duration of the trial, resulting in 75% reduction in cumulative plume deviation (Figure 2C). Remarkably, replacing the high-contrast visual scene with the featureless uniform panorama resulted in decreased tracking accuracy because animals quickly deviated from the odor plume in a manner similar to the no-odor control (Figure 2D and Movie S1 available online). The cumulative plume deviation was not significantly different between the uniform

visual arena with odor and the striped arena without odor, indicating that in the absence of rich visual feedback the flies essentially behave as if there were no odor, highlighting the crossmodal requirements for odor tracking.

We further examined the visual influence on odor-tracking accuracy by activating the odor plume continuously while presenting a sequence of three visual treatments including high-contrast stripes, uniform grayscale, and a second high-contrast treatment. Each fly therefore started within the vinegar plume and was exposed to the three visual stimuli at 20 s intervals. When the striped panorama appeared at the start of the trial, flies maintained their heading into the plume. But once the stripes disappeared, the flies steered out of the plume and began generating saccades. Whereas occasionally they reencounter the plume within the uniform visual panorama, they generally are unable to remain there until the high-contrast pattern reappears, at which point accurate plume tracking resumes. Mean cumulative plume deviation increased significantly between the first high-contrast treatment and the

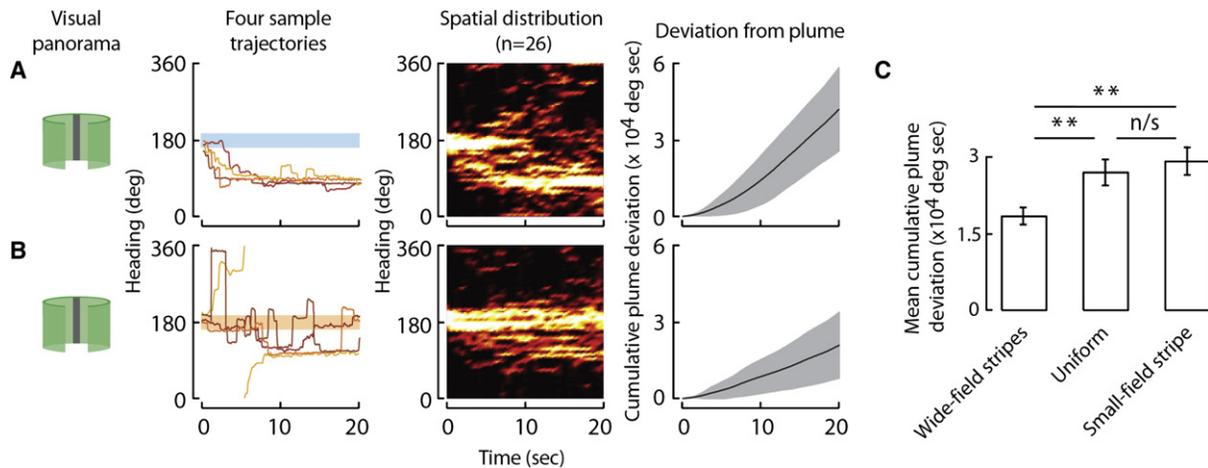


Figure 3. Influence of a Small-Field Object Cue on Active Odor-Plume Tracking

Each fly was visually drawn into the plume as described in Figure 2. Visual stimuli consisted of a single, 30° wide stripe located 90° from the plume. Data are plotted as described in Figure 2. Each fly was presented once, and only once, with all stimulus conditions, which included: (A) lateral stripe and water vapor plume (indicated with blue shading) and (B) lateral stripe and odor plume (indicated with orange shading). (C) Graphs illustrate the effects of three visual treatments on minimizing cumulative plume deviation (n = 26 flies; Paired t test, **p < 0.01). Error bars represent SEM.

uniform arena and then recovered to the initial value for the second high-contrast treatment (Figure 2E).

For the visual manipulation experiments, the order of experimental treatments followed a predetermined sequence and each fly was presented with the sequence once and only once. To examine whether treatment order influenced the results, we repeated the entire experiment with a random block design in which the set of visual and olfactory treatments were randomly shuffled for each individual fly. The randomized experiment disclosed the same results as the ordered experiment; the high-contrast visual panorama significantly reduces the cumulative deviation from the odor plume by comparison to a uniform grayscale panorama (data not shown, n = 26 flies, paired t test, p < 0.02).

Anatomical, physiological, and behavioral analyses suggest that the fly optomotor system is segregated into two parallel channels—one processes wide-field visual motion and the other processes small-field visual and object motion [15–17]. It is thought that these two separate systems contribute to figure-ground discrimination and enable animals to see and track moving objects against a cluttered visual background [18]. Additionally, active stripe fixation during flight may represent the fly’s attempt to approach a suitable landing site, such as a plant stalk. Another remarkable use of small-field vision is demonstrated by home-base foragers, such as ants, that use objects located some distance from food resources or nests as landmarks to navigate return paths to those sites [19]. Here, we show that crossmodal feedback generated by the fly’s movement within a homogeneous wide-field visual landscape enables active plume tracking (Figure 2E). Is the synergistic crossmodal influence on odor tracking specific to wide-field visual signals, or can flies also use small-field visual cues, such as spatial landmarks, to maintain their heading in an odor plume? To examine this idea, we subjected flies to a stationary vertical stripe offset 90° from the odor plume. Flies starting within a control water plume veered out of the plume within several seconds and instead fixated the visual object, thus resulting in a rapidly increasing mean cumulative plume deviation (Figure 3A). Starting a new trial with the vinegar-odor stimulus, the same flies showed a stronger tendency to

stay in or near the plume, resulting in a roughly 50% reduction in cumulative plume deviation (Figure 3B). At first glance, it might appear that the small-field stripe enhances odor tracking by comparison to the no-odor control. However, the critical question is whether a laterally displaced small-field object reduces the cumulative plume deviation by comparison to a uniform panorama, and it does not. The mean cumulative plume deviation for the small-field stripe is equivalent to the measurement for the uniform grayscale panorama (Figure 3C). Accurate plume tracking requires wide-field visual input.

Unlike the propagation of visual or acoustic stimuli, an olfactory signal contains no intrinsic directional information. Therefore, animals often rely on ambient wind cues to determine the route to an odor source. Odor tracking by upwind flight requires visual feedback generated by background motion because an animal cannot easily distinguish ambient wind direction from self-induced airflow during flight [20]. As such, in the absence of wind cues, tethered *Drosophila* provided with a visual stimulus analogous to being carried downwind steer so as to maintain an upwind heading [6, 21]. This response persists whether the animal views the moving ground below or the visual landscape laterally [22]. In addition to directional control, when faced with headwinds, insects such as flies, beetles, bees, and moths regulate their airspeed and altitude by the use of visual cues [23–27], the combination of which enables accurate navigation of a female pheromone plume by a male moth [28–30]. In previous free-flight experiments, it has not been possible to determine whether optomotor stabilization is triggered directly by odor cues or indirectly by wind-driven ground motion. Here, we show that rotational stabilization reflexes are directly activated by odor cues independent of ambient wind cues.

The crossmodal influence of visual feedback on odor tracking in flies provides insight into how complex behaviors are controlled within environments containing nondirectional, weak, noisy, or subthreshold sensory stimuli. Fruit flies have 700 times lower visual spatial resolution than humans [31], and they have five times fewer olfactory receptor types [32]. Yet their ability to find smelly things in visual landscapes as diverse as forests, deserts, and backyard patios would

suggest behavioral performance greater than might be predicted by the sum of the salient sensory inputs. The results presented here show that odor signals activate powerful visual stabilization reflexes to accurately track an appetitive odor plume. The requisite visual feedback cues emerge from the wide-field visual-processing centers of the brain, not the small-field object-tracking centers, thus hinting at possible neuroanatomical substrates. Furthermore, the functional interaction of crossmodal integration for plume tracking in flies is reminiscent of multisensory enhancement (MSE) exhibited by single neurons within the cat superior colliculus [33]. Here, neurons with overlapping receptive fields generally obey a principle known as “inverse effectiveness,” whereby smaller, modality-specific responses are associated with larger, multisensory responses. As such, MSE results in cell excitability that is greater than the mathematical sum of the individual inputs, especially when unimodal input is weak. The superior colliculus forms a tissue map registering spatial information from two sensory modalities. It seems unlikely that visual-olfactory integration in the fly brain occurs with a structurally analogous system but, rather, a functionally analogous one. In gypsy moths, spiking responses within visually selective premotor interneurons are enhanced by sex pheromones [34]. Similarly, the rattlesnake optic tectum contains individual neurons that exhibit nonlinear crossmodal enhancement of visual and thermal responses, presumably to guide prey capture in near darkness [35]. It would appear that crossmodal integration at the behavioral and cellular level represents a functional adaptation for distinguishing and responding to critically important features of a complex sensory environment.

Experimental Procedures

Detailed descriptions of fly preparation, magnetic tether apparatus, video tracking system, and electronic LED visual display are available elsewhere [6, 9, 22]. The infrared Firewire camera used in this study digitized images at 30 Hz (Fire-i). Images were acquired and analyzed by using custom software routines written in MATLAB (The Mathworks, Inc). The visual display used here fully surrounded the fly in azimuth and subtended 60° in zenith. The stationary wide-field grating had a spatial wavelength of 30° and a periodic contrast of 93% at roughly 70 cd m⁻². The small-field vertical stripe was 30° wide. To visually “drag” the flies into the odor plume, the stripe was oscillated about the odor port ±22.5° at 1.6 Hz for 8.5 s.

We used adult female *Drosophila melanogaster* (Meigen), 4–6 days post-eclosion and starved on water for 4–6 hr. The olfactory stimulation system was engineered to accomplish two objectives: deliver odor plumes at the smallest possible flow rate in order to minimize wind cues and deliver narrow plumes such that the animal could easily lose contact and reacquire the odor plume by turning back and forth, thus generating spatial and temporal variations in stimulus exposure—as is the case in free flight [10]. The end of a 4 mm diameter glass tube was mounted 4 mm beneath the fly and was connected to a clear acrylic chamber through which the video camera imaged the fly from below. Room air was drawn downward over the fly through the tube and into the chamber at a rate of 13 l/min (Cole Parmer Instruments). The odor-control system was modified for lower mass flow rates after one described previously [36]. Briefly, odor cues were delivered by a nested “double-barrel” pair of 20G stainless-steel hypodermic tubes (Small Parts, Inc.). The regulated mass flow rate through the system was at 7 ml/min (MFC-4, Sable Systems International). Air was delivered continuously, and one of the paired steel barrels carried saturated water vapor whereas the other carried saturated vinegar vapor, switchable from a gas multiplexer (Sable Systems International). The outlets of the paired barrels were sealed within a plastic pipette tip to generate a single gas plume. The pipettes were mounted on micromanipulators (Siskiyou, Inc.) and positioned 4 mm dorsal and 3 mm anterior to the fly’s head. A prerequisite for analyzing the visual influence on odor tracking is that the odorant used is both attractive and of sufficient concentration to elicit persistent stable tracking. We therefore chose apple cider vinegar, a natural attractant for *Drosophila melanogaster* (“vinegar flies”). In preliminary experiments,

we systematically varied odor concentration and found that 85% vinegar elicited robust and repeatable orientation responses.

We confirmed the structure of the odor plumes by passing opaque “smoke” composed of TiO₂ and HCl (volatilized TiCl₄) through the system and capturing images with video while a fly was suspended in the arena. The resultant plume was roughly the diameter of a fly’s head and flowed evenly and smoothly downward into the vacuum chamber with rapid onset and termination. The most convincing test for the spatiotemporal control and consistency of the odor plume is the fly orientation responses themselves. The spatial restriction of the plume is evident in the width of the orientation histogram which at half-maximum is 18° (Figure 1C). We frequently replaced the odor-exposed Teflon tubing and delivery ports to minimize the adsorption of odorants within the apparatus. Yet, the no-odor orientation histogram showed subtle peaks at 0° and 180°, indicating that either (1) flies linger at the plume even after the odor cues are completely terminated, (2) residual odorant takes a short time to clear from the delivery system, or (3) flies are mildly engaged by the water plume or the subtle wind cue. However, the lack of significant anemotaxis, which during free flight accompanies very low wind speed [10, 37], suggests that the apparatus does not produce an overt wind stimulus. Taken together, these results show that the attractive odor is the most salient sensory feature in the arena.

Supplemental Data

One movie is available at <http://www.current-biology.com/cgi/content/full/18/4/270/DC1/>.

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