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# Extracting spatial information from temporal odor patterns: insights from insects

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Extracting spatial information from temporal stimulus patterns is essential for sensory perception (e.g. visual motion direction detection or concurrent sound segregation), but this process remains understudied in olfaction. Animals rely on olfaction to locate resources and dangers. In open environments, where odors are dispersed by turbulent wind, detection of wind direction seems crucial for odor source localization. However, recent studies showed that insects can extract spatial information from the odor stimulus itself, independently from sensing wind direction. This remarkable ability is achieved by detecting the fine-scale temporal pattern of odor encounters, which contains information about the location and size of an odor source, and the distance between different odor sources.

#### Addresses

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#### Introduction

In open, aerial environments where odor plumes disperse by turbulent diffusion [1], the release of odorants<sup>1</sup> into the air results in a plume that extends and widens downstream of the source (Figure 1a) [2–7]. Large-scale air movements cause the plume to meander, and smallerscale turbulent air movements break up the plume into discrete filaments. As a result, an animal located downstream of the source encounters odor packets of high odorant concentration interspersed with periods of zero or subthreshold concentration (blanks) (Figure 1b) [2]. While the average odorant concentration of odor packets decreases with increasing distance from the source, the concentrations between individual packets vary greatly [2]. Estimating the distance to the source from odor concentration, therefore, requires averaging over multiple packets. This takes time and is less reliable than in low-or no-wind conditions where molecular diffusion creates smooth odor concentration gradients that instantaneously point toward the source. Far from the source, detecting the timing of odor packets predicts distance better than detecting odor concentration [8].

Research has repeatedly shown that, in turbulent environments, surging upwind upon detecting an odor and casting crosswind otherwise is a fundamental strategy for reaching an odor source [9]. In its simplest form, this surge-cast strategy only relies on local information: encounters with discrete odor packets (Figure 1b) indicate when to surge and the wind direction indicates where to orient. However, the temporal pattern of odor packets also contains information about the location (Figure 1c) [2,4–8], size [10], and the number of and distance between odor sources [11-13]. A long-standing question has been whether and how animals exploit the spatiotemporal structure of odor plumes to make better-informed decisions about approaching resources or avoiding danger [8,14,15]. This review focuses on temporal odor patterns in open, aerial environments and evaluates evidence of insects' ability to extract spatial information from odor stimuli alone, independent of wind direction detection. As the review covers studies on different insects, behaviors, and olfactory stimuli, we aim to identify possible mechanisms rather than universal ones.

## Insects can resolve fine-scale temporal odor patterns

When an odor plume hits olfactory receptors in the insect antenna, the plume's spatial pattern of discrete filaments transforms into a temporal pattern of odor packets and blanks (Figure 1b). These odor concentration fluctuations can exceed 100 Hz, as measured by a stationary sensor [16], with individual odor encounters lasting only a few milliseconds [2]. Insects' motion and active odor sampling behaviors such as antenna flicking further increase the rate of odor fluctuation [17]. Therefore, high temporal precision of olfactory processing is crucial for insects to

 $<sup>^1</sup>$  An 'odorant' is a single volatile chemical compound. We use the term 'odor' for odorants released by one odor source.





Turbulent diffusion creates spatiotemporal odor patterns that convey source distance information. (a) Photograph of a meandering odor plume visualized with TiCl<sub>4</sub> smoke. (b) A typical time series (arbitrary units, a.u.) of odorant concentration at a specific point in space. Red triangles represent encounters with filaments (odor packet) and filament clusters (clump), when the local concentration surpasses the detection threshold of a sensor (e.g. a physical detector or insect olfactory receptor neurons, dashed line). (c) Horizontal section through an odor (NH<sub>3</sub>) plume with color-coded intermittency. The intermittency decreases with increasing downwind distance from the odor source and plume centerline (dashed line).

(b) Adapted from Ref. [2]. (c) Adapted from Ref. [6].

extract spatial information about odor sources from temporal odor patterns.

Recent research has shown that insects indeed exhibit high temporal precision in olfactory processing, exceeding previous estimates. Olfactory receptor neurons can respond to odorants within less than 3 ms and exhibit less than a millisecond of jitter between the first odor-evoked spikes [18], and they can resolve odorant concentration fluctuations surpassing 100 Hz [19,20]. Additionally, adaptation mechanisms in olfactory receptor neurons ensure precise detection of the timing of odor packets across a broad range of concentrations [21]. This concentration invariance of temporal precision is likely important in turbulent plumes where the concentration of odor packets is distributed as a power law [2]. Projection neurons, the postsynaptic partners of olfactory receptor neurons, may even display faster response dynamics than olfactory receptor neurons [22].

Temporal precision is also important for the rapid encoding of odor identity, which can take place in just tens of milliseconds, potentially through reading out spike rate changes across the earliest-responding neurons or differences in response latencies across neurons [23]. Additionally, downstream neurons in the mushroom body have short integration time windows and can respond precisely to odorant onsets [24,25]. The high temporal precision of neural odor responses enables insects to rapidly identify odors. For example, mosquitoes can identify 30-ms CO<sub>2</sub> packets [26], and fruit flies can identify and behaviorally react to specific odors within 85 ms of exposure [27].

#### Where is the odor source?

In turbulent environments, most animals locate odor sources by combining odor and wind detection, surging upwind when encountering odor, and casting crosswind when losing the plume [9]. This strategy can be successful even if the odor is only used to detect the edge of the plume and surges and casts emerge from sensori-motor reflexes, as demonstrated in flying flies navigating narrow odor plumes [28]. However, recent studies with fruit flies and mosquitoes in wind tunnels discovered a history dependence in flight decisions during odor tracking [29]. This suggests that insects not only detect whether they are inside the odor plume but also can hold some of that information in memory and use it to modulate navigation over timescales longer than individual odor crossings.

Relevant to odor source localization is the frequency of odor packets, the duration of blanks, and the intermittency (the proportion of time the odor concentration exceeds the detection threshold<sup>2</sup>) (Figure 1b and c). Walking and flying moths [30–33], fruit flies, and mosquitos [28,29,34,35] bias their motion upwind in re-

 $<sup>^2</sup>$  In common usage, 'intermittent' refers to a signal that is repeatedly interrupted by periods of no signal. In physics, this is quantified as 'intermittency', which is the proportion of time the signal is on. This definition can be confusing because a large 'intermittency' means the odorant is present most of the time. For example, a continuous odor stimulus would have an intermittency of 1

sponse to both frequency and intermittency of odor encounters, and when a blank is too long, they cast (when flying) or stop or initiate a search (when walking). Computational studies showed that there is a trade-off in using frequency and intermittency and suggest animals should actively modulate how they weight these two temporal features of the odor stimulus [36]. Indeed, in walking flies, intermittency dominates upwind motion in environments with high-duration, low-frequency odor packet encounters [34], whereas frequency dominates in low-duration, high-frequency environments [35]. Moreover, walking flies exhibit both temporal novelty detection [37] and offset response [34], meaning that when a fly encounters a clump of odor packets (Figure 1b), it can respond differently to the beginning and end of that clump than to fluctuations within [37]. These findings suggest that flies modulate their behavioral response according to the temporal statistics of odor packets, and thereby extract spatial information and use it for source localization.

Insects can also detect odor concentration gradients by comparing signal intensity between their two antennae [38,39] and use this information for odor source localization. In turbulent plumes, this is likely useful close to the source, where a meandering but continuous plume is emanating (Figure 1a). Further downstream from the source, turbulent air motion randomizes the concentration gradient direction, making it less informative for navigation [8]. However, bilateral olfactory sensing can still be useful because it enables insects to detect the direction of motion of odor packets from the temporal correlation of the signal between their two antennae in a computation analogous to detecting motion direction in vision [40]. Owing to turbulent diffusion [1], odor packets typically move away from the plume's centerline (Figure 1c) [6,7,41]. Consequently, detecting this odor motion reveals the direction toward the centerline of the plume, offering a navigational cue independent of wind direction, which enhances flies' navigation capabilities (Figure 2) [40].

While these studies show that the local spatiotemporal structure of an odor plume can modulate insects' behavior, whether the larger-scale spatiotemporal structure of odor plumes can do so is less clear. The overall shape of an odor plume and the spatiotemporal statistics of odor packets within it vary as a function of downwind and crosswind distance from the source, as well as distance from the boundary or floor. For an animal moving toward the source, the odor plume narrows, and the frequency of odor encounters and the intermittency increase (Figure 1c) [3,4,6]. And when moving crosswind toward the centerline of the plume, the fluctuation intensity decreases, and the intermittency increases (Figure 1c) [6,7,41]. Consequently, by integrating statistics from odor encounters over time, animals may be

able to 'climb' these gradients of signals statistics toward the source [42]. However, this navigation strategy requires retaining information in memory to enable comparison of odor encounters over time. Moreover, sufficiently far from the source, odor packets are infrequent, making such a gradient-ascent strategy more difficult. In this case, an 'infotaxis' strategy could be more effective, where the animal balances random exploration for accumulating information about the potential source location and exploiting that knowledge to direct their search toward the odor source [43,44].

#### How large is the odor source?

Close to the source, most concentration fluctuations result from the meandering of the plume (Figure 1a) [4]. A larger odor source produces a more homogeneous plume (Figure 3a) with larger intermittency and smaller fluctuations of the concentration, while a smaller source produces a more filamentous plume (Figure 3a) with smaller intermittency and larger fluctuations of the concentration [10].

There is limited evidence regarding insects' ability to detect an odor source's size through olfaction. A. aegypti mosquitoes engage in strong upwind flight upon brief and fluctuating encounters with CO<sub>2</sub> in filamentous plumes (Figure 3b). Conversely, skin odors in filamentous plumes do not induce upwind flight, but they do so when presented in a homogeneous plume, resulting in longer and more continuous odor encounters (Figure 3b) [26,45]. The origin of these differences in behavior is unknown. One interesting possibility is that mosquitoes search for CO2 and skin odor sources that match the size of their hosts [45]. Brief and sparse  $CO_2$ encounters would suggest that the  $CO_2$  is emitted from a small source, such as the mouth and nostrils, while longer and more continuous skin odor encounters would indicate release from a larger body. Note that variations in temporal odor patterns associated with size and distance can be similar. For example, continuous odor encounters can arise because the source is large [10] or because it is close [4] or both. Therefore, size detection could depend on the context, for example, a mosquito could extract size information by comparing the temporal patterns of concurrent CO<sub>2</sub> and skin odors.

## Do mixed odorants come from the same or different sources?

Olfaction allows animals to identify odor sources without actually visiting them. But does it also tell them where these sources are relative to each other? A natural odor source typically emits a mixture of odorants whose ratios determine the perceived odor identity. Molecular diffusion may change odorant ratios over time because diffusivity depends on molecular weight. But this effect is thought to be negligible because odor dispersal via





Detecting the direction of odor motion improves source localization. (a) To disentangle the effect of odor motion and wind stimuli, and to have high precise temporal control over the olfactory stimulus, the flies' olfactory receptor neurons expressing channel rhodopsin were optogenetically activated by projecting a video of a real odor plume onto them (left). The plume video was played either normally or in reverse. Reversing the playback reverses the sign of the spatiotemporal correlations and therefore of the perceived odor motion direction but maintains the statistics of odor intensity and gradients. Trajectories of flies during normal playback (middle) and during reverse playback (right). Black/gray denote successful/unsuccessful trajectories. (b) Flies are more likely to reach the source in normal playback (magenta bar), demonstrating that odor motion sensing enhances odor source localization. The probability density functions (pdf) of flies' lateral (y) position, in the downwind (left) or upwind (right) end of the arena. (c) Flies turn against the sum of the directions of the wind and of the odor motion. The back square and gray and black circles indicate the fly body and left and right antennae, respectively. The curved arrows indicate rotations of the fly's heading direction. (a) Adapted from Ref. [40].

molecular diffusion is much slower than via turbulent diffusion [2] (but see Ref. [46] for conflicting evidence). Therefore, odorants from a single source reach insect antennae simultaneously. However, when odors from multiple sources mix, they form plumes with varying spatiotemporal structures (Figure 4a) [2,12,47,48]. This results in differences in arrival times and concentration fluctuations of odorants from different sources (Figure 4a and b), reducing the temporal correlation between odor encounters (Figure 4c) [13].

Animals could exploit these temporal cues to perceptually segregate mixed odors from different sources [11], a process analogous to concurrent sound segregation based on stimulus-onset asynchrony [49]. Indeed, studies on mate choice [50–52], host plant selection [53], and foraging [54–56] suggest that insects perceive two odorants as separate sources when their onsets are asynchronous and as one source when their onsets are synchronous. For example, a male corn earworm moth takes off for a search flight when it encounters packets of a female corn earworm moth's sex pheromone component (A), even when it is mixed with sex pheromone packets (B) of another moth species. However, when packets of A and B are released from the same source, the moth does not take off. This behavior has been explained by the synchrony between A and B, indicating that they originate from the same source — a moth of a different species [50]. Similarly, honey bees and fruit flies prefer a mixture of an aversive and attractive odorant when the odorants arrive with a few-millisecond difference (Figure 4d–e), indicating that the sources are spatially separated [54,55].

However, animals could use other cues to segregate odorants from different sources. For example, they could recognize the target odorant during periods of its pure, unmixed presence or use spatial sampling to detect





Mosquitoes favor small-source  $CO_2$  plumes and large-source skin odor plumes. (a) Homogeneous, turbulent, and filamentous plumes were generated in wind tunnel. (b) Mean percentage of mosquitoes flying upwind when stimulated with different concentrations of  $CO_2$  (left) or skin odor (right). Mosquitoes are more attracted to fluctuating, filamentous  $CO_2$  plumes and homogeneous skin odor plumes. (a) and (b) adapted from Ref. [45].

spatial differences of odor concentrations across both antennae [38,39] or even across a single antenna (see review about spatial receptive fields in insect antennae in this issue [57]). A study in fruit flies suggests they use temporal odor patterns to segregate odor sources [55]: when an attractive odorant A and an aversive odorant B are presented asynchronously, flies prefer this asynchronous mixture over a synchronous mixture of A and B (Figure 4d and e). And this preference persists even when A is never present in its unmixed form (asynchronous mixture B33A versus synchronous mixture AB). It remains unclear how mixtures from one source and multiple sources differ perceptually. Stimulus-onset asynchrony may support odor source segregation by making the odor mixture perception less synthetic (where the mixture is perceived as a unit) [58] and more analytic (where the mixture is perceived as a collection of individual odorants) [59]. Alternatively, stimulusonset asynchrony may just make any mixture more attractive without adding spatial information. Another open question is whether animals can use temporal cues to segregate unknown odors without innate or learned meaning, similar to the process of blind source separation [60]. A study in honey bees suggests that segregating unknown odors is more difficult than segregating known odors, because it requires stimulus-onset asynchrony in the range of seconds [61] compared with milliseconds for odors with innate or learned meaning [50,51,54,55].

#### **Future directions**

Odor-guided behavior arises from the changes in odor stimuli that are produced by behavior. For example, turning leads to a different odor stimulus than not turning. Therefore, to understand how animals extract spatial information from odor stimuli, simultaneous measurement of both unrestrained animal behavior and the odor stimulus is necessary. However, capturing encounters between animals and odor stimuli in turbulent plumes is challenging. Olfactory measurement devices lack spatial resolution, and they lack either temporal resolution or odorant specificity [7,62] needed to resolve the fast stimulus dynamics of natural odor plumes [2]. Approximations are currently employed, such as adding visible tracers to the odor plume [35] or using a video projector for optogenetic stimuli, but this method is limited to two-dimensional odor plumes (Figure 2a) [40]. Another approach involves measuring the behavior of fixed animals in virtual reality while delivering naturalistic odor stimuli [63], but existing odor delivery devices fail to replicate the fast stimulus dynamics found in natural environments due to odorant-specific adsorption and desorption rates inside the delivery device [13,64,65]. To overcome these limitations, it is crucial to develop new odor-measuring and delivery devices capable of capturing millisecond-scale rise times and durations of odorant stimuli, regardless of the specific odorant used.

While there is growing evidence that insects use temporal odor patterns to extract spatial information about odor sources, the underlying neural mechanisms remain elusive. Recent research on the central complex and its role in maintaining and updating goal direction during navigation [66] makes this an exciting time to ask how insects combine temporal cues (frequency, intermittency, and temporal relation between different odor stimuli) and spatial cues (odor motion and gradient directions), along with wind direction, to update an estimate of their direction relative to the source and modulate navigation. It is also critical to clarify the role of active sampling behaviors, such as antennal flicking, in extracting spatial information, and whether insects can detect other spatial features of odor sources such as their height, shape, or motion.





Insects detect temporal odor patterns that convey information about the distance between odor sources. (a) Horizontal section of plumes from two sources (dyes in water). Magenta and green traces show changes in dye concentration along the dashed line. The two plumes mix as they travel downstream, but the temporal pattern of both plumes differs. (b) As the distance between two odor sources increases, the correlation between their

temporal patterns decreases. Left: A dual-energy photoionization detector simultaneously measures two odorants at a 40-cm distance, either from a single source or separated by 50 cm, under turbulent airflow conditions in the lab. (c) Correlation coefficients for recordings of odorants from the same source and for sources separated by distances ranging from 10 to 50 cm. (d-e) Asynchronous stimulus onset enhances the attractiveness of mixed odorants with opposing valences, indicating that stimulus-onset asynchrony facilitates odor source segregation. (d) Valve states generating odorant pulses of the attractive odorant A (green), the aversive odorant B (magenta), the synchronous mixture AB, and mixtures with 33-ms stimulus-onset asynchrony (B33A, A33B). (e) Approach probability for mixtures of odorants with conditioned meaning, using butanedione and ethyl acetate equally often as positive- (A) and negative- (B) conditioned stimuli.

(a) Data from Ref. [48]. (b) and (c) data from Ref. [13]. (d) and (e) adapted from Ref. [55].

#### **CRediT** authorship contribution statement

Paul Szyszka: Conceptualization, Visualization, Writing - original draft, Funding acquisition. Timothy L Edwards: Conceptualization, Writing - review & editing, Funding acquisition. **Thierry Emonet:** Writing – review & editing.

### **Data Availability**

No data were used for the research described in the article

### **Declaration of Competing Interest**

The authors declare no conflict of interest.

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