PERSPECTIVE

Active sensing in a dynamic olfactory world

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1 Introduction

This Perspective highlights the shift from the classic picture of olfaction as slow and static to a view in which dynamics play a critical role at many levels of sensing and behavior. Olfaction is now increasingly seen as a "wide-bandwidth temporal sense" (Ackels et al., 2021; Nagel et al., 2015). A parallel transition is occurring in odor-guided robot navigation, where it has been discovered that sensors can access temporal cues useful for navigation (Schmuker et al., 2016). We are only beginning to understand the implications of this paradigm-shift on our view of olfactory and olfacto-motor circuits. Below we review insights into the information encoded in turbulent odor plumes and shine light on how animals could access this information. We suggest that a key challenge for olfactory neuroscience is to re-interpret work based on static stimuli in the context of natural odor dynamics and actively exploring animals.

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2 Fast odor signals in a turbulent physical space

The odorant concentration at a sensor is a time series that results from a reformatting of the spatiotemporal structure of an odor field (Fig. 1) by processes that operate prior to transduction, including flow dynamics (Fig. 1a), motion of the organism (Fig. 1d), and processes intrinsic to the organism, such as sniffing and antennal motion. With regard to flow, several physical mechanisms interact. After release into a flow, odors are transported downstream by the mean flow (Fig. 1a). Stirring alters the macroscopic structure of the odor field, imparting spatiotemporal structure. Simultaneously, molecular diffusion eradicates spatial patterns by destroying odor gradients. The resulting odor field develops as a balance between molecular diffusivity and the intensity of stirring (Crimaldi & Koseff, 2001). Since the aim of this perspective is to highlight the evidence for, and likely functional relevance of, high temporal resolution olfaction, we focus our discussion on more dynamic and intermittent odor landscapes (e.g. all freestream panels, Fig 1a). However, we also note the importance and relevance of "slower" olfactory processes, including gradient following schemes ((Catania, 2013) and references therein), that are well-suited to more static odor landscapes (e.g. nearbed isokinetic panel, Fig. 1a).

The spatiotemporal structure of an odor field is thus reformatted into temporal fluctuations registered by a sensor, with both a finer spatial structure or faster relative motion (flow-to-sensor) leading to higher-frequency fluctuations (Fig. 1b). The intermittency factor (γ, fraction of time the local concentration is above some threshold, Fig 1c) is commonly used to describe these fluctuations but does not directly quantify the frequency content. The signal can be further reformatted by the sensor itself - active sensing. Examples include motion of the entire organism (e.g., walking or flying, Fig. 1d), or of a sensory appendage (e.g., antennal motion or turning of the head). Sniffing is another form of active sensing, since it modifies the local flow-field causing odor structures to be
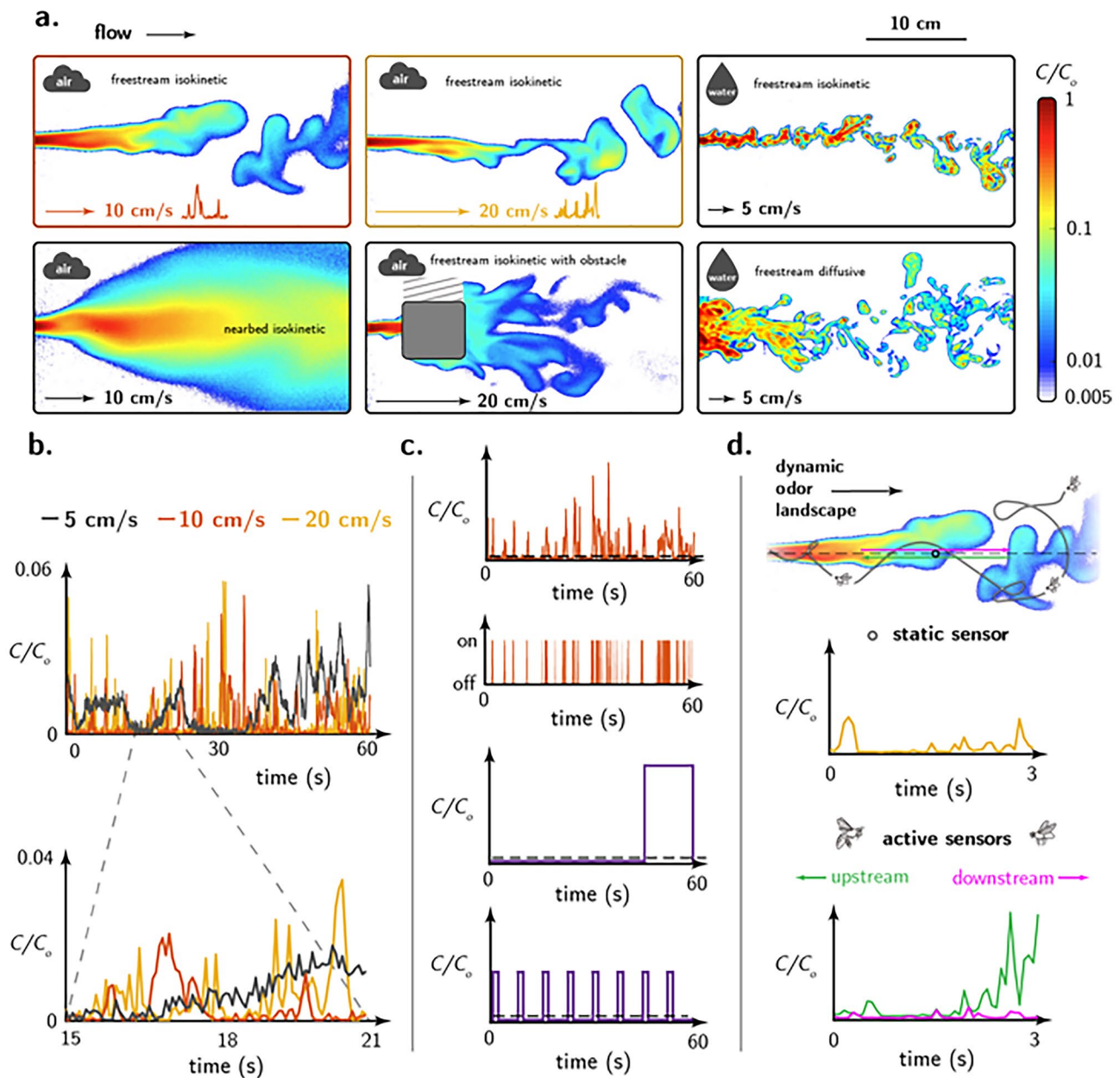
Fig. 1 Odor landscapes and temporal reformatting of spatiotemporal structure. **a.** Normalized instantaneous odor concentration fields measured by planar laser-induced fluorescence illustrate diverse odor landscapes in air (left & middle columns) and water (right column) for varying release conditions and flow speeds. Cross-hatching signifies a data gap from laser shadowing behind the obstacle. **b.** Concentration fluctuations across flow speeds show how changes in delivery rates of odor filaments of some characteristic length to a sensor yield appreciable differences in the statistics of temporally reformatted signals (top panel). A 10X magnified view of a six second window highlights this disparity (bottom panel). All time-series were taken on the mean plume centerline at differing downstream distances to match the total advection (diffusion/mixing) times from the source. **c.** (top panel) The 10 cm/s time-series from panel b has intermittency $\gamma =$ 0.25 for concentration threshold $c_T =$ 0.005 (estimated noise floor, dashed black line), seen also in the corresponding binarized signal (second panel). Two synthetic time-series (third and bottom panels) also have $\gamma =$ 0.25, but all signals vary notably in frequency and amplitude content. **d.** Moving through odor landscapes is an active sensing modality where the information content of the signal is modified by sensor kinematics (top panel, black line shows a hypothetical trajectory). This is seen in concentration time-series from one static sensor (middle panel, black circle in top panel), and two active sensors (bottom panel, green & magenta arrows in top panel) moving upstream (downstream) through the same plume along straight trajectories (arrows, upper panel) on the mean plume centerline (dashed black line, upper panel) at 5 cm/s absolute velocity. All sensors have the same mean position over their three second trajectories (black circle symbol, top panel).

advected past receptors. Active sensing is a form of signal processing, since it modifies the frequency content of the odor signal even prior to transduction —either increasing it (via enhanced relative motion of the sensor) or decreasing it (via enhanced mixing resulting from sensor-induced stirring). Thus, its role in olfaction may resemble that of whisking in somatosensation, or fixational eye movements in vision: transforming the spatiotemporal pattern of the natural input into a temporal pattern whose characteristics facilitate processing (Ahissar & Arieli, 2001; Rucci & Victor, 2015).

While the physics of stirring and diffusion governing odor field dynamics are identical in air and water, aqueous odor fields typically have finer-scale spatial structure since diffusivities there are orders of magnitude lower than in air. In fact, a large body of literature details aspects of olfaction in aquatic crustaceans and vertebrates (Webster & Weissburg, 2009). While the focus of this perspective is on air-mediated olfaction, the commonality of the underlying physics indicates the value of studies in an aqueous environment for elucidating universal principles of odor transport, dispersion, and reception by sensors.

3 Evidence that animals process fast signals

Insects and mammals are able to track the dynamics of fast odors signals. In insects, the response latency in olfactory receptor neurons (ORNs) is approximately 2 ms (Szyszka et al., 2014), which allows receptor neurons to follow fast concentration dynamics (Brown et al., 2005; Geffen et al., 2009; Kim et al., 2010). Odor onset asynchronies as short as 6 ms suffice to drive behavior and generate distinguishable responses to different odors in early processing in the antennal lobes (Stierle et al., 2013). This sensitivity could help insects to separate intermingled odors from different sources. Accordingly, second order neurons in the insect brain encode complex dynamics of odor stimuli (Kim et al., 2015), and the premotor output neurons have latencies of 60 to 80 ms (Strube-Bloss et al., 2012).

In mice and rats, odor processing is rapid and temporally precise, though not quite at the level seen in insects. Odor detection and discrimination can occur rapidly within few 100 ms (Abraham et al., 2004; Uchida & Mainen, 2003). Mice can detect precise timing of optogenetically delivered stimulation to ORNs, and discriminate latency differences of as little as 25 ms (Smear et al., 2011)). With direct, patterned stimulation of mitral/tufted cells, the threshold is reduced to 13 ms (Rebello, 2014). Duration differences of as little as ~10 ms can also be detected (Li et al., 2014). Thus, the mammalian olfactory system could represent optogenetic stimuli at a time scale of several 10s of Hz (Chong, 2020). Moreover, recent work shows that OB cell populations can follow temporal patterning in natural plumes (Lewis, 2021),

and fast temporal properties of odor stimuli such as intermittency, frequency and phase (Ackels, 2021; Gumaste et al., 2020) can be accurately recognized (Fig. 1b, c), supporting odor source separation (Ackels, 2021).

4 Active sensing imposes dynamics upon odor signals

Insects actively move their antennae towards locations of higher odor concentration, which affects the dynamics of neural odor representation (Huston et al., 2015). Wing flapping during flight also imposes dynamics on odor sampling by the antennae (Li et al., 2018). Mammals sample odorants by sniffing, which are periodic events (2-15Hz) bringing the odorants in the air in contact with the olfactory mucosa. Neural activity of ORNs, mitral/tufted cells and inhibitory neurons of the OB is precisely timed relative to each sniff cycle (Wachowiak, 2011). Hence sniffing may function as a neural reference of a signal that is decoded within several tens of milliseconds and includes bulbar fast LFP gamma activity (40-100Hz) (Wachowiak, 2011). Sniffing also appears to drive whisking, another rhythmic exploratory behavior in rodents, as well as hippocampal theta-like respiratory rhythm (Kurnikova et al., 2017; Moore et al., 2013) particularly during odor-guided navigation (Findley, 2021). The sniff rate also affects the processing of the odorants: while slow sniffing provides a summated representation of odorants, rapid sniffing enhances odor representation during learning (Jordan et al., 2018a) and allows differentiation by rapid adaptation in ORNs and MCs (Eiting & Wachowiak, 2020; Verhagen et al., 2007). Movement of the nose relative to the odor plume will also affect odor dynamics, strongly extending the high frequency spectrum when moving upstream (Fig. 1b, d), while leaving intermittency unaffected (Fig. 1c). Meanwhile, sniff-invariant concentration discrimination has also been reported (Jordan et al., 2018; Shusterman et al., 2018), consistent with latency or primacy-based encoding of odor quality (Margrie & Schaefer, 2003; Wilson et al., 2017).

5 Multisensory integration of fast odor signals

In both mammals and insects, there is evidence for convergent processing of mechanosensory and chemosensory information. Specifically, studies suggest that olfactory neurons process both mechanosensory and chemosensory information simultaneously (Grosmaitre et al., 2007; Tuckman et al., 2021). The effect that mechanosensory input has on the olfactory neurons may allow for better recovery of the underlying temporal plume structure, for example, by subthreshold

summation or adaptively scaling the sensitivity of the system to the informational features of the odor plume.

6 Stereo-olfaction

The mammalian olfactory system also allows for the rapid detection of the spatial origin among lateralized sources across both nares. Rats, whose nares are separated by a few mm, can be trained to localize odors within 1-2 sniffs, or as short as 50ms, mediated by side-specific bulbar responses (Rajan et al., 2006). This appears to depend on both internasal time and intensity differences (ITD, IID), analogous to auditory localization by inter-aural differences. In humans self-motion perception appears to be subconsciously biased by non-trigeminal binaral odor cues (Wu et al., 2020), though for conscious direction perception trigeminal co-stimulation appears critical (Kobal et al., 1989). Furthermore, mice show rapid spontaneous nose movement toward the stimulated nostril (Esquivelzeta Rabell et al., 2017) within a single sniff, and it depends on intact Anterior Commissure (AC), connecting the first interhemispheric odor processing in the Accessory Olfactory Nucleus (AON) (Esquivelzeta et al., 2017). Indeed, neurons in the AON pars externa are excited by ipsi-nostril and contra-nostril-only stimulation with odorants of similar quality during each respiratory cycle (Kikuta et al., 2010). Evidence is also accumulating that stereo-olfaction can contribute to odor-driven navigation (Catania, 2013; Khan et al., 2012; Liu et al., 2020; Marin et al., 2021).

Insects and other invertebrates also use bilateral comparisons across antennae in localization of odors. Trail following in ants, for example, is disrupted if their antennae are crossed (Hangartner, 1967). Removal of one antenna reduces odor localization and induces compensation in movements of the remaining antenna (Draft et al., 2018). In the fruit fly bilateral antennal comparisons are important for orientation toward an attractive odor or away from a repulsive odor (Wasserman et al., 2012). In moths, a delay as short as 50 ms in arrival of the female sex pheromone at one antenna relative to the other will bias turning behavior (Takasaki et al., 2012), suggesting a fast bilateral comparison of inputs from the antennae.

7 Behavior and navigation models

High-bandwidth sampling in olfaction has theoretical advantages for navigation and olfactory scene segregation. One way that rapid sampling could be harnessed for navigation is that intermittency (Fig. 1b) is a cue to location in a plume (Connor et al., 2018; Crimaldi & Koseff, 2001; Schmuker et al., 2016). However, so far there is no direct evidence that animals use intermittency to navigate. For example, insects seem to change their direction far more frequently than would allow for stable estimates of intermittency at each location (Cardé, 2021). Conversely, many aspects of fruit fly search can be modeled by navigation algorithms that combine a simple state model with continuous updating of orientation based on instantaneous sensing of odor concentration (Álvarez-Salvado, 2018). Additionally, moment-by-moment updating may aid navigation in noisy environments by destabilizing limit cycles that would otherwise prevent a successful search (Riman et al., 2021).

Rapid sampling also enables detection of odor filaments. As an organism moves, a filament's spatial structure is reformatted into a rapid temporal fluctuation above the mean odor concentration -- precisely the kind of temporal feature that is captured by an olfactory receptor (Nagel et al., 2015) that adapts to recent history (Victor et al., 2019). How sensor movement and sampling in general might affect or even benefit odor coding in a complex spatiotemporal odor environment is a topic of ongoing investigation.

Navigation -- and olfactory-guided behavior in general -- could be confounded by multiple odor sources. Hopfield, 1991 suggested that odors emanating from spatially separate sources usually generate distinct spatio-temporal distributions, whereas co-located odor sources will result in co-incident odor encounters. The temporal structure of odorant percepts imposed by their filamentous structure may thus be instrumental to figure ground-segregation. More generally, recognition of temporal coincidence of odorant encounters may be critical to solving the problem of olfactory scene analysis (Ackels et al., 2021; Rokni et al., 2014).

8 Implications for neural processing from the evolution of olfactory systems

Olfactory systems of insects and mammals have similar system-level properties for processing of fast dynamic odor signals (Nowotny et al., 2005; Strausfeld & Hildebrand, 1999; Touhara & Vosshall, 2009). However, given differences in molecular and functional properties of insect and mammalian odorant receptors (Benton et al., 2006), it is likely that system-level similarities have arisen via convergent evolution. Independent convergence onto the same circuit-level solution could indicate that there is a restricted range of fundamental solutions for tracking fast odor signals. If confirmed, this finding would have important implications for understanding the biological principles of using chemical signals to drive action, and for odor-sensing robots.

9 Summary

The objective of this Perspectives article is to highlight the many ways in which dynamics play a key role in the structure of olfactory environments, how olfactory signals are sensed, and how they are used. Odor plumes are complex because of turbulence, and animals use a variety of active sensing and neural processing capabilities to extract important information on fast time scales about odor identity and localization from those plumes. Strengthening cross-disciplinary bridges among biology, theory, computational modeling and engineering can catalyze new generalizable knowledge about the sense of smell.

Declarations

Conflict of interest The authors declare no conflict of interest.

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