

A new angle on odor trail tracking

Siddharth Jayakumar^{a,b} and Venkatesh N. Murthy^{a,b,1}

Animals navigate by making a series of decisions using external stimuli and any internal model (or map) of the world they may have formed. Many animals, including ants, dogs, and rodents, spontaneously track scent trails, which are chemical cues that form navigational guides that allow animals to locate food, mates, and landmarks like their homes (1–6). Tracking odor trails is a nontrivial problem since cues are detected intermittently due to potential complexity of the trail as well as the nature of the sensory apparatus. Importantly, future locations of the trail are “invisible” and must be predicted based on current and past information (unlike in vision, where one can simply see the future locations). In PNAS, Reddy et al. (7) present a general algorithmic framework to understand odor trail tracking.

Previous work in a variety of organisms ranging from insects to humans points to a characteristic zig-zag movement over a scent trail (1, 2, 5). Such zig-zag movements, or casting, have been described extensively in flying insects (8) and are thought to be part of their search strategies to discover the source of an odor. Casting movements are complemented by upwind surges upon odor detection (8). While purely odor-guided navigation has been discussed extensively, other sensory modalities may also play fundamental roles—for example, optomotor anemotaxis (8). Walking insects also exhibit odor-guided anemotaxis toward attractive odors, and there is an exciting surge in research on this behavior (9, 10).

Trail tracking occurs under different constraints compared to windborne odor tracking, where turbulence leads to highly dynamic odor landscapes, unlike the more stable odor distribution in trails—some exceptions include so-called plume tracking, where the plume can be thought of as a trail (11–14). Dogs and wolves can track trails with remarkable accuracy over long distances, perhaps even for miles (6, 15). Intuitively, tracking is composed of an initial

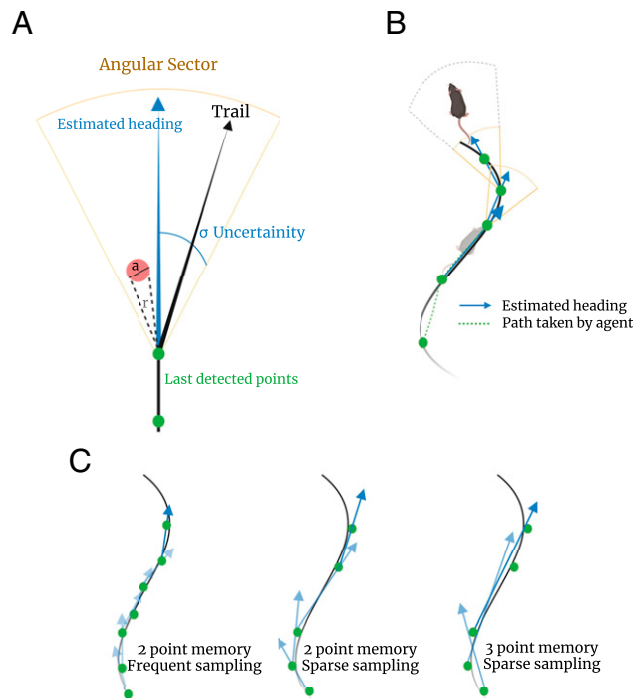


Fig. 1. Schematic of the sector search algorithm described in Reddy et al. (7). (A) The polar coordinate system which describes trail tracking in episodes of searching for the trail using an estimate of the heading (here based on two recent contacts with the trail). The angular width of a search is given by σ . The rate of angular searching in the space is a function of the sensor size a and the distance r . (B) A schematic of how an agent, in this case a mouse, searches for a ground-based trail using headings estimated from the two recent points of contact with the trail or two-point memory. The angular sectors are shown for successive pairs of contacts. (C) Tracking as a function of sampling frequency and memory. In the regime estimating heading with two points, an agent who samples frequently (moving at lower forward velocity) has a better estimate than one with higher velocity and samples sparsely. In the latter regime, an agent estimating using more memory (for example, a three-point estimate) would estimate better. The figure was created using BioRender.

^aDepartment of Molecular & Cellular Biology, Harvard University, Cambridge, MA 02138; and ^bCenter for Brain Science, Harvard University, Cambridge, MA 02138

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¹To whom correspondence may be addressed. Email: vnmurthy@fas.harvard.edu.

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foraging phase to locate the trail, followed by an estimation of the trail heading and subsequent tracking. Trail tracking has been documented in the laboratory in rodents and ants, which display oscillatory casting, whose amplitude increases upon encountering breaks or loss of the trail (2, 3, 5). The studies highlighted above, however, have not been able to describe an underlying algorithmic framework for understanding trail-guided navigation. Previous models to explain casting assume oscillations to be intrinsically generated and control the exposure of the sensor to the stimulus (16) or are thought to arise from bilateral or temporal gradient estimation for chemotaxis (2, 17, 18). These models generally rely on cue detection for tracking and do not take trail geometry into account, which can carry important information. Importantly, previous models do not have robust predictions about what the animal should do when it loses the chemosensory cue and do not prescribe potential strategies to reacquire lost trails.

Reddy et al. (7) present a normative theory of odor trail tracking that goes beyond conventional chemotaxis. The authors propose a search strategy where an agent estimates local heading based on previous contacts with the trail to define an angular sector extending from the most recent contact with the trail (Fig. 1). The angular sector defines a mean heading direction and the associated uncertainty at any given moment in time, so that search for the trail can proceed within that angular sector. They use this framework to provide a quantitative description of trail tracking, while providing experimentally testable predictions.

Reddy et al. (7) begin by elegantly framing the challenges that are faced by an agent that tracks odor trails. During tracking, an animal or agent decides when and where to sample the odor and also builds an internal representation of the trail based on the ensemble of odor detections to guide future decisions. The authors ask what an ideal agent should do to follow a ground-based trail. Using their theoretical formulation and through simulations the authors show that a reinforcement learning agent can learn to track efficiently without losing trails while recapitulating naturally observed casting behaviors. They proceed to provide an intuition on how the oscillations previously reported arise as a function of probability distribution of the heading and the interdetection interval. The authors also provide insights into balancing tracking speed while not losing the trail and derive bounds for speed–accuracy trade-off based on trail geometry and interdetection interval.

Another open question in understanding navigational strategies is the role of active memory in retaining past contacts of the trail. The authors explain that an agent that tracks should maintain an internal model retaining some amount of the past contacts with the trail, allowing it to navigate across the intermittency naturally imposed on trails by sampling strategies (such as antennal movement in insects or sniffing in rodents) as well as various factors in the environment. Reliance on memory or internal model for tracking works because natural trails are expected to have nonrandom structures. An analogy in vision is the realization that visual experience is not simply a succession of white-noise frames but smoothly changing images, which allows the brain to make predictions about the future. Reddy et al. (7) use tools from statistical and polymer physics to make explicit analytical predictions of how the agent should integrate information from past contacts with the trail to make the best guess about the trail heading. The statistics of casting arises naturally in the model as a solution to minimizing the probability

of losing the trail altogether and maximizing the speed of tracking—this result contrasts with earlier models (2) where casting is simply baked into models in an ad hoc manner.

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The work of Reddy et al. (7) is exemplary in its conceptual framing of the problem, which allows both analytical and numerical analysis. A good theory not only offers a normative explanation for interesting phenomena but also suggests crisp and feasible experimental predictions. The authors go on to describe explicitly some testable predictions for experimentalists. One prediction is the dependence of the amplitude of casting on the correlation length of the meandering trail encountered. If the agent or animal encounters a long stretch of rather straight trail, followed by a break, casting amplitude will be small and grow slowly. On the other hand, if the animal has tracked highly curved trails just before a break, casting amplitudes should rapidly grow larger. Another interesting question is the relation between trail structure and the limit of when an agent would stop attempting to track. A key question that could be answered by experiments is about the length of the memory of past trail encounters: Do animals store any of the prior contacts and, if so, how many contacts? Careful experiments with curved or forked trails and breaks can be used to test these ideas. Visual neuroscience has benefitted from a deeper understanding of the natural statistics, which allows vision to be modeled as extracting invariances in the visual world (19). Knowledge of the natural statistics of odor trails may lead to a similar understanding of the olfactory invariances extracted by animals.

Developing theoretical frameworks to understand behavior is a vital complement to the growing efforts in data-driven automated analysis of behaviors using computer vision and deep networks (20–22). The latter research direction is exciting and is often presented as hypothesis-free discovery of behavioral modules, but generative models of behavioral strategies promise deeper understanding. This paper is also likely to inspire further work on agent-based models for other continuous behaviors in animals, in particular partially observable Markov decision processes (23). For example, a natural extension of the current work might involve realistic situations where there are distracting odors in the background (either as airborne cues or as competing cues on the ground). It will be of interest to determine how the sector search strategy, especially an implementation using reinforcement learning, should be adapted for noisy and conflicting backgrounds.

A final point is about the neural implementation of the sector search strategy. The algorithm requires a sensorimotor loop with some sort of short-term memory. If we consider rodents, which are amenable to neuroscientific experiments, a first step might be the detection of the odor (or a lack thereof) during a sniff. This detection must then be compared with previous detections to obtain a vector direction for heading. Reorienting to the estimated heading direction may first occur for the head, since inertial forces are smaller for head movements than for full-body movements. These considerations point to interactions among olfactory sensory regions, navigational circuits such as the entorhinal cortex and hippocampus, working memory

areas such as prefrontal cortex, and the cortical and subcortical motor regions. The work of Reddy et al. (7) offers strong

impetus and direction for a study of neural mechanisms in odor-guided navigation.

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