Optimal encoding of odor concentration for olfactory navigation is approximated by the Hill nonlinearity

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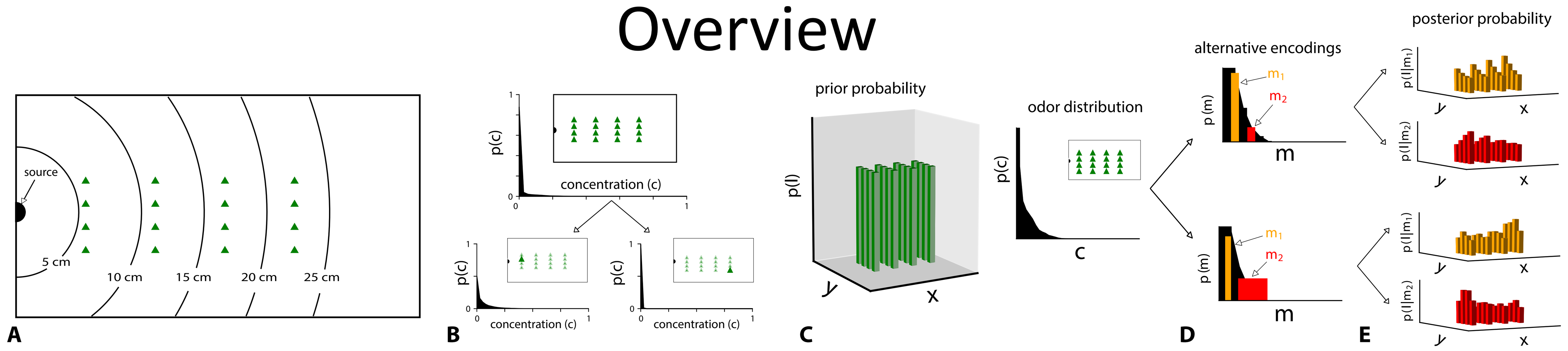
Introduction

Olfactory navigation is a sensorimotor behavior that is critical to the survival of a wide range of organisms. It is made computationally challenging by the turbulent nature of natural olfactory plumes. Evolutionarily successful organisms accomplish olfactory navigation by making navigation decisions on a moment-by-moment basis. These decisions are necessarily based on a limited knowledge of the odor plume. Limitations arise not only because measurements are restricted to sensor's locations, but also because the sensors have limited accuracy and bandwidth. Our focus here is how these limited resources are best used. We take an information-theoretic approach: how can odor concentration be encoded into a fixed number of bits in a way that maximizes information about location within a plume?

Overview

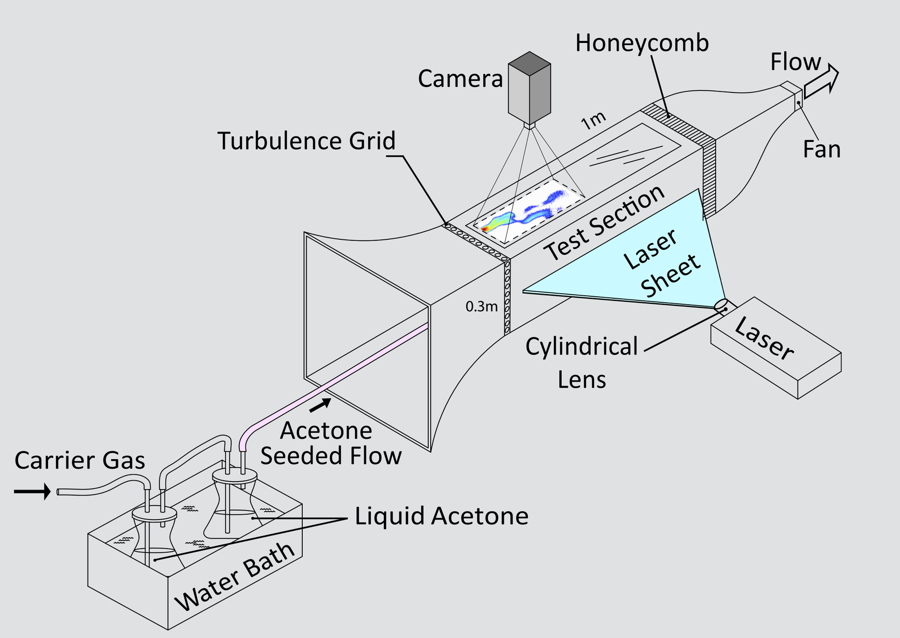


A: Odor concentration is measured at multiple grid locations (triangles) within a dynamic odor plume.
B: Since the odor concentration varies with time, each location yields a distribution of odor concentrations. The large histogram shows the distribution of odor concentrations across all grid points; the two smaller histograms show the distribution of odor concentrations at two example grid points.

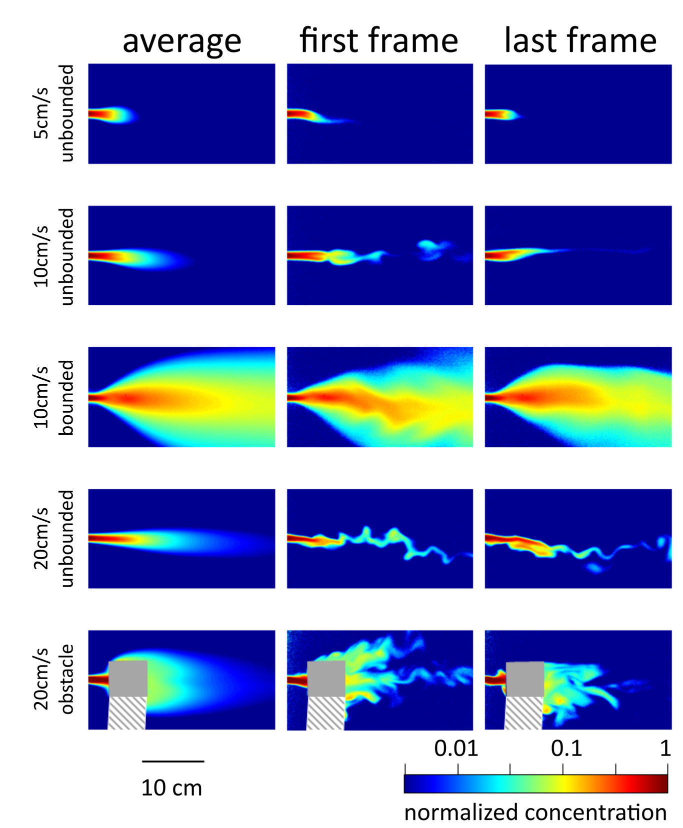
C-E: Evaluation of schemes encoding odor concentration. **C:** Locations across the grid points are assigned equal *a priori* probability. **D:** An odor sample is obtained at a randomly-chosen grid point, and encoded into a code word that represents a discrete range of odor concentrations. Several alternative discretizations are considered. **E:** For each code word, the *a posteriori* probability of location within the grid is computed via Bayes Theorem. For each discretization, we then compute the Shannon mutual information between location and code word. Modified from (Boie, Connor et al. 2018).

Experimental Methods

Spatiotemporal Measurement of Odor Concentrations in a Turbulent Air Plume

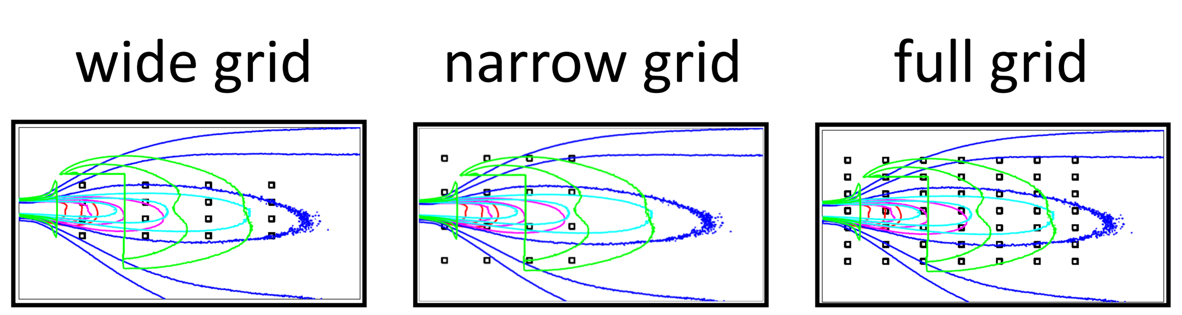


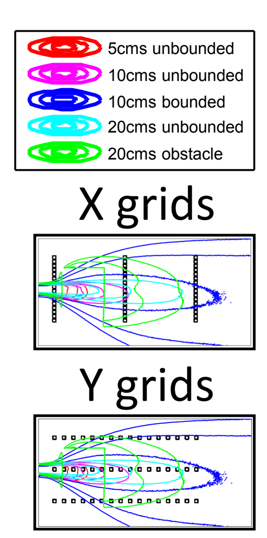
An odor surrogate (acetone made neutrally buoyant by mixing with air and helium) was isokinetically released into a wind tunnel at the center of its entrance. Turbulence was induced by an entrance grid (6.4 mm diameter rods and a 25.5 mm mesh spacing, followed by a 15 cm long honeycomb section). Fluorescence was induced with a 1 mm thick light sheet from a Nd:YAG 266nm pulsed laser. Fluorescence, proportional to acetone concentration, was imaged using a high-efficiency sCMOS camera. Modified from Connor et al., 2018.



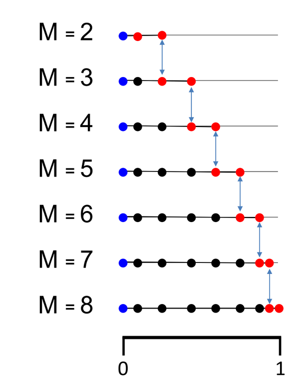
Five olfactory environments. Average odor intensity (first column), and snapshots of odor intensity on the first and last data frames (last two columns). The color scale is logarithmic, ranging 0.003 to 1 (equal to the inlet concentration). For the bounded dataset, a false floor was placed just under the release point. For the obstacle dataset, the obstacle is indicated by the solid gray square; a portion of the plume could not be imaged because of obstacle's shadow (hatched parallelogram).

Sampling Grids. Three two-dimensional grids (**below**), superimposed on contour lines corresponding to average odor concentrations of 0.1, 0.03, and 0.01 times the inlet concentration. One-dimensional sampling grids (**right**) in X and Y directions. Analyses at these grids yielded similar results (not shown).



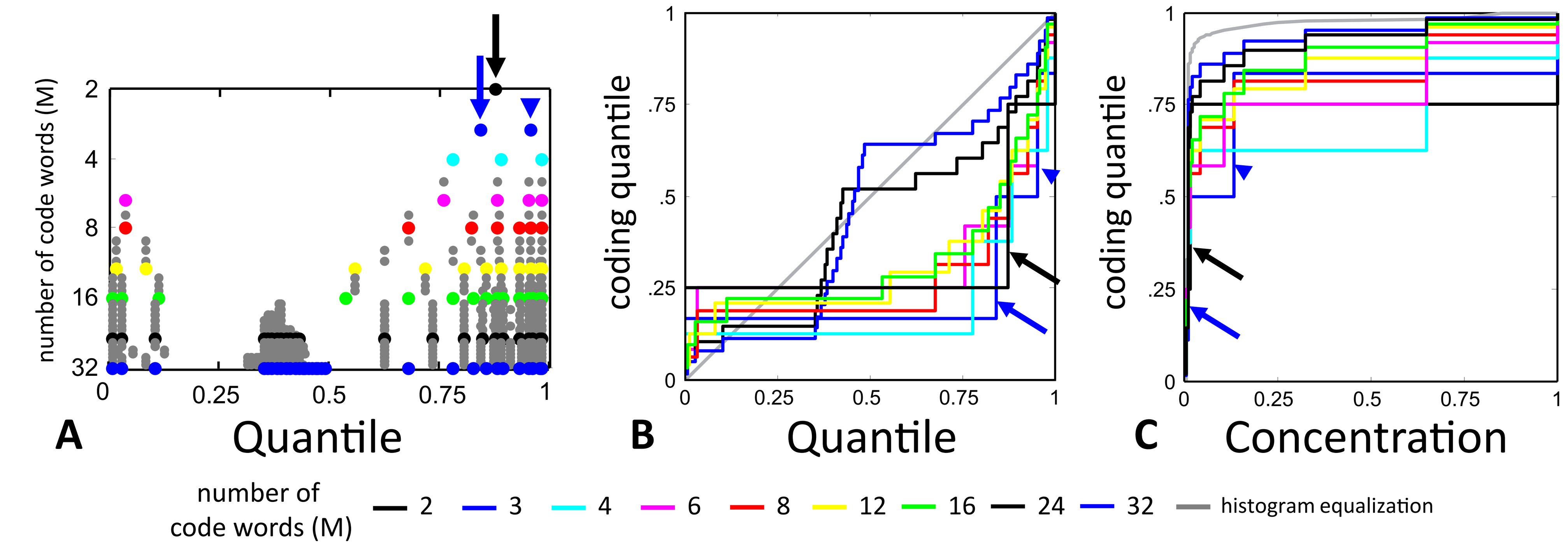


Algorithm



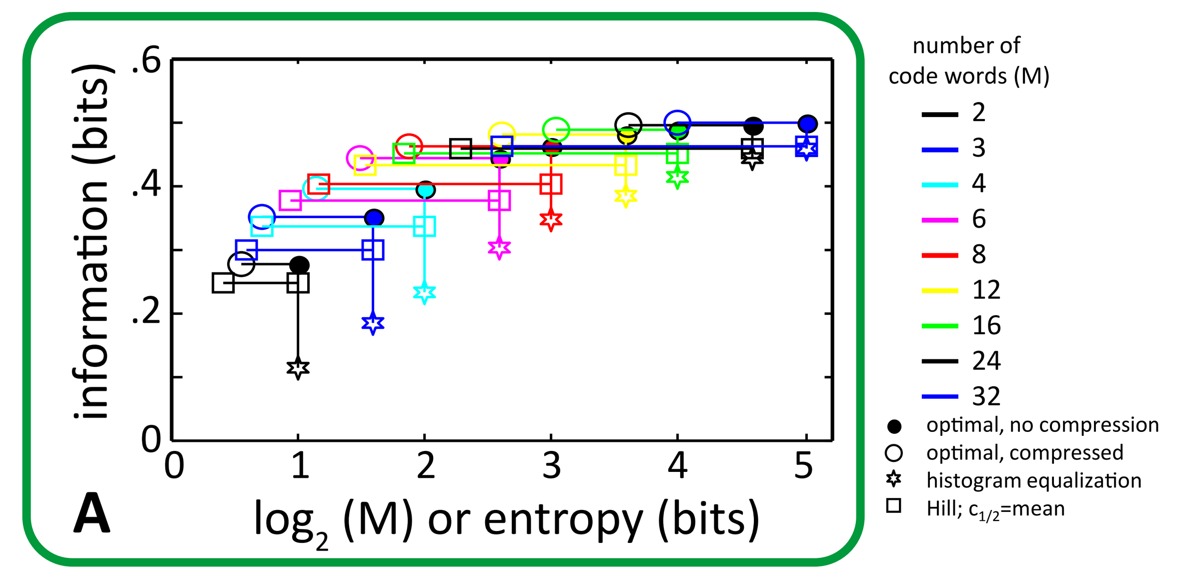
Dynamic programming strategy for determining the discretization of a range into *M* code words that maximizes the Shannon information about an underlying variable (location).

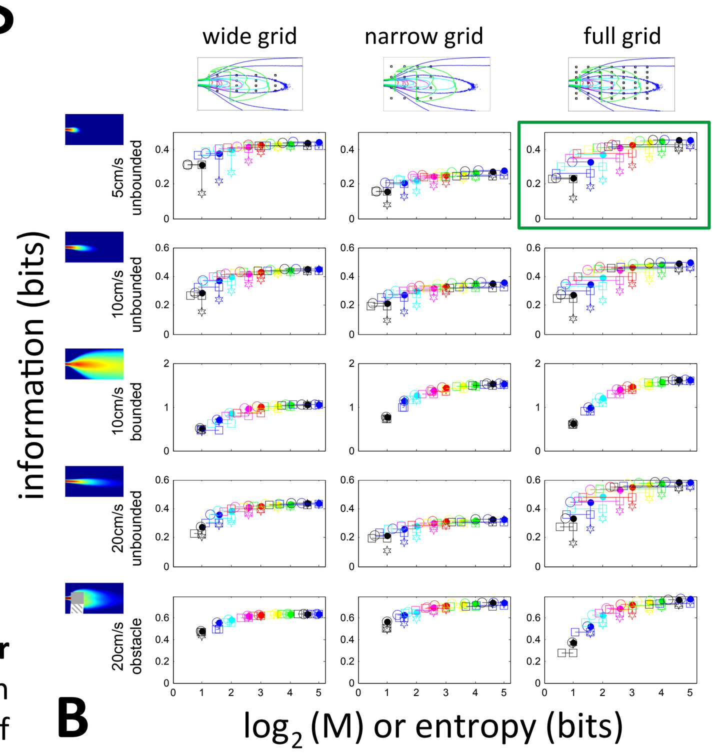
The key observation is that in an optimal discretization of an interval, any sub-interval is optimally discretized. This holds because of the chain rule for entropy. The optimal discretization of the entire interval can then be built from a library of optimal discretizations of sub-intervals. Initially, a library of optimal discretizations of [0 *x*] into 2 segments is constructed (blue and red symbols). Iteratively, each library is used to build a library of optimal discretizations containing one additional segment.



Optimal segmentations for the 10 cm/sec unbounded environment, full grid. A: Positions of the cutpoints, for 2 to 32 code words (*M*). For each value of *M*, there are *M*-1 cutpoints, which separate the concentration range into segments corresponding to the code words. **B:** stepwise nonlinearities corresponding to selected values of *M*. As shown by the arrows for *M*=2 (black) and *M*=3 (blue), the nonlinearities in **B** have a step increment of height 1/*M* at the cutpoints in **A.** Histogram equalization corresponds to the diagonal. **C:** As in **B,** but plotted as a function of normalized concentration, rather quantile.

Results

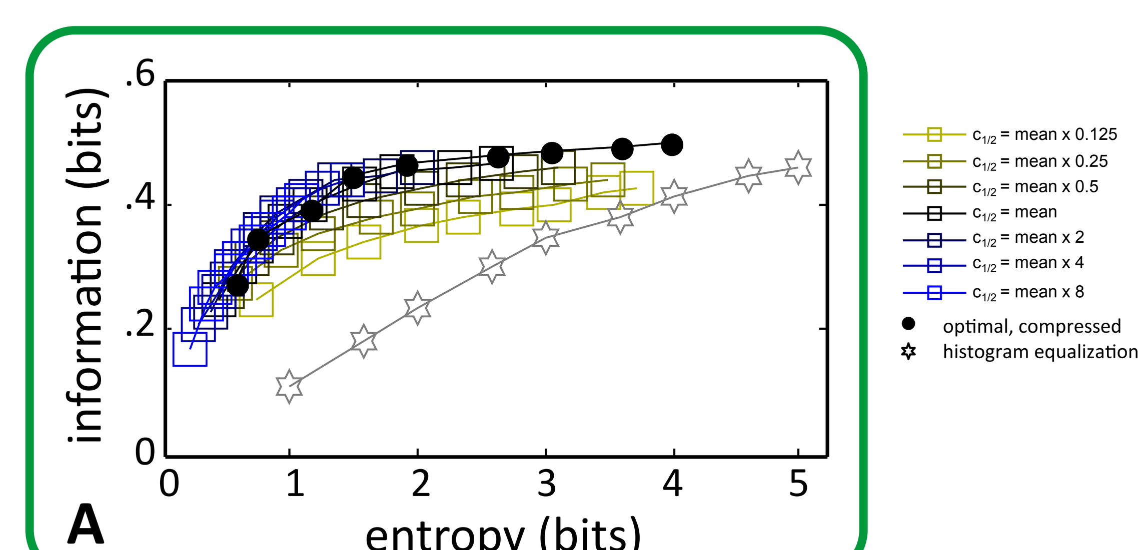




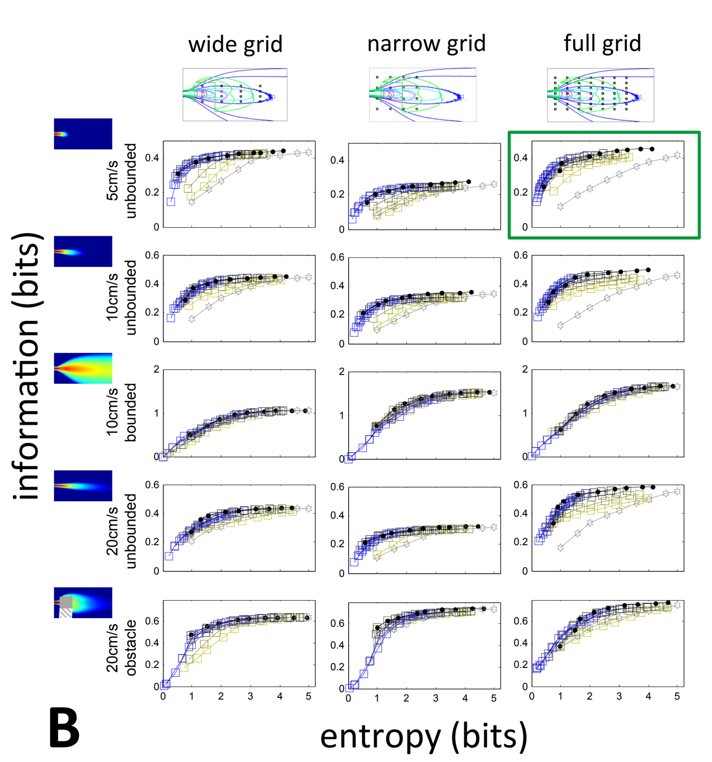
Information transmitted about location by the histogram equalization (HE) code is far from optimal; the Hill nonlinearity code is close to optimal. Circles: information transmitted by the optimized code as a function of $\log_2(M)$, where *M* is the number of code words (filled symbols) or as a function of the entropy of the code (open symbols). Hexagrams: information transmitted by the HE code. For HE, entropy is equal to $\log_2 M$. Open squares: performance of codes in which the Hill nonlinearity is followed by uniform segmentation into *M* code words. Positions of the two squares along the abscissa indicate $\log_2 M$ and the entropy of the code word distribution. **A:** 10 cm/sec unbounded environment sampled with full grid; **B:** five environments and three grids.

Hill Nonlinearity $f([X]) = \dfrac{[X]}{c_{1/2} + [X]}$

$[X]$: odorant concentration
$c_{1/2}$: semisaturation constant
$f([X])$: bound fraction



Information transmitted about location by the Hill nonlinearity is maximized when the semi-saturation constant $c_{1/2}$ is near the mean concentration in the environment. Black: $c_{1/2}$ equal to the mean across grid points. Blue: $c_{1/2}$ larger than mean. Yellow: $c_{1/2}$ smaller than mean. Filled circles: optimal code for location. Hexagrams: HE code. Abscissa: entropy of code word distribution. **A:** 10 cm/sec unbounded environment sampled with full grid; **B:** five environments and three grids.



Summary & Conclusions

- We used a combined experimental and theoretical approach to analyze optimal coding strategies for the purpose of olfactory navigation.
  - Planar laser-induced fluorescence was used to measure spatiotemporal characteristics of turbulent plumes in air.
  - A new dynamic programming algorithm was used to identify optimal coding schemes.
- Histogram equalization, the optimal strategy for transmitting information about concentration, is sub-optimal for transmitting information about location. For location, gentler nonlinearities yield greater information per code word.
- The advantage of a more gently saturating nonlinearity is even greater when compressibility of the code word stream is taken into account.
- Optimal behavior is approximated by a Hill receptor binding nonlinearity, with binding constant $c_{1/2}$ at the mean odor concentration.

References

Boie, S. D., E. G. Connor, et al. (2018). "Information-theoretic analysis of realistic odor plumes: What cues are useful for determining location?" PLoS Computational Biology 14(7): e1006275.

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