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NEUROCOGNITIVE COMPUTING LAB

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Novelty detection by density estimation in the fruit fly olfactory circuit

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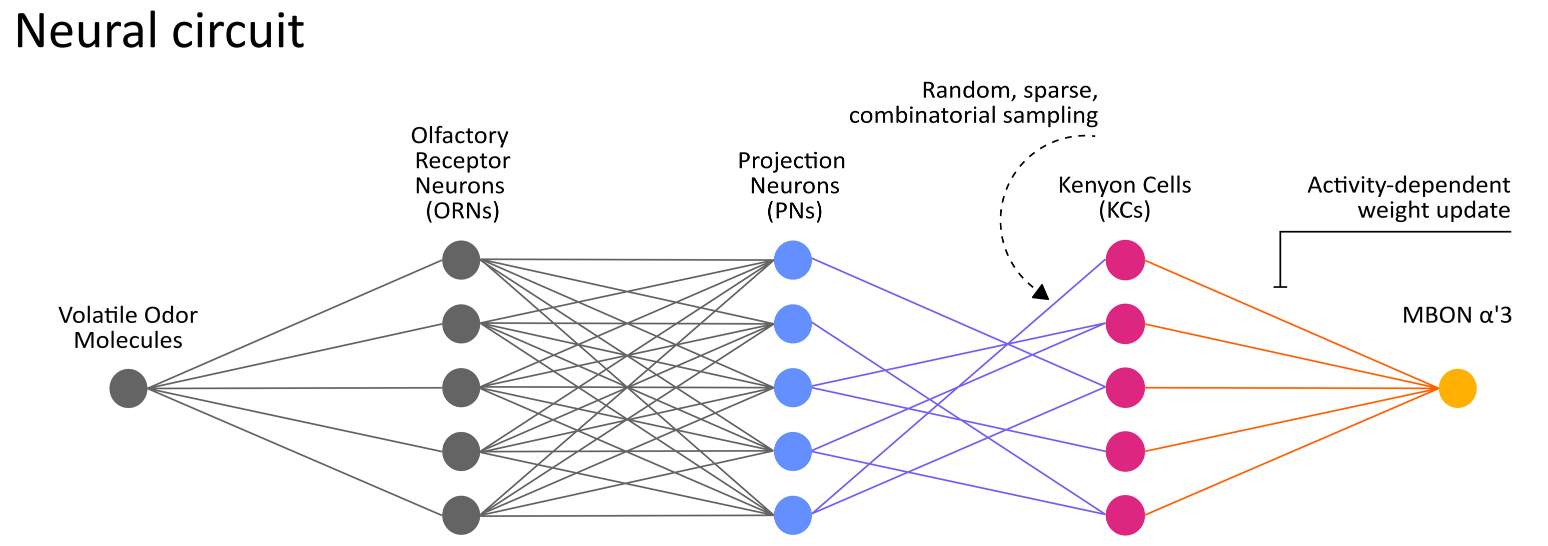
1. Introduction

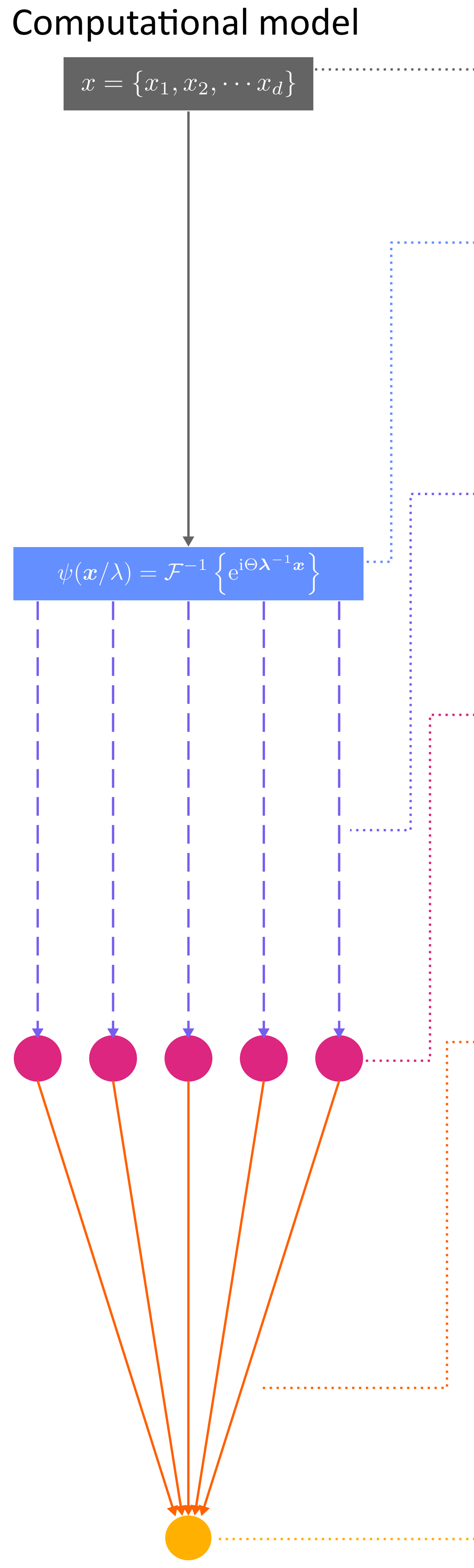
The capacity to recognize an unfamiliar situation is essential for survival. In the insect mushroom body, a single feedforward circuit controls the alerting response to novel odors, but the high-level algorithm being executed remains unclear. Previous work has shown how the locust mushroom body circuit could act as a probability density estimator. Here we investigate the extent to which this model applies to the neurobiology of the fruit fly, a widely-used animal model in neuroscience.

2. Interpreting the locust KC-MBON α'3 circuit as a kernel density estimator

Neural circuit



Computational model



Input: sample

A real-valued sample from the world, $\boldsymbol{x}$, is drawn from some unknown generating distribution $\mathcal{S}$ and provided as input to the network. The distribution can be defined over any number of features d for vector input with elements $\{x_1, x_2, \cdots x_d\}$:

$$\boldsymbol{x} \sim \mathcal{S}$$
$$\boldsymbol{x} = \{x_1, x_2, \cdots x_d\}$$

Projection

The input is projected onto a manifold lying on the surface of the unit hypersphere with fixed dimensionality, D:

$$\psi(\boldsymbol{x}/\lambda) = \mathcal{F}^{-1}\left\{e^{i\Theta\boldsymbol{\lambda}^{-1}\boldsymbol{x}}\right\}$$

Where λ is a diagonal, non-negative matrix whose entries $(\lambda_1, ...\lambda_d)$ are user-specified parameters defining the length scale of the representation, Θ is a $D \times d$ matrix, and $\mathcal{F}^{-1}$ denotes the inverse Fourier transform. Θ is constructed of a set of column vectors θ_j, each comprising a collection of frequencies. Elements $\theta_{i,j}, i = (1, ..., (D-1)/2)$ are drawn from a uniform distribution over the range $[-\pi, \pi]$ with $\theta_{0,j} = 1$. θ_j are then made conjugate symmetric to ensure that the inverse Fourier transform is real-valued.

Random, sparse, combinatorial sampling

The preferred directions of neurons in the hidden layer, modelling N Kenyon Cells (KCs), is specified by E, a $D \times N$ real matrix with columns corresponding to vectors drawn from a uniform distribution over the surface of the hypersphere. Each e_n can therefore be decomposed into a sum of B vectors that are non-orthogonal with the representational manifold $\psi(\boldsymbol{x}_b/\lambda)$, with respective scaling factors α_b, and a component that is approximately orthogonal to it:

$$e_n = \sum_{b=1}^{B} \alpha_b \psi(\boldsymbol{x}_b/\lambda) + e_{\text{orthogonal}}$$

50000 Kenyon Cells (KCs)

The activity of the n^{th} KC, a_n, is the rectified result of the dot product between e_n and $\psi(\boldsymbol{x}/\lambda)$, less some bias ξ. Due to the high-dimensional vector representation, the contribution of pseudo-orthogonal components are negligible, and the result approximates the contribution of vectors aligned with the manifold:

$$a_n = \text{ReLU}(\psi(\boldsymbol{x}/\lambda) \cdot e_n - \xi)$$
$$a_n \approx \text{ReLU}\left(\psi(\boldsymbol{x}/\lambda) \cdot \sum_{b=1}^{B} \alpha_b \psi(\boldsymbol{x}_b/\lambda) - \xi\right)$$

The dot product between vectors in this latent space induces a sum of approximate sinc kernels in the domain. The sinc function can be corrected to provide an admissible kernel for density estimation through rectification with an appropriate scalar bias, which is precisely the transformation performed by a rectified linear neuron:

$$a_n \approx \max\left\{0, \sum_{b=1}^{B} \alpha_b \text{sinc}(\|\boldsymbol{x} - \boldsymbol{x}_b\|) - \xi\right\}$$

Activity-dependent weight update

One approach to estimating the probability density of an observation $\boldsymbol{x}$ under the unknown generating distribution $\mathcal{S}$ is to construct a kernel density estimator using K samples drawn from $\mathcal{S}$ and a non-negative kernel function f_h, to produce the estimator $P(\boldsymbol{x} \sim \mathcal{S}) = \frac{1}{K}\sum_{k=1}^{K} f_h(\boldsymbol{x} - \boldsymbol{x}_k)$, where h is the bandwidth of the estimator. This definition can be rewritten due to the fact that kernel functions can be approximated by the dot product between vectors in some higher-dimensional space defined by mapping ϕ from the domain:

$$P(\boldsymbol{x} \sim \mathcal{S}) = \frac{1}{K}\sum_{k=1}^{K} f_h(\boldsymbol{x} - \boldsymbol{x}_k)$$
$$\approx \phi_h(\boldsymbol{x}) \cdot \frac{1}{K}\sum_{k=1}^{K} \phi_h(\boldsymbol{x}_k) \quad = \quad \phi_h(\boldsymbol{x}) \cdot \mathbb{E}[\phi_h(\boldsymbol{X})]$$

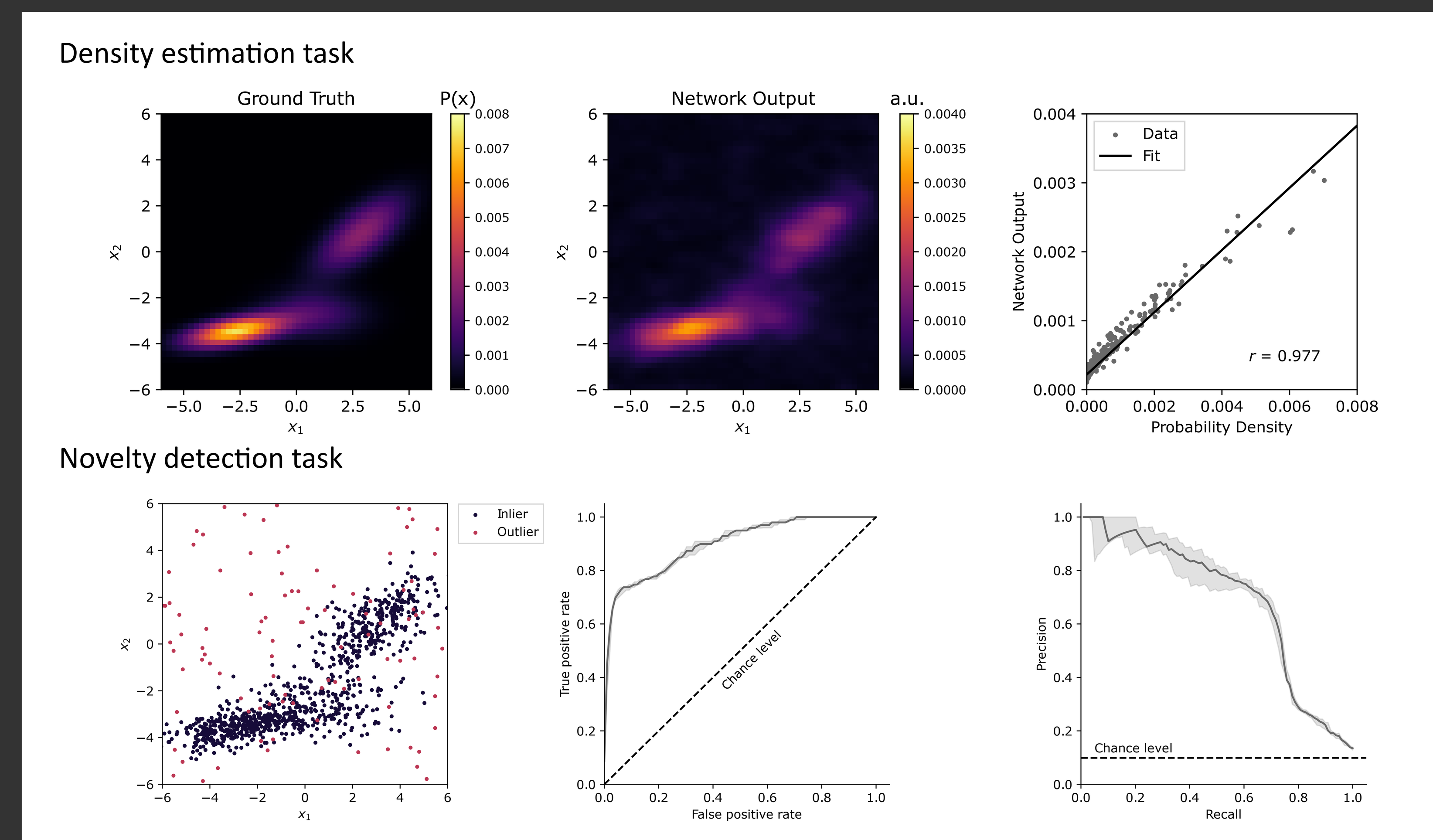
The expectation quantity $\mathbb{E}[\phi_h(\boldsymbol{X})]$ refers to the mean vector of the embedding, and $\boldsymbol{X}$ is a database of K samples. In this way, the mean vector provides a compressed representation of the distribution to evaluate the density at some point. In this model, we can identify $\phi_h(\boldsymbol{x}) = \mathcal{A}(\psi(\boldsymbol{x}/\lambda))$, where $\mathcal{A}(\cdot)$ describes the projection of the SSP input into the space of activities in the KC layer. Therefore, applying the update rule

$$\Delta w = \frac{a_n}{\sum_m a_m}$$

at each observation will enable learning of a vector aligned with the mean vector $\mathbb{E}[\mathcal{A}(\psi(X/\lambda)]$, which is just the KC activities averaged across samples in the dataset, X. As this update rule is based solely on presynaptic activity in KCs, it is consistent with the biological mechanism of KC-MBONα'3 synaptic weight modulation by dopaminergic neurons (Hattori et al 2017). Normalization across neuron activities, meanwhile, ensures that samples contribute equally to the overall estimate, as the representation can cause differences in total activity in the KC layer from sample to sample.

Output: probability estimate

3. Locust circuit model performs density estimation and novelty detection



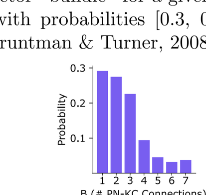
4. Fruit fly circuit modelling: incorporating neurobiological details reproduces KC responses

1. Respect PN-KC connectivity patterns

KCs receive input from 1-10 PNs (Gruntman & Turner, 2008). We model this by first sampling vectors from the manifold of the latent representation, and constructing KC encoders by equally-weighted combinations of these vectors:

$$e_n = \frac{1}{B}\sum_{b=1}^{B} \psi(x_b/\lambda)$$

The number of components in a vector "bundle" for a given cell, in turn, were drawn from a discrete distribution over the range [1,7] with probabilities [0.3, 0.25, 0.2, 0.1, 0.05, 0.05, 0.05], in rough agreement with the actual data (Gruntman & Turner, 2008).



2. Match observed sparsity

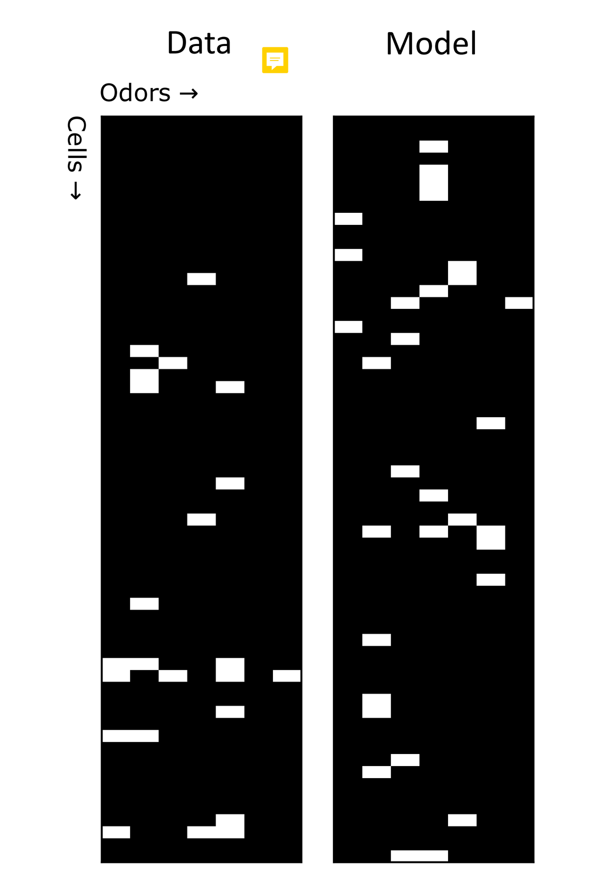
In the fruit fly, KCs are 94% sparse; or have an average response probability of 6% (Turner et al, 2008). To mimic this activity, we derived a relationship between bias on the ReLU neuron ξ, the dimensionality of the representational manifold D, and the proportion of the input space for which individual neurons are active, on average. It may be shown that ρ is related to D and ξ through:

$$\rho = \frac{1}{2} I_{1-\xi^2}\left(\frac{D-1}{2}, \frac{1}{2}\right) \qquad \xi \leq 0$$

Where I is the regularized incomplete beta function, and which may be rearranged to solve for ξ given fixed $D = 1024$ and a desired ρ:

$$\xi = \sqrt{1 - I_{2p}^{-1}\left(\frac{D-1}{2}, \frac{1}{2}\right)}$$

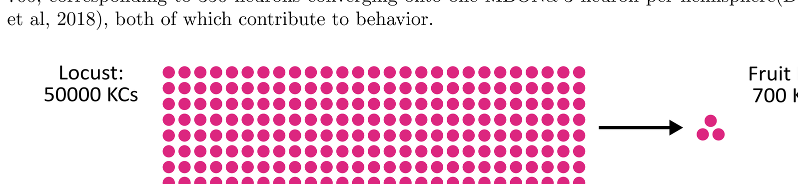
Where I^{-1} is the inverse of the regularized incomplete beta function.



5. Fruit fly circuit modelling: imposing constraints preserves novelty detection computation

3. Reduce KC population size to match that of D. Melanogaster

The locust model estimated probability density with 50000 KCs, however the size of the fruit fly mushroom body is much smaller. We imposed this constrain by setting the KC population size to 700, corresponding to 350 neurons converging onto one MBONα'3 neuron per hemisphere(Dasgupta et al, 2018), both of which contribute to behavior.



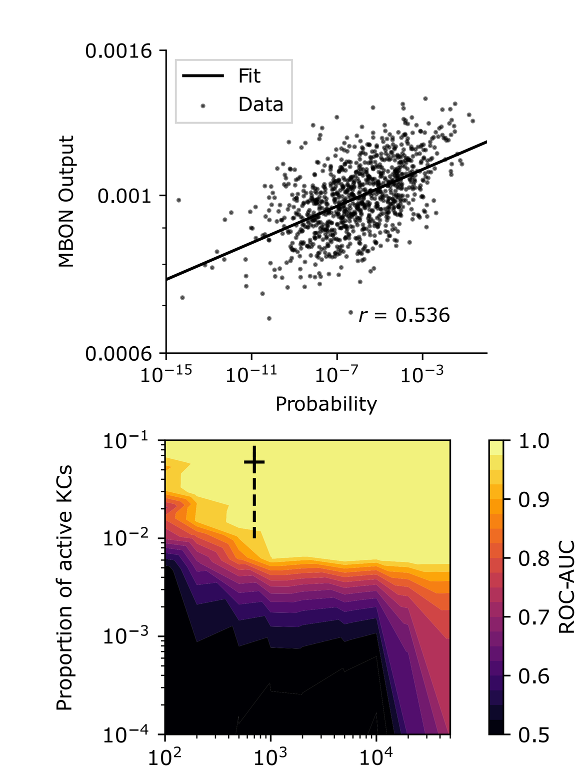
The scatterplot on the right shows a monotonically increasing relationship between network output and the ground-truth probability, indicating that a basic capacity for density estimation has been preserved.

4. Compute without normalizing across neuron activities

The computational model uses a learning rule that relies on normalizing activities across KCs. To our knowledge, however, direct experimental evidence for normalization is lacking. We therefore assess performance with a weight computation based on only on an individual KC's activity averaged across samples in the dataset:

$$w_n = \frac{1}{K}\sum_{k=1}^{K} a_{k,n}$$

The plot to the right shows the performance landscape as measured by the area under the curve of the receiver-operator characteristic (AUC-ROC) with this learning rule on a 50-dimensional novelty detection task, over a range of sparseness and population sizes. The + marker indicates the actual average operating point of the fruit fly, and the dotted line indicates a range of sparsity levels observed.



6. Conclusion

Density estimation is a promising proposal for the algorithm underlying insect novelty detection. These findings uphold this interpretation by showing how it applies when constrained by the neurobiology of the fruit fly. We therefore offer a viable alternative to the Bloom filter interpretation (Dasgupta et al, 2018).

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