Local pairwise correlations and network states in cat primary visual cortex

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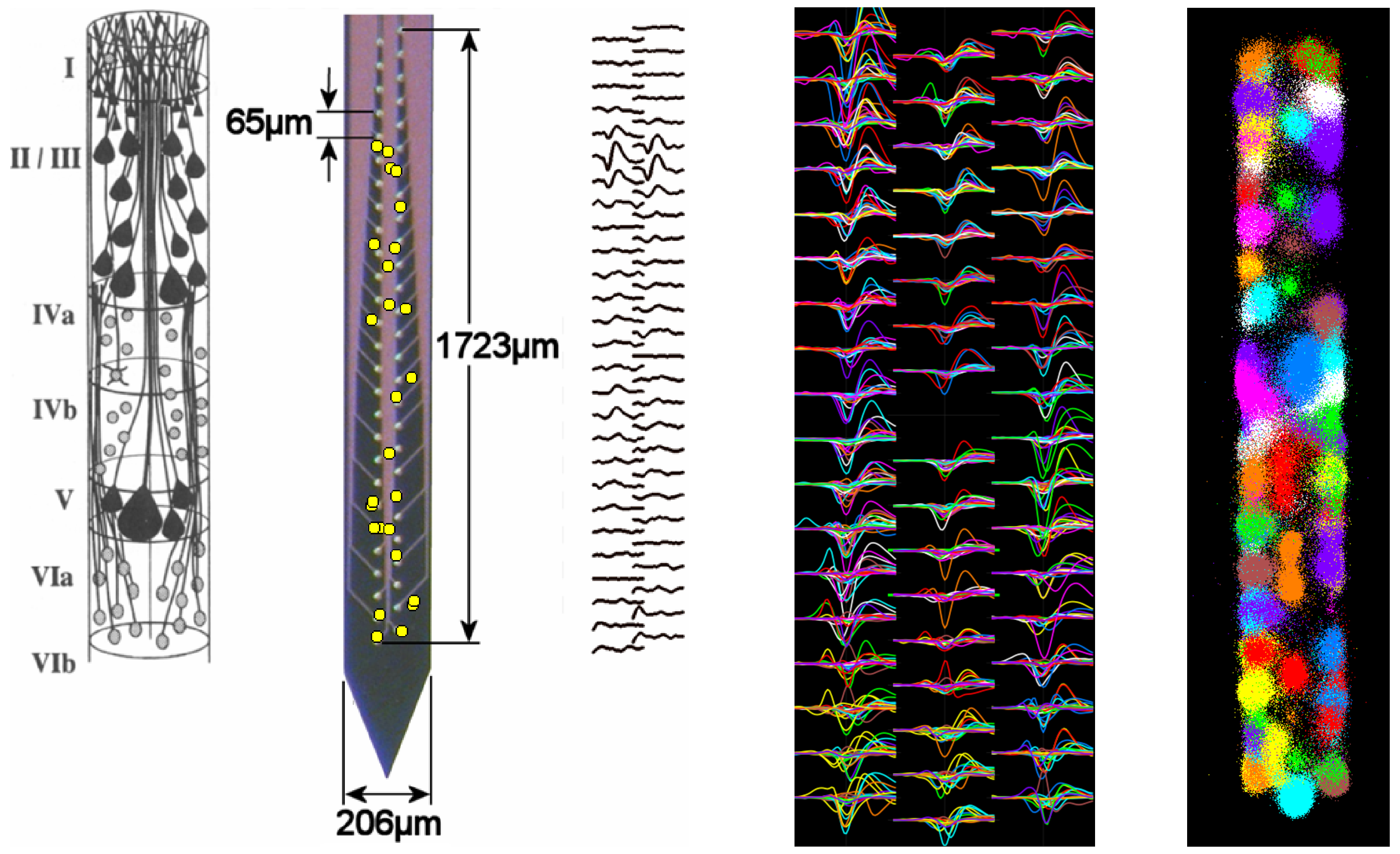
Introduction

Schneidman et al. (2006) showed that weak pairwise correlations are prevalent in retinal ganglion cell (**RGC**) networks *in vitro*, and that their influence on network behaviour is significant, yielding predictions of network state probabilities orders of magnitude better than if the cells were assumed to be independendent. Furthermore, the influence of higher-order correlations was deemed insignificant. Shlens et al. (2006) additionally found that not only pairwise, but *local* pairwise correlations were sufficient to explain RGC activity. These results point to useful simplifications that reduce what could be a combinatorial explosion involving many higher-order neuronal correlations into a much more tractable (local) pairwise problem. This makes analysis considerably easier for the experimenter, and perhaps decoding easier for downstream areas in the brain.

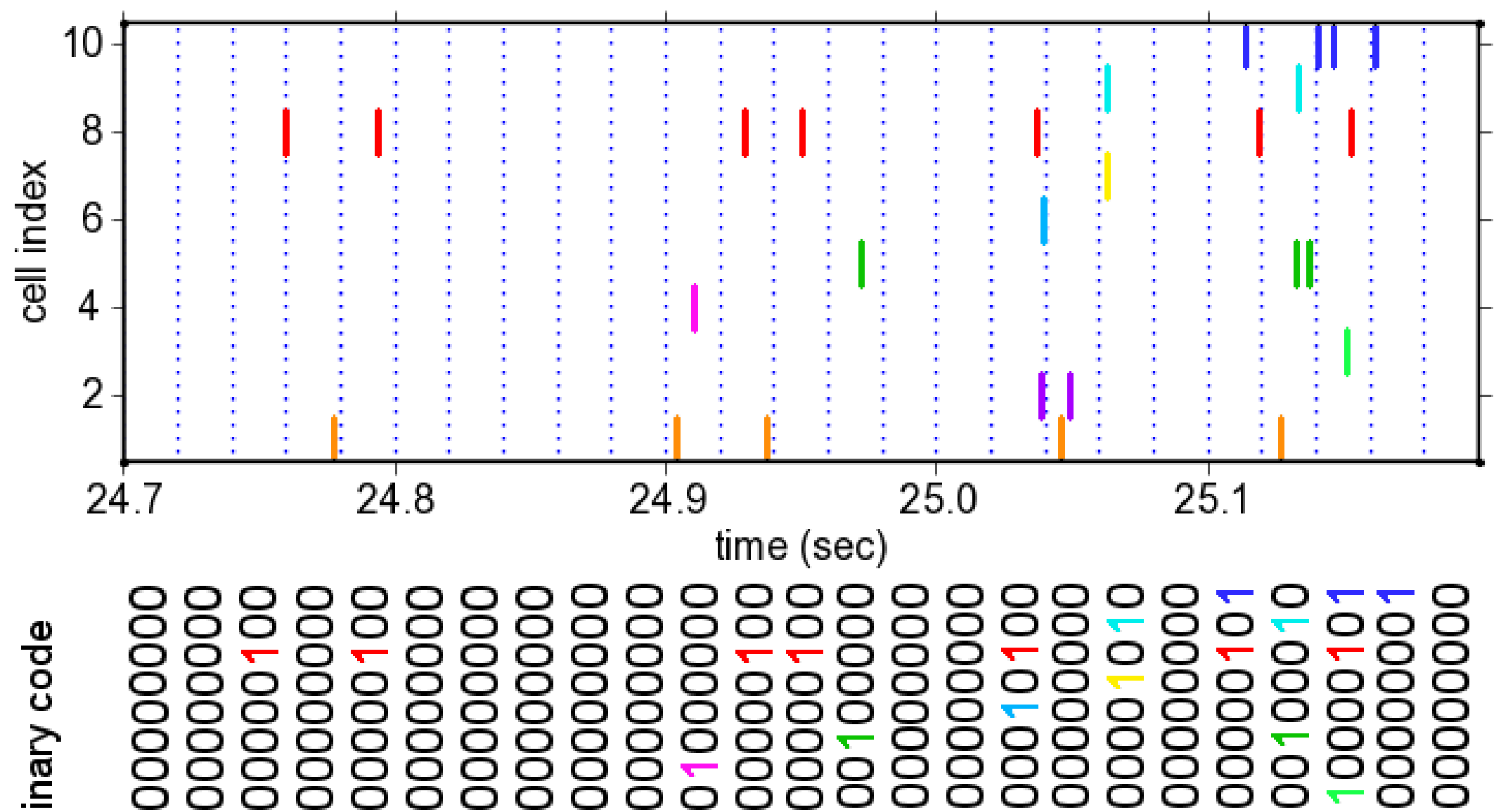
We wondered: **do these results generalize to *in vivo* cortical networks?**

Methods

We recorded extracellularly from up to 150 multiple units in area 17 (**V1**) of anesthetized cat using silicon polytrodes[3] (*below*) and a variety of natural and artificial visual stimuli.



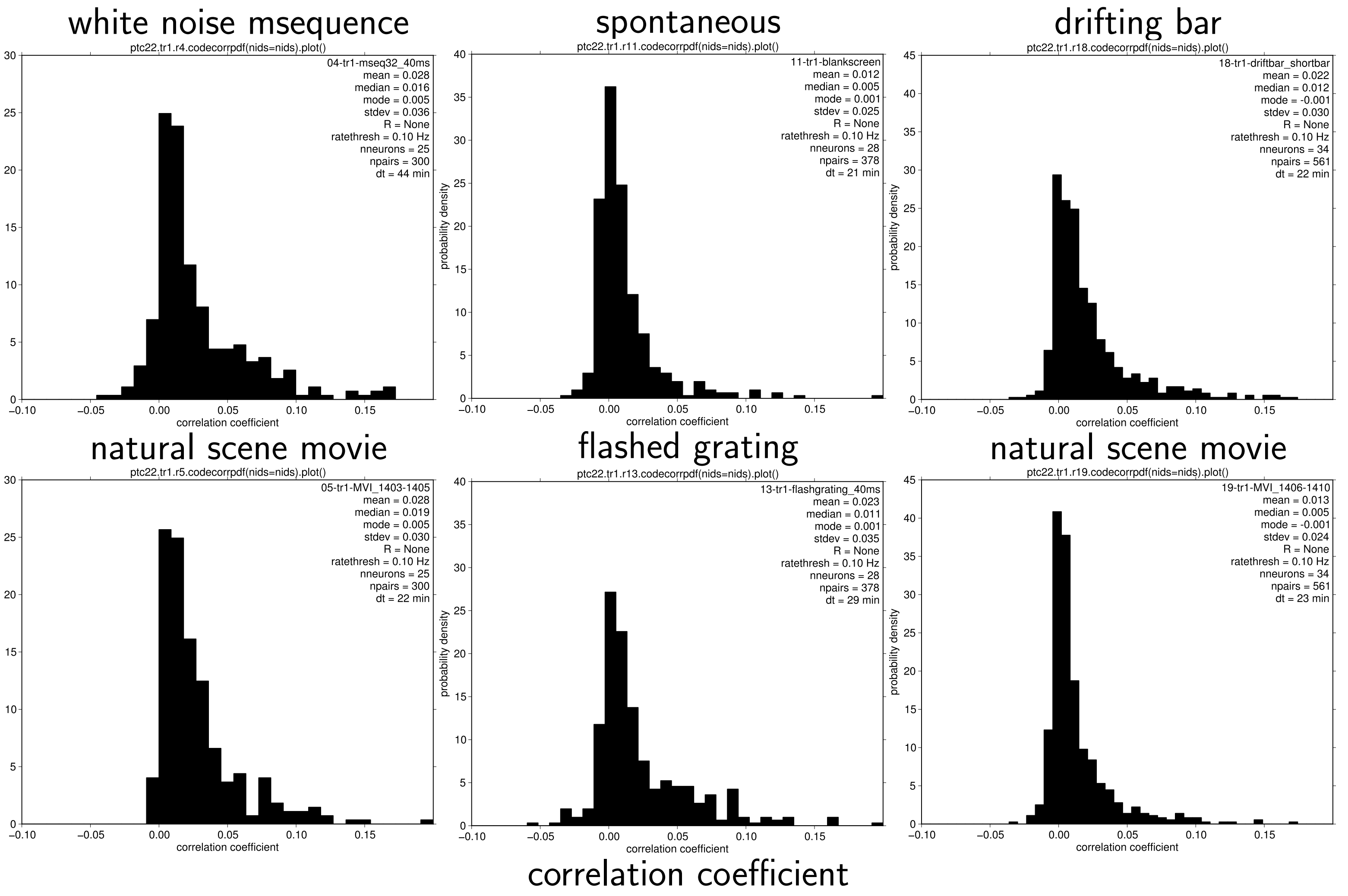
Spike trains were binned and digitized to create temporal binary codes (*rows, lower panel*). If a neuron spiked one or more times within a time bin, its activity was represented by a 1 in that bin. Otherwise, its activity was represented by a 0. Taking the binary codes of all the neurons together, the **network state** at any time bin could then be represented as a binary word of length N neurons (*columns, lower panel*).



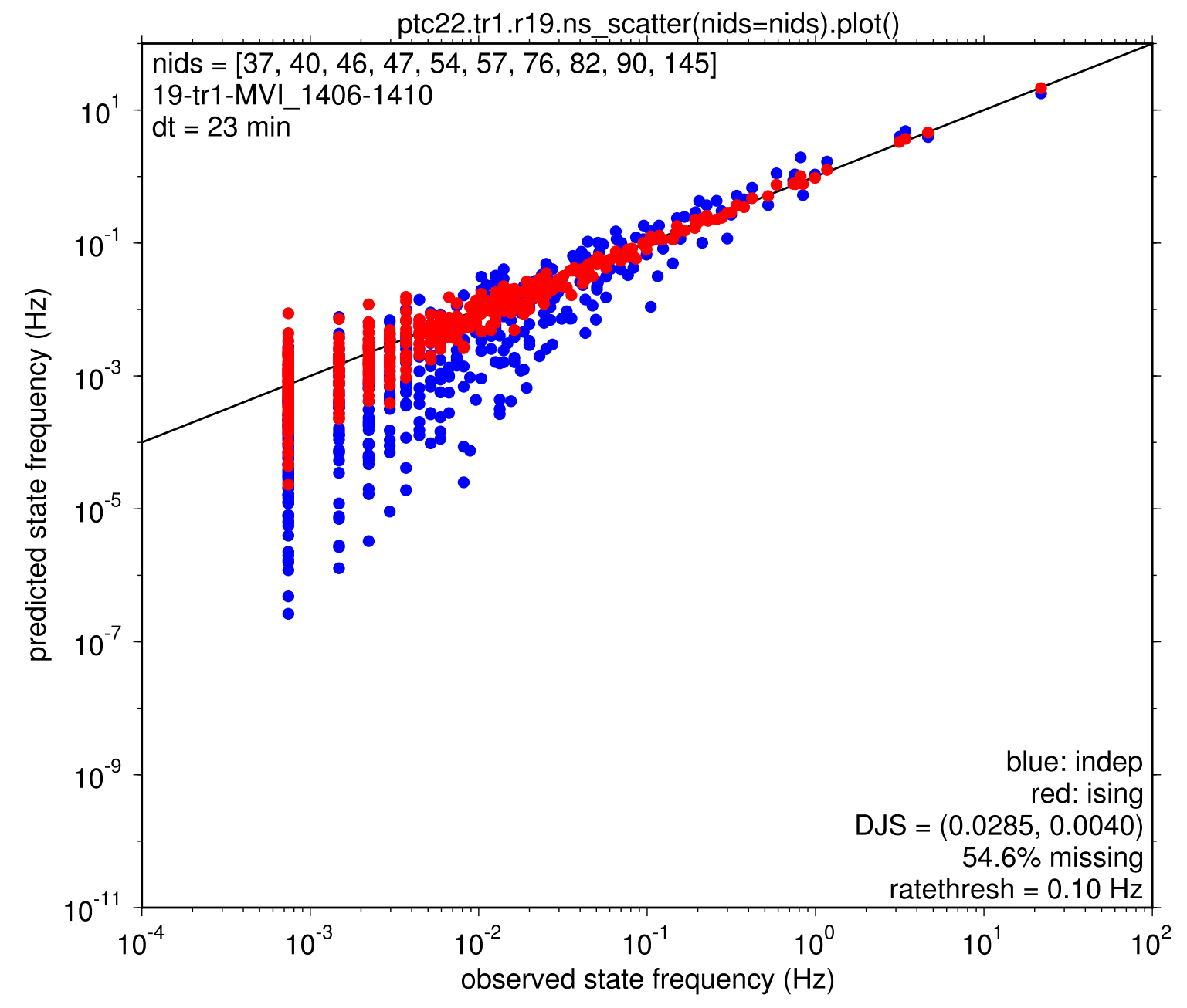
$$\rho = \frac{\overline{xy} - \bar{x}\bar{y}}{\sigma_x \sigma_y} \qquad (1)$$

The correlation coefficient (ρ) of a pair of neurons was calculated by **Eq 1**, where x and y are the binary codes of the two neurons, and $\overline{xy}$ is the mean of the element-wise product of the two codes. ρ was calculated for all possible neuron pairs. 0s are replaced with -1s when calculating ρ.

Results



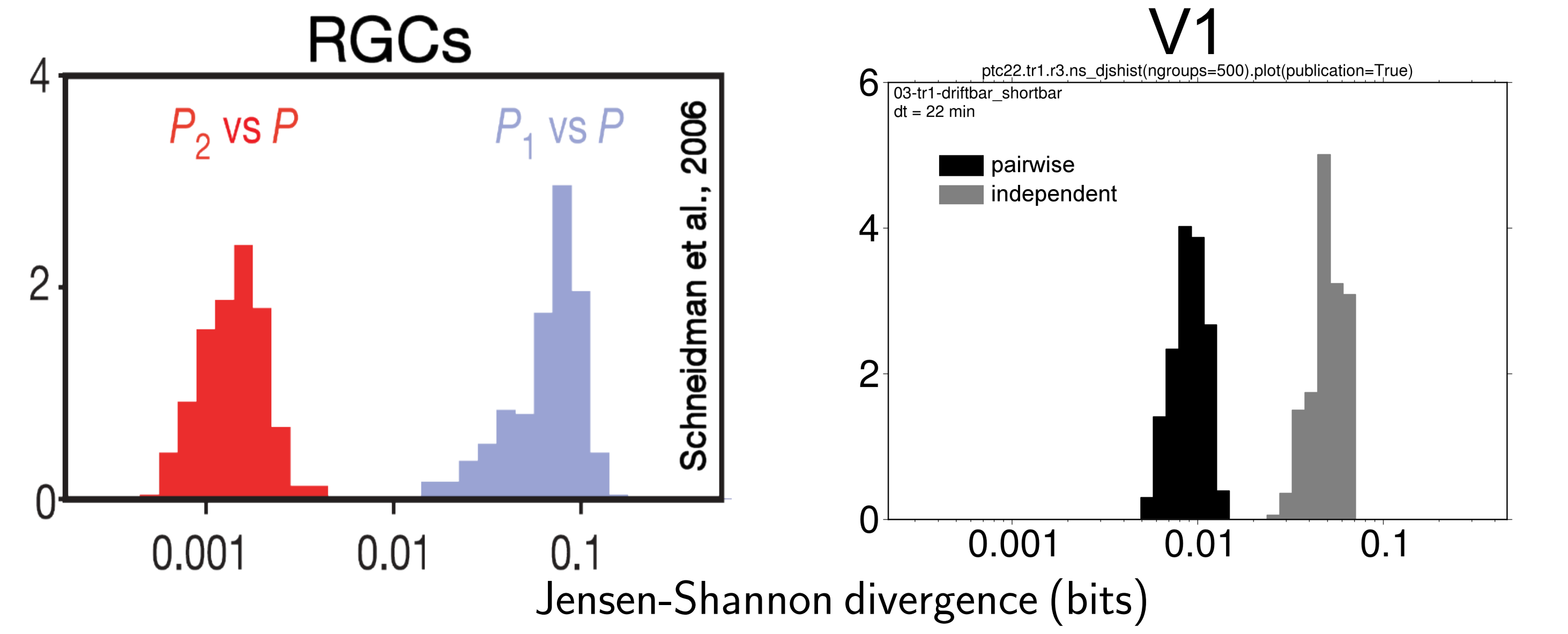
We found $\bar{\rho} \sim 0.01$–0.05, slightly higher than $\bar{\rho} \sim 0.01$ in RGCs[1]. ρ distributions in V1 were generally independent of the visual stimulus. This suggests that much of the correlations observed here are not from visual common input.



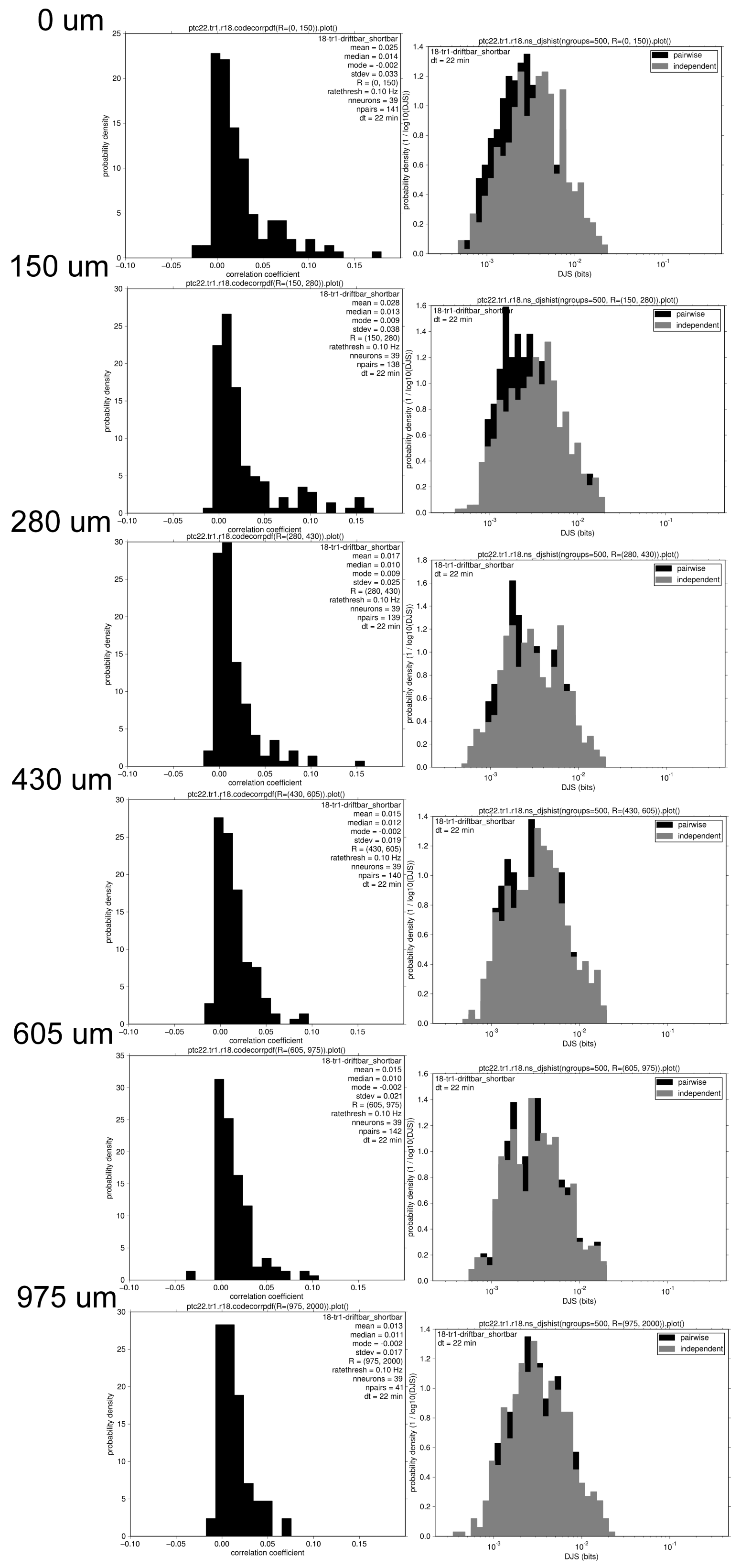
Network state frequencies were scatter plotted (*right*), comparing actual frequencies to those predicted for a given model. For the independent model, network state probabilities are the product of the neuronal state probabilities ($P(101...) = P(1)P(0)P(1)...$). The maximum entropy pairwise model additionally takes into account probabilities of cell pairs being simultaneously active, while maximizing total entropy to prevent introduction of any higher-order correlations. As in RGCs[1], the independent model (*grey*) was orders of magnitude off in many of its network state frequency predictions, and the pairwise model (*black*) performed much better. For the pairwise model, the probability P of a specific network state is given by

$$P(\sigma_1, \sigma_2, ..., \sigma_N) = \frac{1}{Z} \exp\left[\sum_i h_i \sigma_i + \frac{1}{2}\sum_{i \neq j} J_{ij}\sigma_i\sigma_j\right], \qquad (2)$$

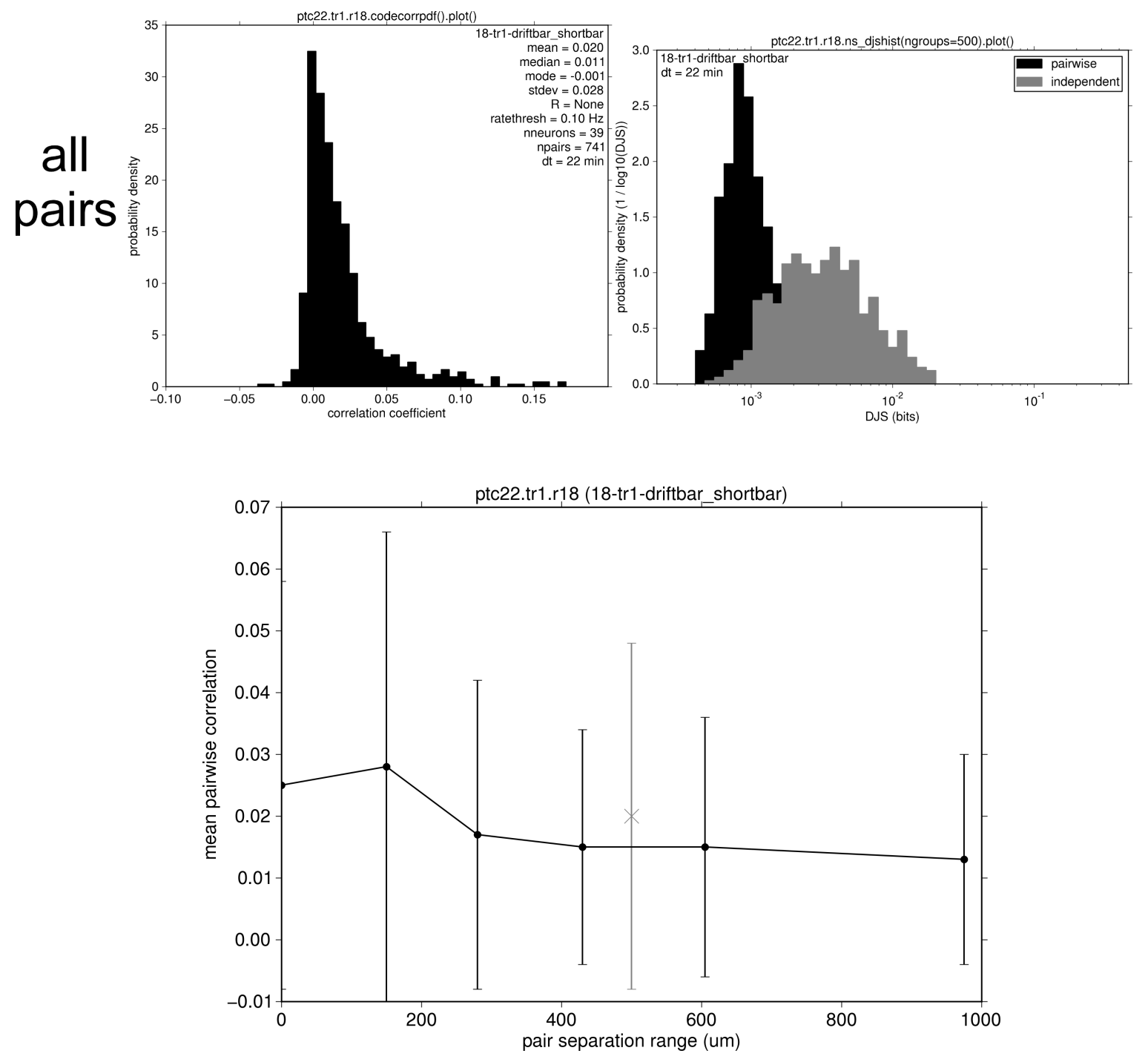
where σ_i is the binary state of neuron i, N is the number of neurons, h_i is the activity weight, J_{ij} is the interaction weight, and Z is the normalizing partition function. The model was fit in Python (`scipy.maxentropy`, conjugate gradients).



Jensen-Shannon divergence (D_{JS}, *above*) was used to measure the amount of network state frequency scatter of a given model from the $y = x$ ($prediction = data$) line. D_{JS} was calculated for 100s of groups of $N = 10$ neurons. The independent model resulted in similarly high prediction scatter in both RGCs and V1. The pairwise model reduced prediction scatter in V1, but not as much as in RGCs. D_{JS} for the pairwise model in V1 was ∼ an order of magnitude higher than in RGCs.



We also calculated *local*[2] correlation coefficient distributions, where only pairs of neurons separated by specific ranges were considered. ρ means generally increased with decreasing pair separation (*left*). This suggests that pairwise correlations tend to be strongest between nearby cells. Next, the pairwise model was limited to local pairwise correlations. When given only distant cell pairs, the model did poorly, but as cell pairs became more local, model performance improved. However, it performed best when given all possible cell pairs. This suggests that local pairwise correlations are the most important ones in predicting network state frequencies.



Conclusions

- V1 has weak pairwise correlations, though they seem stronger than in retina
- A pairwise maximum entropy Ising model does a good job of explaining network state probabilities, but not as good as in retina
- Local pairwise correlations are stronger, and local pairs are more effective at predicting network states than distant pairs
- It's likely that higher than second order correlations are at work in cortex

References

1. Schneidman E, Berry II MJ, Segev R, Bialek W (2006) Weak pairwise correlations imply strongly correlated network states in a neural population. *Nature* 440:1007.
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