Accounting for network states in cortex: are (local) pairwise correlations sufficient?

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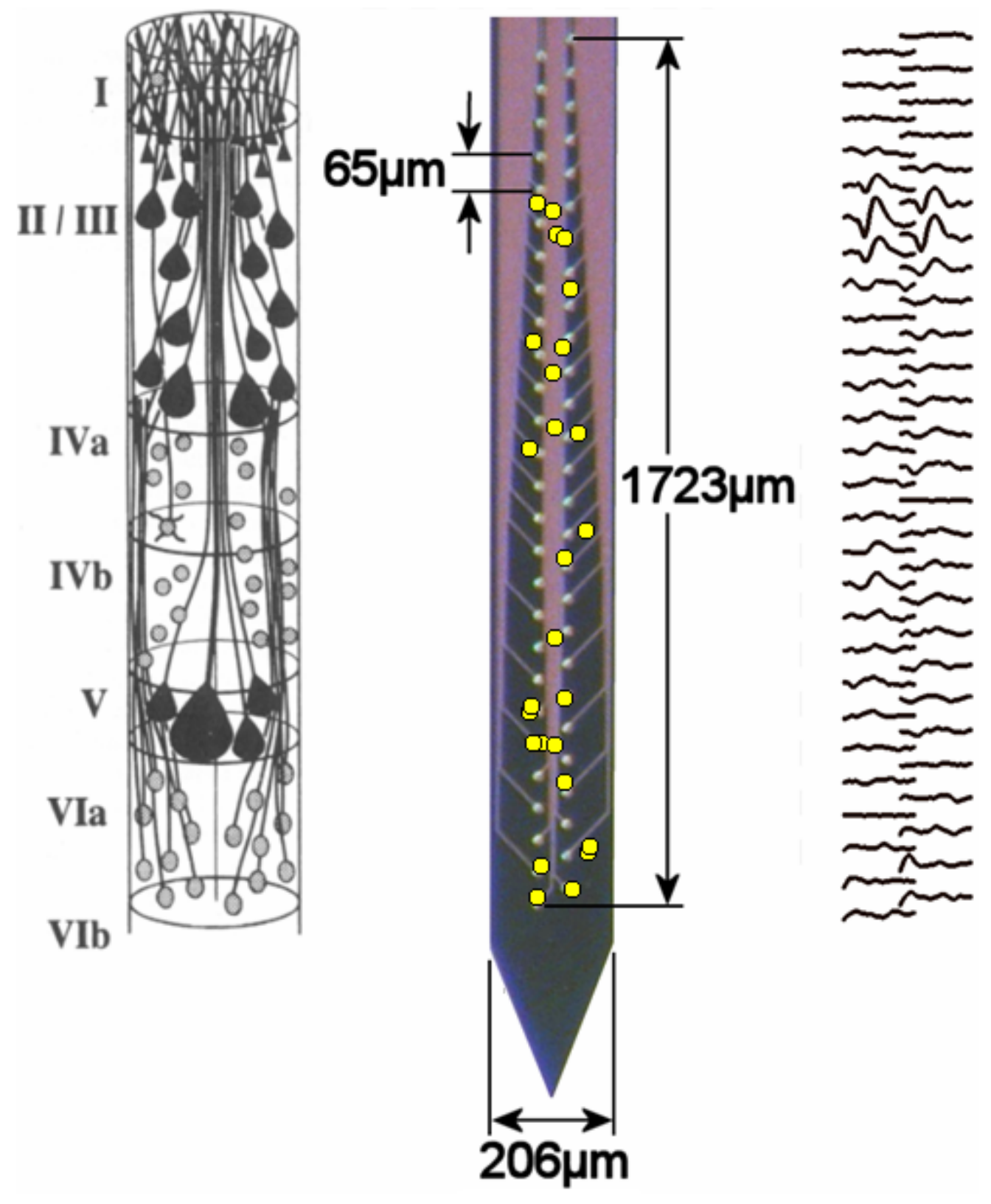
Introduction

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 are assumed to be independent. 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.

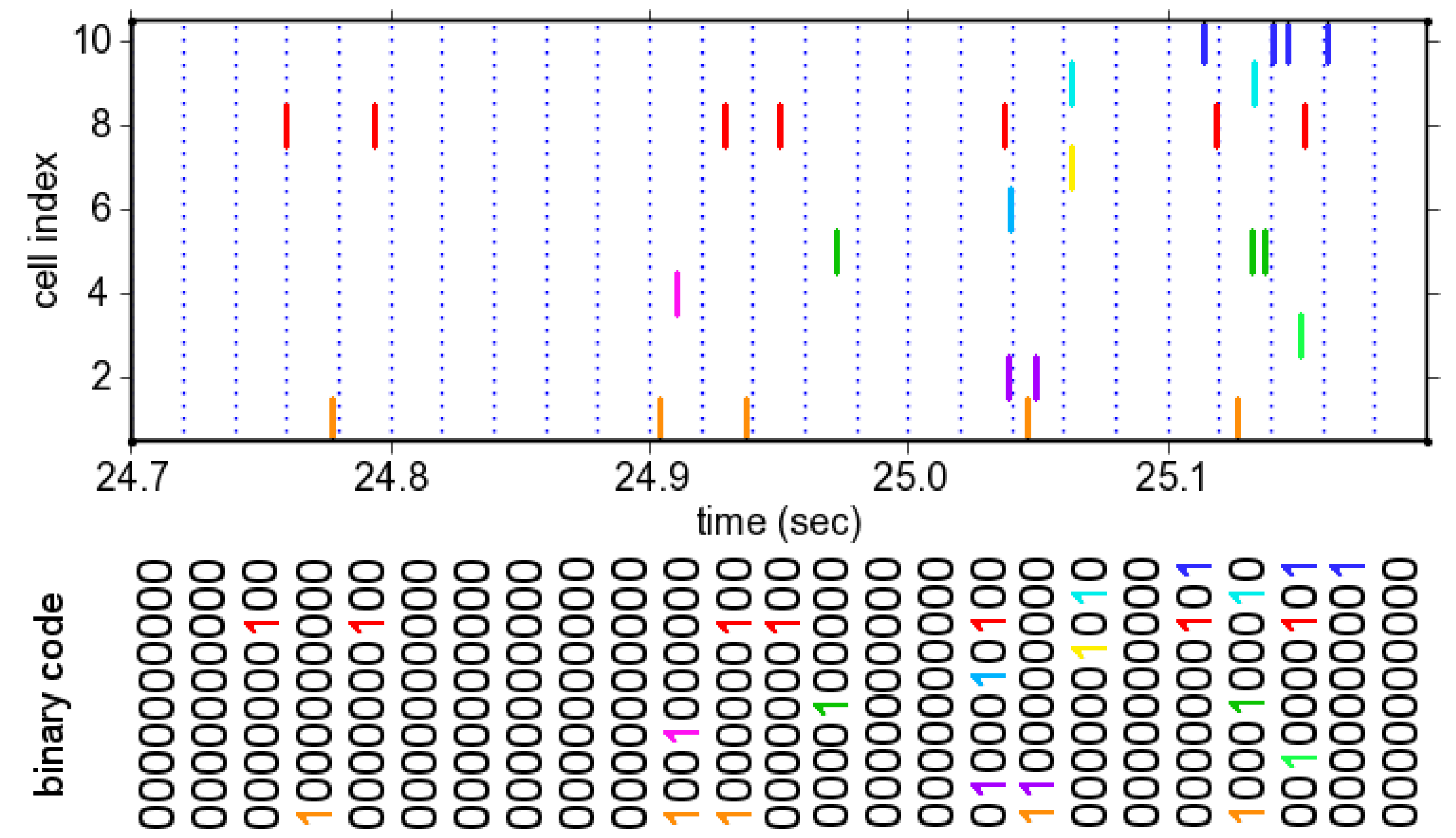
We wondered: **do these results generalize to *in vivo* cortical networks?**

Methods



We recorded extracellularly from multiple units in area 17 (**V1**) of anesthetized cat using silicon polytrodes^3 (*right*) and a variety of natural and artificial visual stimuli. We also recorded with multiple tetrodes in awake behaving rat pre-frontal cortex (**PFC**) during a radial arm maze task.

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



Typically, groups of $N = 10$ neurons and bin widths of $T = 20$ ms were used. Results were insensitive to changes of $\sim$ an order of magnitude of these parameter values. Results were also insensitive to temporal bin phase.

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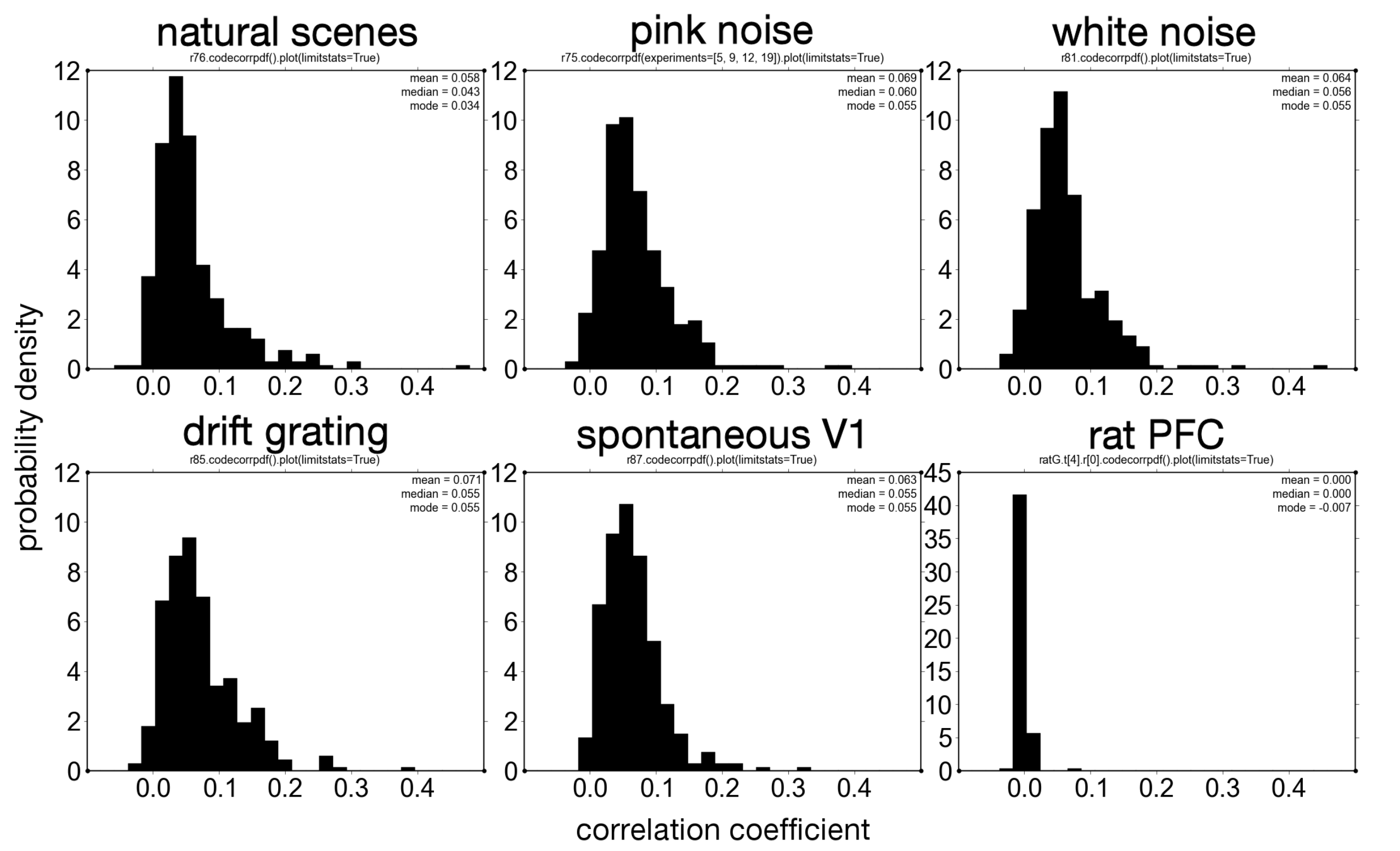
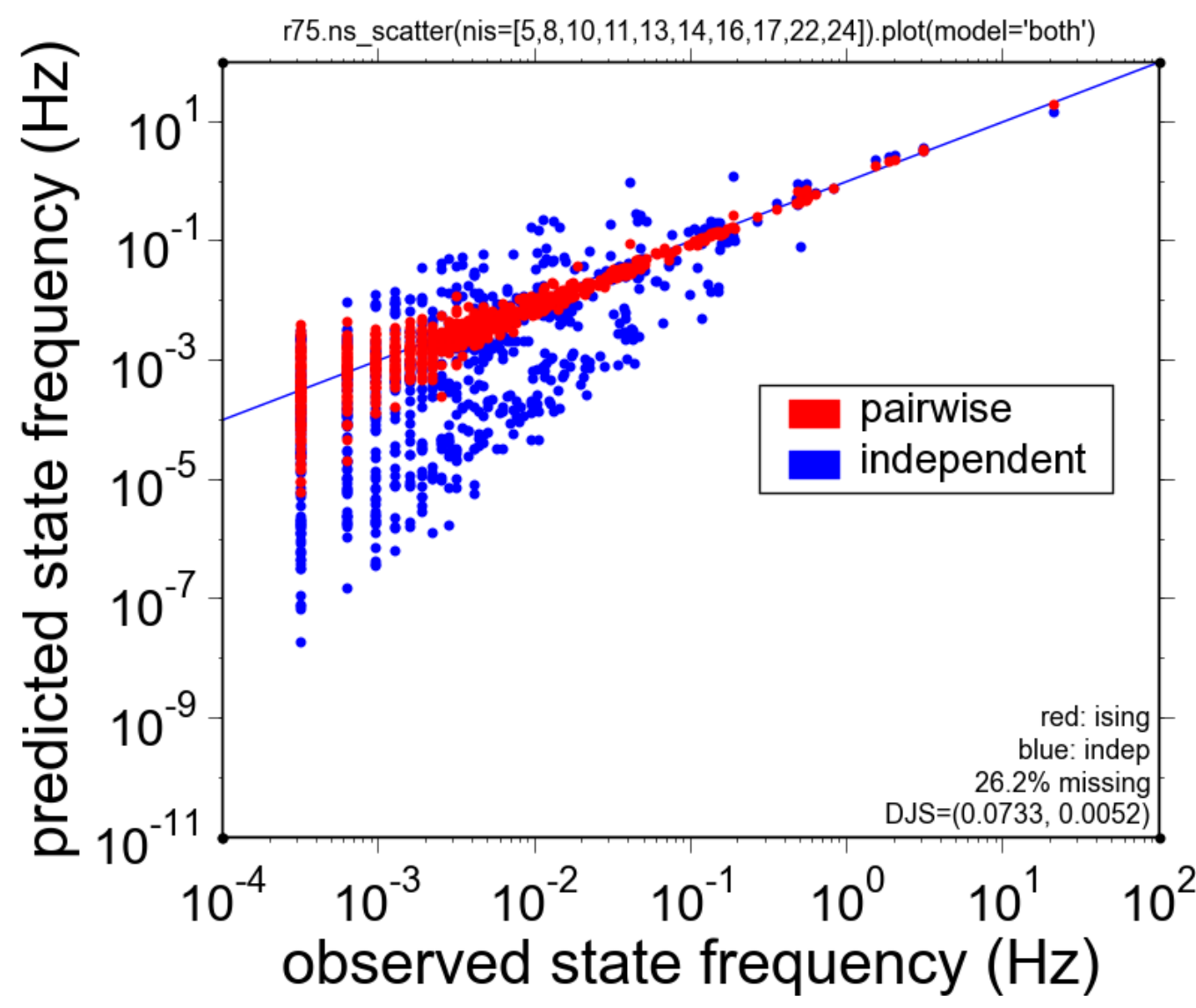
$$\rho = \frac{\overline{xy} - \bar{x}\bar{y}}{\sigma_x \sigma_y} \qquad (1)$$

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.

Results



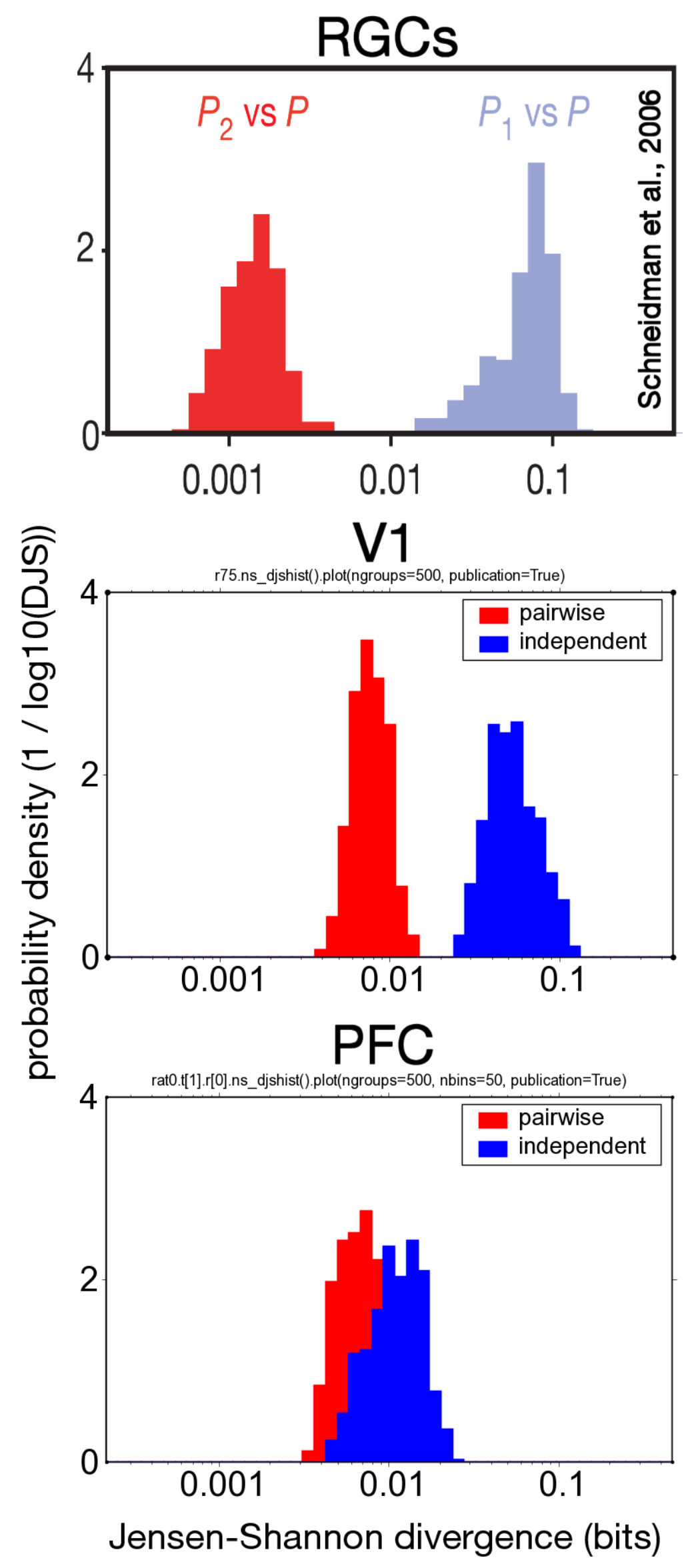
In V1, $\bar{\rho} \sim 0.05$–0.07, substantially more than $\bar{\rho} \sim 0.01$ in RGCs[1]. Furthermore, ρ values in V1 were generally independent of the visual stimulus used. This suggests that spatial correlations in stimuli such as natural scene movies are removed by the time they reach V1. In comparison, rat PFC had no correlations whatsoever ($\bar{\rho} = 0.00$). This might be related to the highly sparse firing we found in PFC.



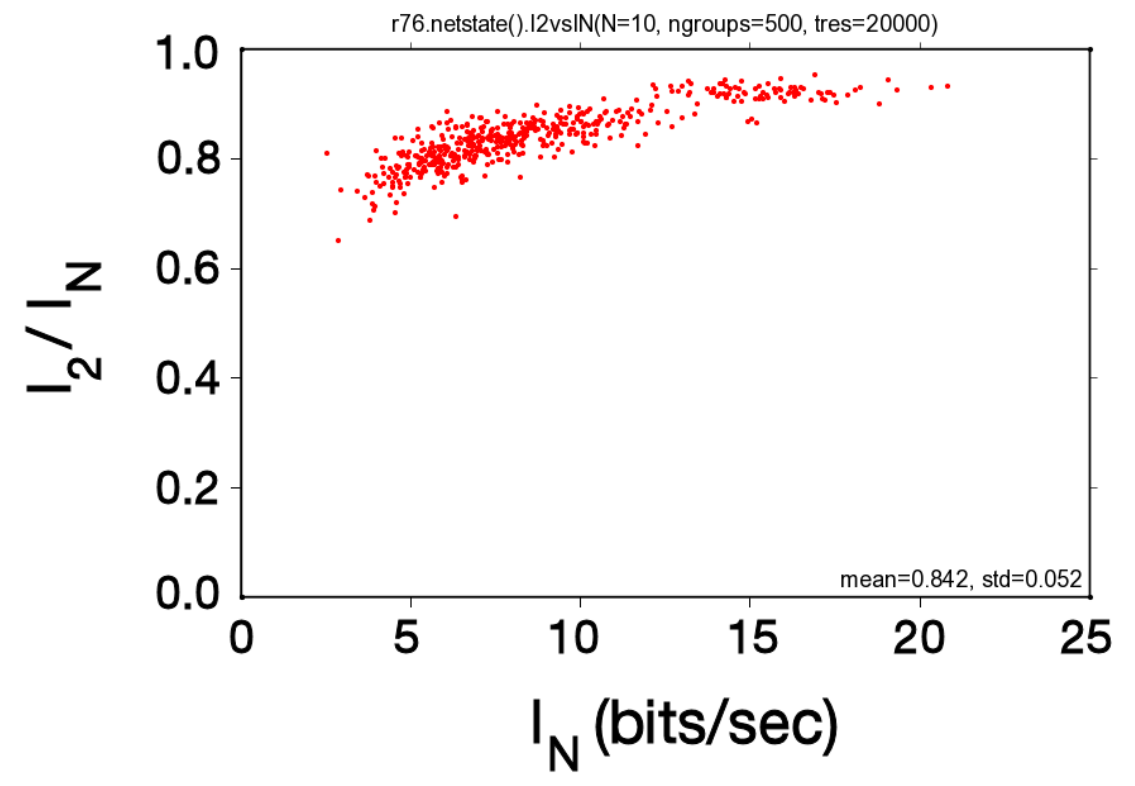
Network state frequencies were scatter plotted (*right*), comparing actual frequencies to those predicted for a given model. For the independent model, network state probabilities are the product of the neuronal state probabilities ($P(101...) = P(1)P(0)P(1)...$). The maximum entropy pairwise model additionally 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 (*blue*) was orders of magnitude off in many of its network state frequency predictions, and the pairwise model (*red*) 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.maxent`, conjugate gradients).

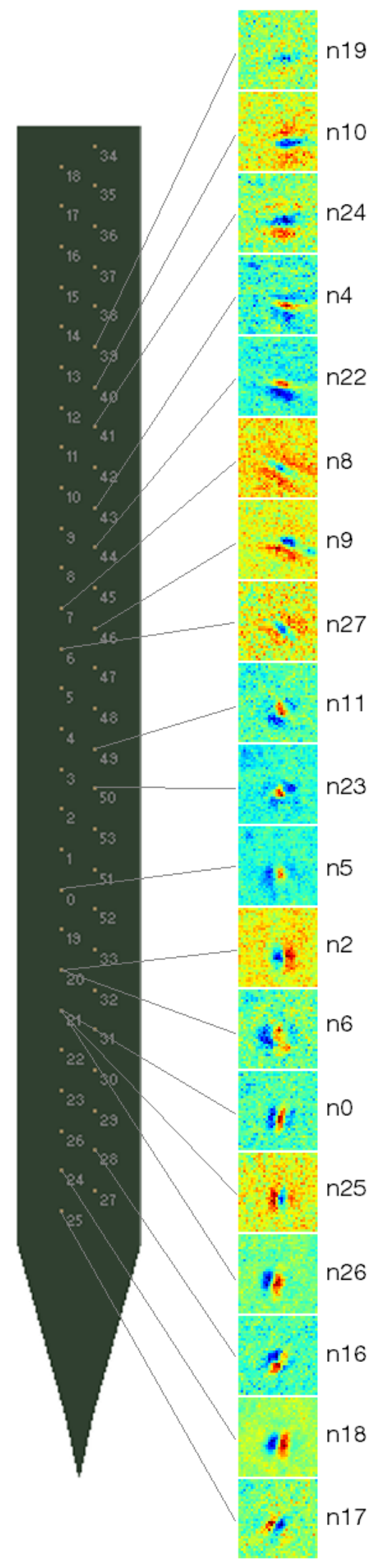


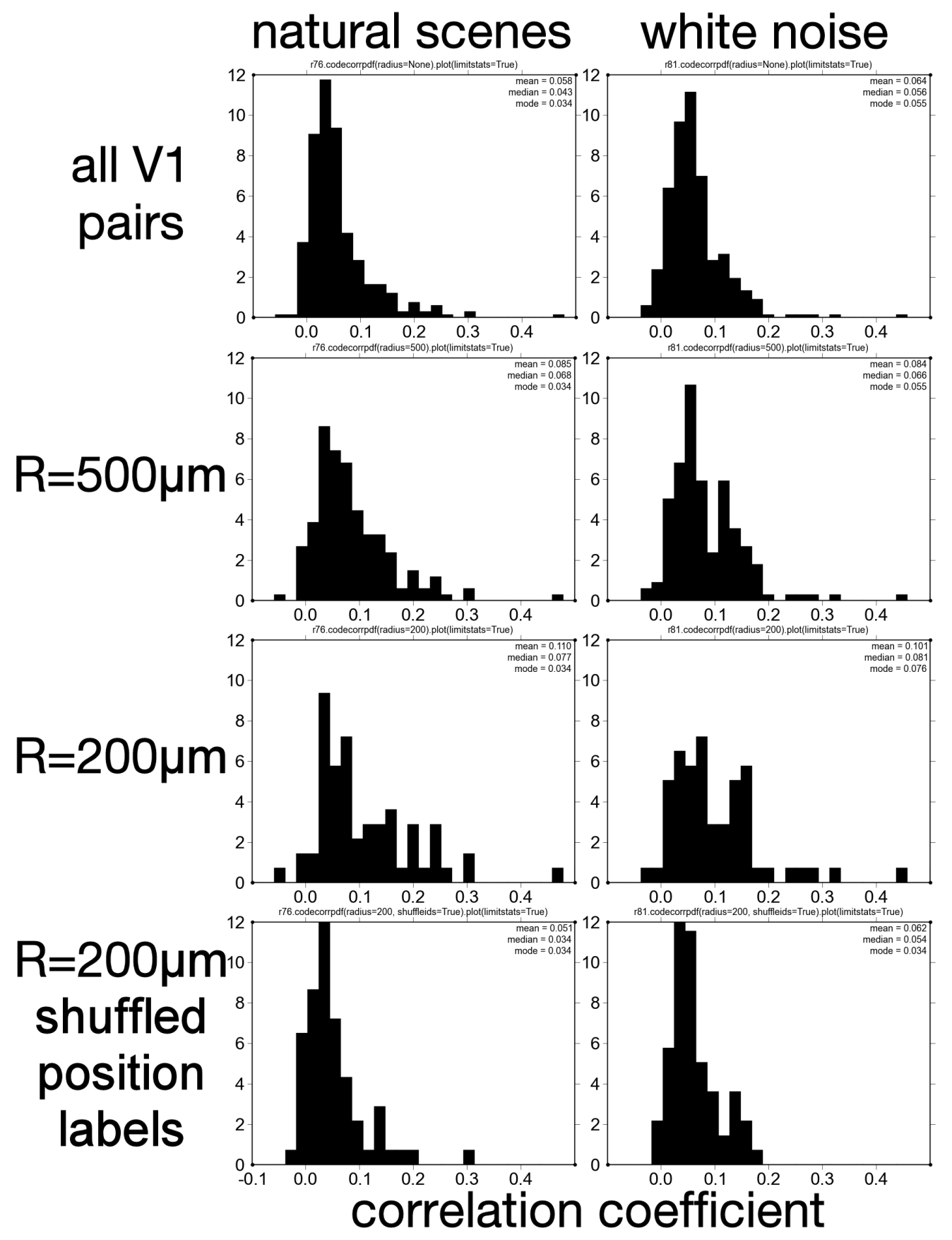
Jensen-Shannon divergence (D_{JS}, *right*) was used to measure the amount of network state frequency scatter of a given model from the $y = x$ ($prediction = data$) line. D_{JS} was calculated for 500 groups of $N = 10$ neurons. The independent model resulted in equally high prediction scatter in both 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 $\sim$ an order of magnitude higher than in RGCs. In rat PFC, the pairwise model showed almost no improvement over the independent model. This is sensible, given that pairwise correlations in PFC were non-existent (*left*).



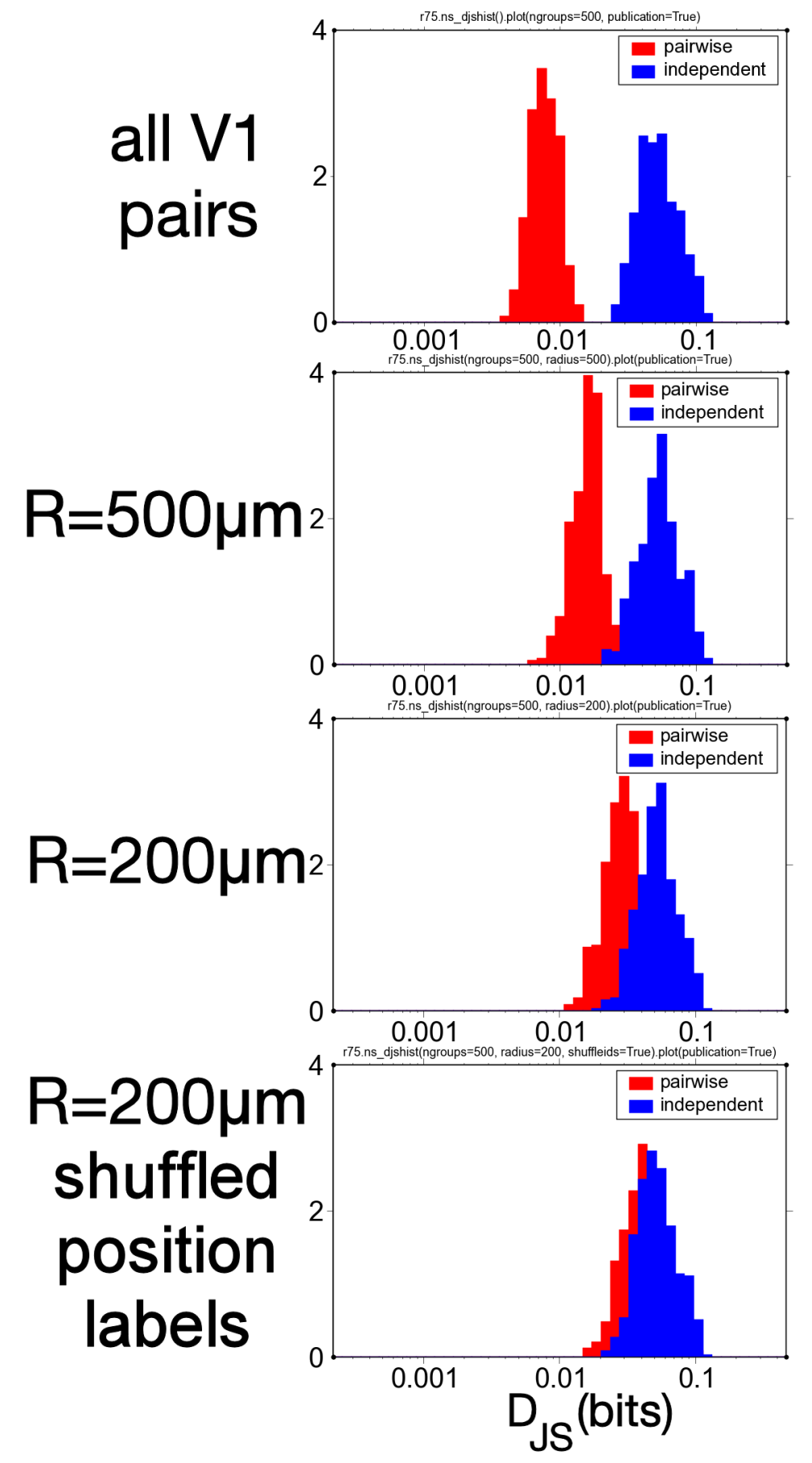
In V1, the pairwise model accounted for 80–85% of reduction in entropy due to correlations (*above*), $\sim$ 10% less than in RGCs[1]. I_2 and I_N are, respectively, entropy reductions due to pairwise correlations and those due to all order of correlations. Again, these were calculated for 500 groups of $N = 10$ neurons.

Results shown here came from a 26 neuron transcolumnar recording (*right*). We expect stronger pairwise and higher-order correlations in columnar recordings, and we expect that these will make the pairwise model perform worse, further differentiating the results in V1 from those in RGCs.





We also constrained the analysis to *local* pairwise correlations[2], where only pairs of neurons within a radius R were considered. ρ distributions generally broadened with decreasing R (*left*). Shuffling neuron positional labels mostly recovered distribution shape. This suggests that pairwise correlations tend to be strongest between nearby cells.



Next, the pairwise model was limited to local pairwise correlations. As R decreased, the pairwise model was given fewer ρ values, and network state frequency prediction gradually degraded (*right*). At $R = 200\mu$m, only a small fraction of possible ρ values were available. Given these, the pairwise model performed only marginally better than the independent model (*3rd panel*). After shuffling neuron position labels, the same small fraction of ρ values was provided to the pairwise model, but now the cells were randomly distributed in space. Non-locality, on top of a scarcity of ρ values, wiped out any advantage the pairwise model had over the independent model (*bottom panel*). This suggests that local pairwise correlations are the most important ones in predicting network state frequencies.

Conclusions

- Pairwise correlations were weak *in vivo* in V1, but were stronger than reported *in vitro* in RGCs. Their strengths were generally invariant to different visual stimuli with different spatiotemporal structure. In awake behaving rat PFC, pairwise correlations were non-existent.
- In V1, ignoring pairwise correlations and assuming independence resulted in poor predictions of network state frequencies. In V1, using a pairwise maximum entropy model greatly improved these predictions, but by $\sim$ an order of magnitude less than in RGCs. The pairwise model offered no improvement in rat PFC.
- It was suggested that weak pairwise correlations may be important and sufficient for explaining neuronal network states in non-RGC networks[1,2]. Here we show *in vivo* that pairwise correlation strengths are different in cortex, that they depend on cortical area (and perhaps species/anesthesia), and that as a result, they need not always be important or sufficient for explaining network state frequencies.
- Local pairwise correlations in V1 seem to be the strongest, and have the greatest influence on network state frequencies. However, unlike in RGCs[2], local pairwise correlations on their own seem insufficient to explain network behaviour in V1.
- Pairwise correlation strengths seem key: too weak and they have no influence (awake behaving rat PFC); too strong and a pairwise model becomes less effective (anesthetized cat V1), perhaps because as pairwise correlations increase past some threshold, higher-order correlations inevitably arise[4].

References

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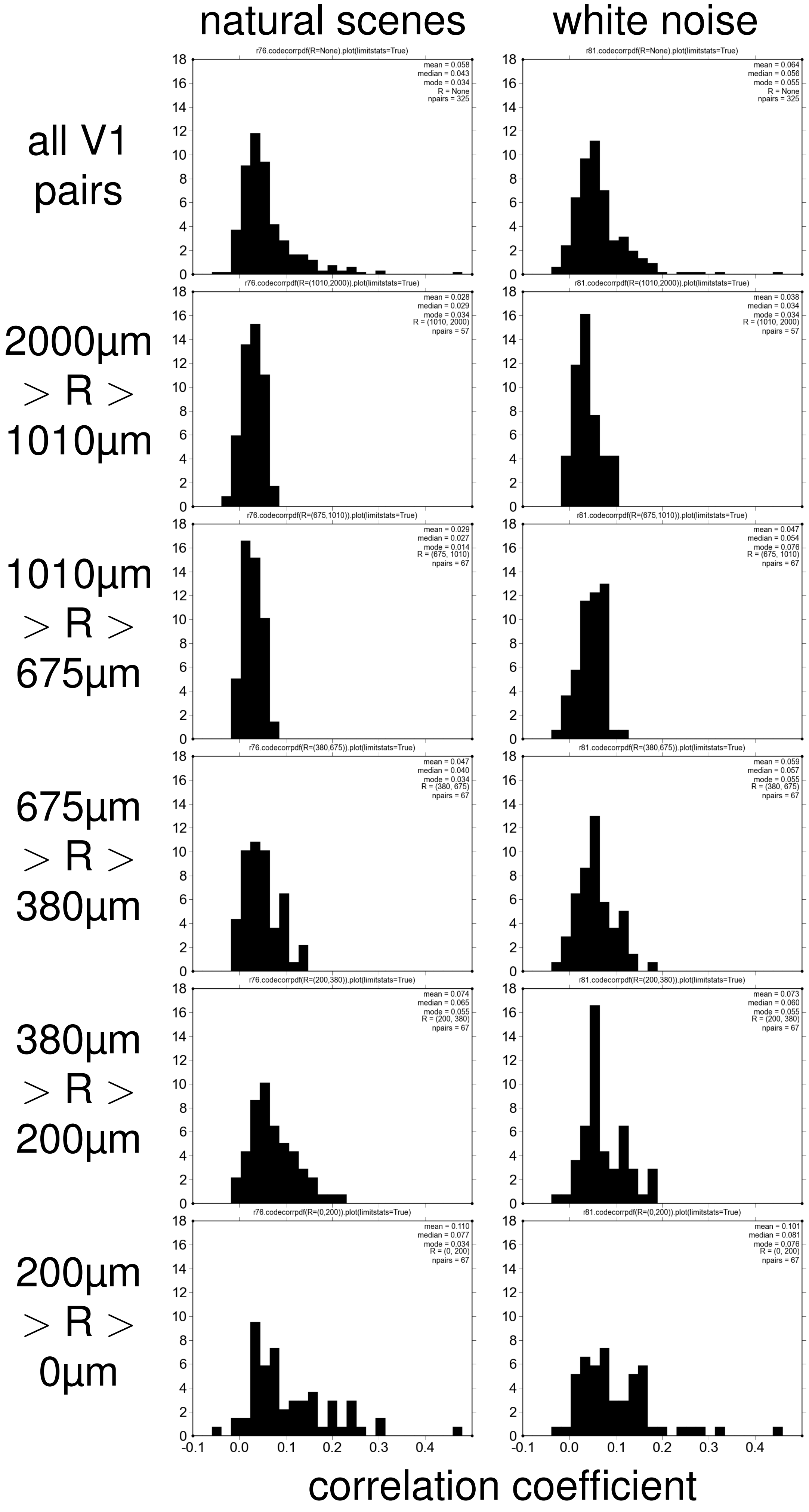
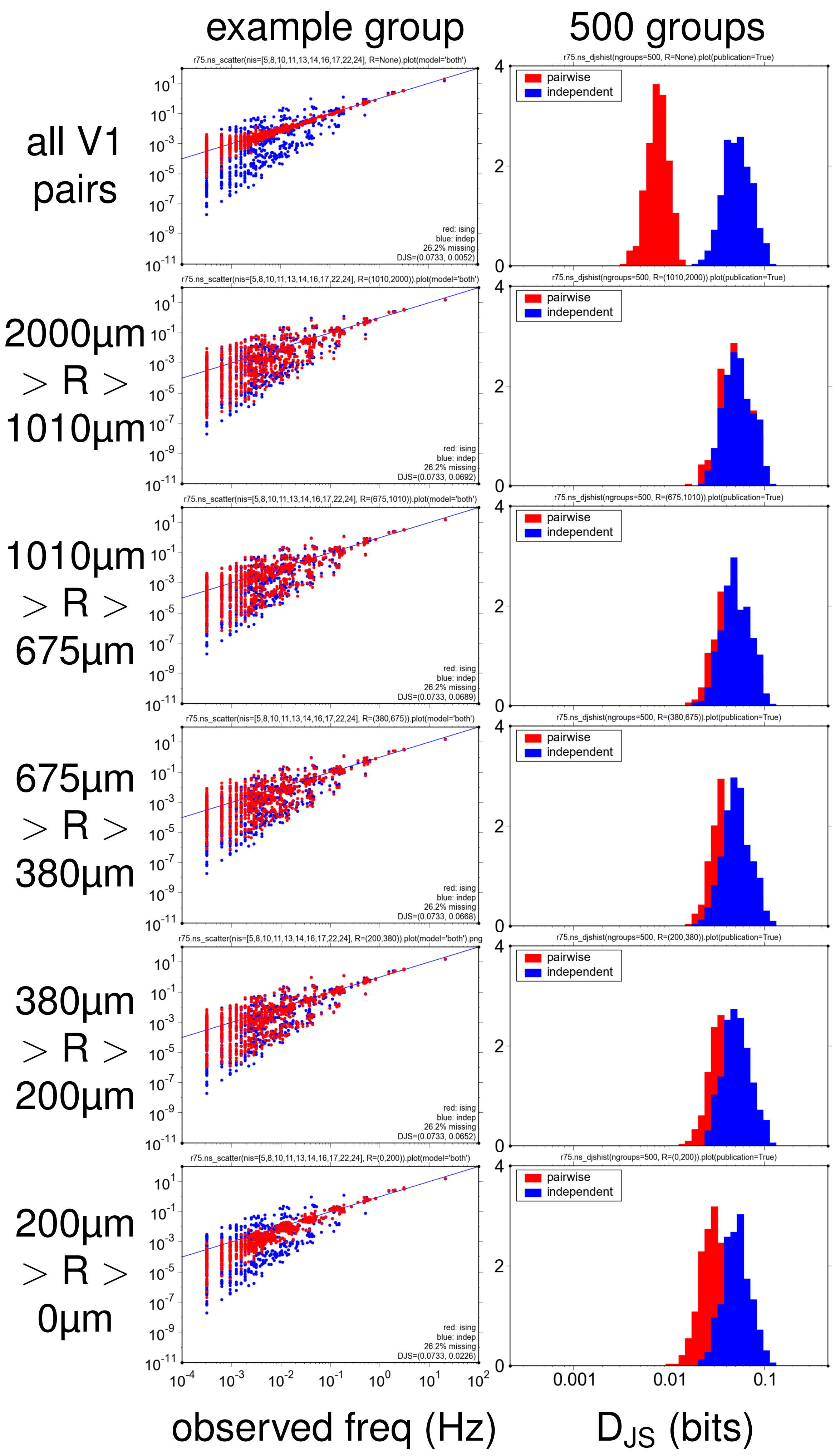
Poster and addendum available online at: `http://swindale.ecc.ubc.ca`



To further distinguish between the influence of separation distance and number of included cell pairs, analysis was restricted to pairs whose separation fell within a specific range of inner and outer radii of an annulus. Annular radii were chosen such that the number of cell pairs within that range of separation was $\sim$ constant. For comparison, row 1 consisted of all $N = 325$ cell pairs. Row 2 had $N = 57$ cell pairs. Rows 3–6 had $N = 67$ cell pairs each.

As the annulus became more local and separation distance decreased, ρ distributions broadened and higher ρ values became more prominent (*bottom*).



When given only distant cell pairs, the pairwise model performed poorly (*rows 2–5*). As cell pairs became more local, the pairwise model did better (*bottom*), but it performed best when given all possible cell pairs (*top*).