Heterogenous firing rate dependencies in simultaneously recorded neural populations in cat area 17

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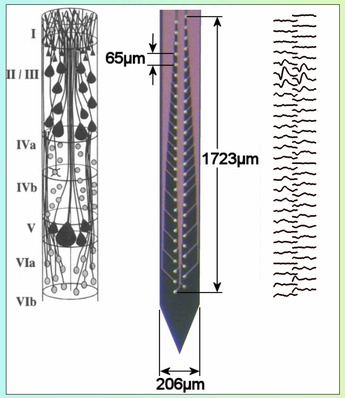
Introduction

In the retina, it has been shown that cells act as independent encoders, where the spike trains are generally independent across cells (Nirenberg et al, 2001). We wanted to see what kind of dependencies, if any, might exist in the firing rates of cells in primary visual cortex.

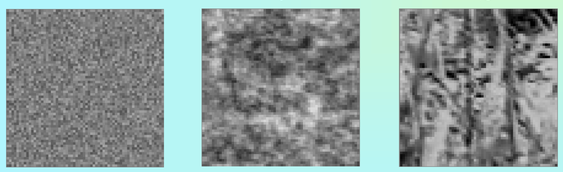
Barlow's original efficient coding hypothesis suggests that cells in cortex should respond independently. But a more recent view is that as one moves from retina to the much larger visual cortex, "redundancy must increase, because information cannot be created," (Barlow 2001), and that the purpose of expansion is to represent the input in a more convenient way for later use. Perhaps this redundancy might reveal itself in firing rate dependencies (correlations, or perhaps other types) in neuronal populations in cortex.

Methods

We used silicon polytrodes with closely spaced electrode sites (50-75 um) to simultaneously record from dozens of cells over multiple cortical layers in area 17 in anesthetized cat (Blanche et al, 2005). Electrode sites were closely spaced so as to isolate many adjacent cells within the recordable volume of roughly 2000 x 200 x 130 um.



We stimulated with white noise (wn), pink noise (pn, 1/f amplitude spectrum), and contrast normalized natural scene (ns) movies on a 200Hz monitor. Stimulation area was about 3X the classical receptive field area. Receptive fields (RFs) were mapped using spike triggered averaging of an msequence noise or sparse bars stimulus, for simple and complex cells respectively.

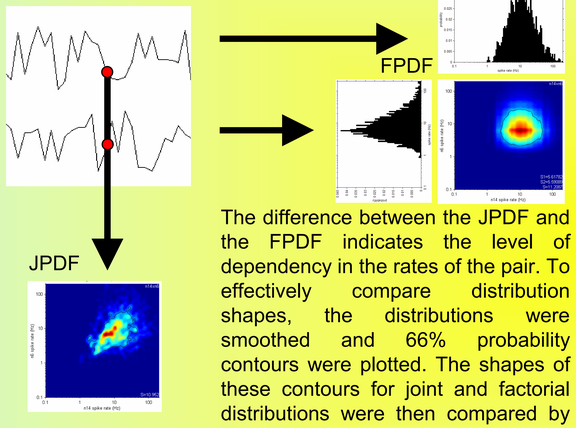


We calculated instantaneous firing rates instead of PSTH rates because we wanted to track rate dependency over time, not over trials. Due to spontaneous variations in brain state and depth of anesthesia, the two are not necessarily the same.

Instantaneous rates were calculated using partially overlapping bins of varying duration such that a fixed number of spikes n fell in each bin. We set n=4, but results did not differ for different values of n (n=2 gives ISI spike rate).

The joint firing rate probability distribution function (JPDF) for each cell pair was constructed by stepping through every time point in the rates of both cells and building up a 2D histogram of joint rate probabilities. Rates were binned on a log scale.

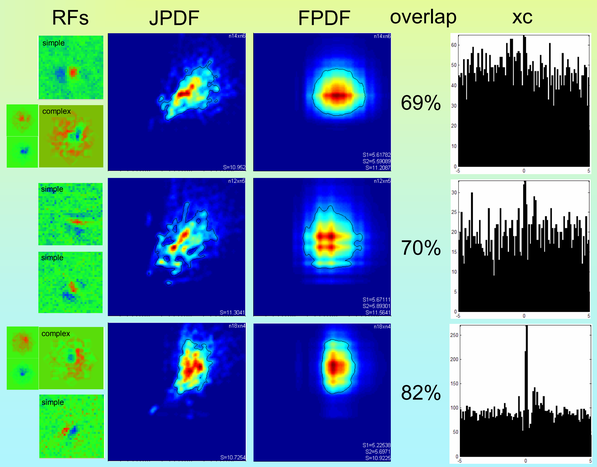
The factorial firing rate probability distribution function (FPDF) was calculated by first finding the rate distribution for each cell separately, and then taking the outer product of the two distributions. Doing so assumes that the rates are independent.



The difference between the JPDF and the FPDF indicates the level of dependency in the rates of the pair. To effectively compare distribution shapes, the distributions were smoothed and 66% probability contours were plotted. The shapes of these contours for joint and factorial distributions were then compared by measuring their percentage of overlap.

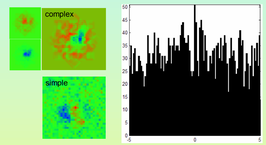
Results

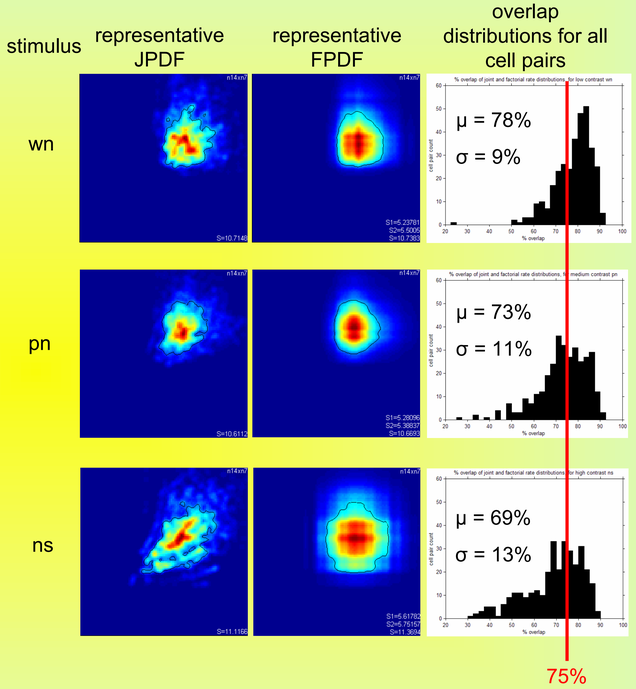
Of 325 cell pairs, we found that some showed dependency, and others did not. The presence/absence of cross correlogram (xc) peaks did not seem to predict dependency.



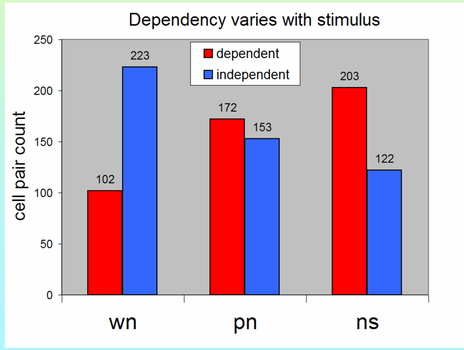
Moreover, we found that the amount of dependency varied with stimulus type.

Receptive fields and cross correlogram for representative cell pair:





A percent overlap threshold of 75% was chosen to classify cell pairs as either dependent or independent. This classification criterion matched qualitative impressions of whether the JPDF and FPDF looked significantly different.



Responses to ns saturate at low contrast, to pn at medium contrast, and to wn at high contrast. As responses saturate, variance in firing rates decreases. Without variance, covariance is not possible. To roughtly normalize for variance in firing rates, we used low contrast ns, medium contrast pn, and high contrast wn movies for the above comparison.

Discussion

- Some, but not all, cell pairs in primary visual cortex show dependency (mostly correlation) in their firing rates. Also, the number of dependent cell pairs and their degree of dependency, as measured by the overlap of their JPDFs and FPDFs, increases as the stimulus changes from wn, to pn, to ns movies.
- Dependencies run against Barlow's original efficient coding hypothesis, but then again, the brain needs to do more than efficiently transmit info from one area to the next – it needs to compute, not just transmit (see Barlow, 2001).
- Presence or absence of dependencies between cell pairs may reveal more about neural architecture than cross correlation analysis alone.
- ns > pn > wn result makes sense: ns and pn have greater redundancy in their pixel values than wn, so cells can afford to have more redundancy (dependency) during ns and pn than during wn stimulation.

Future work:

- Linear receptive field model: because both ns and pn have the same (1/f) amplitude spectrum, the additional dependency is conceivably due to higher order statistics in ns movies. The difference could still come out of a simple linear RF model, say if the RFs of the cell pair are colinear in space and time, matching contiguous features in ns such as moving edges, that do not exist in pn.
- The experiments were not run to test dependency specifically, the stimuli were quite short, only 2 minute movies – we need more spikes to build better rate distributions.
- Further recordings will have accurate histology and/or CSDs to confirm cortical layer positions, preferably with more simultaneously recorded cells to increase cell pair count. Perhaps cell pair dependency is a function of layer position.
- What kind of dependency exists during spontaneous activity (no stim)? Could wn be inhibiting dependency below baseline?
- Normalize the mean and variance of each cell's rate from 0 to 1 to better remove confound of rate variance (and saturation) of cells with covariability of cell pairs.

References

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