Cornell University

Assessing the importance of correlated firing using large populations of neurons

Marsha Meytlis[1], Illya Bomash[1], Jonathan Pillow[2], and Sheila Nirenberg[1]

1 Dept. of Physiology and Biophysics, Weill Medical College, Cornell University, New York, USA, 2 The University of Texas, Austin, USA

Introduction

The role of correlated firing for representing information has been a subject of much discussion. Several studies in areas including retina, visual cortex, somatosensory cortex, and motor cortex, have suggested that it plays only a minor role, carrying less than 10% of the total information carried by the neurons [3,5-7]. A limiting factor of these studies, however, is that they were carried out using pairs of neurons; how the results will extend to large populations isn't clear. Recently, new methods for modeling network firing patterns have been developed [8]. These open the door to answering this question for more complete populations of cells. Pillow et al [8] used this approach to assess the importance of correlations in primate retina. Using a binary checkerboard stimulus, his group decoded ganglion cell responses when correlations were and were not included. Their results showed that 32.9 +/- 0.5% of the information about the stimulus could be obtained when correlations were included, and 27.2 +/- 0.5% when they were not. While this constitutes a gain, the gain is several fold smaller than what might be expected from extrapolations using the pairwise data [see Ref. 8, Fig, S9 or attachment to this poster]. Here we performed the same analysis on mouse retinal ganglion cells, using cells with correlations as high as those found in primate retina [8]. The results showed that 25.5 +/- 1.35% of the information about the stimulus could be obtained when correlations were included, and 22.6 +/- 1.45% when they were not. An even smaller difference was found when the same analysis was performed on natural scenes.

These results suggest generalization. The pairwise analysis in many brain areas in several species show that correlations account for very little of the total information (<10%) [3,5-7]. Now, in retina in two species, the analysis with large populations show a similar result, that correlations still account for a small fraction of the total information.

Figures 1 and 2 show the reliability of the data, that is, that the cells in our datasets are clearly and consistently driven by the stimulus.

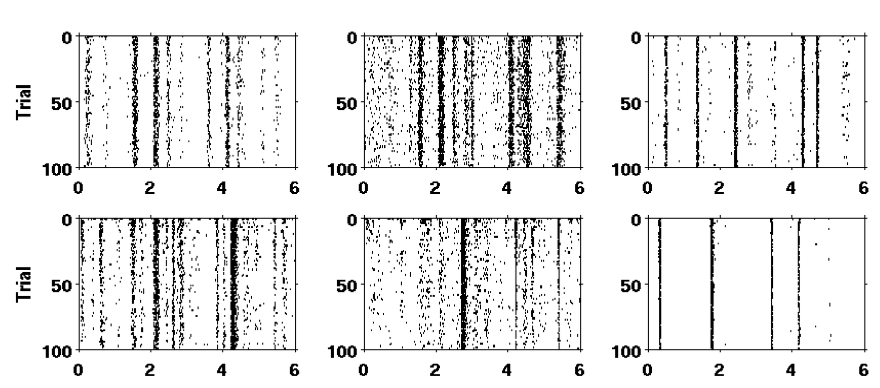

Fig 1. Typical ganglion cell responses to the movies. Each raster plot shows the response of a ganglion cell to 100 repeats of a movie. Each plot is from a different cell. The top and bottom rows are from different retinas.

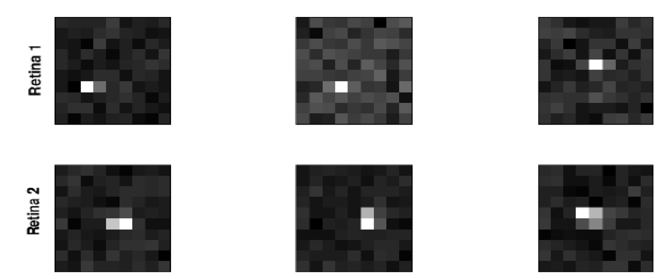

Fig 2. Typical Spike Triggered Averages (STAs) from 6 different ON cells from 2 retinas. The spatial component of the full STA which contains the peak of the STA is shown.

Figures 3-5 show the properties of the correlations in our model system, the mouse retina:

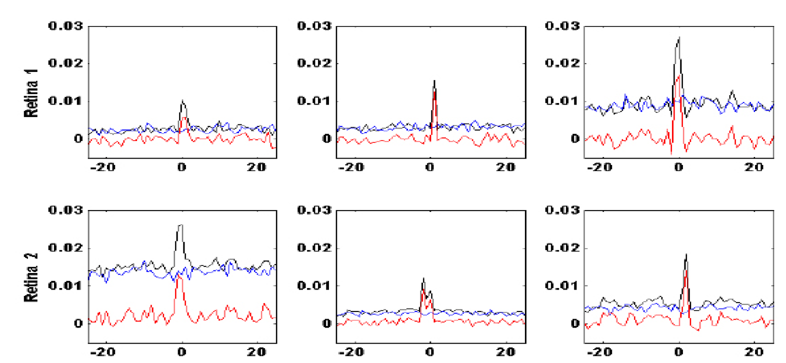

Fig 3. Typical cross-correlerograms for pairs of mouse ganglion cells from 2 retinas. A cross-correlerogram gives the firing rate of one cell relative to spikes generated by the other. Black, the raw cross-correlerogram; blue, the shifted (stimulus) cross-correlerogram; red, the noise cross-correlerogram. The stimulus cross-correlerogram gives the correlations produced only by the stimulus and is generated by presenting the stimulus multiple times and cross-correlating the responses of the cells when they 'saw' the stimulus at different times. The noise cross-correlerogram is the raw cross-correlerogram minus the stimulus cross-correlerogram.

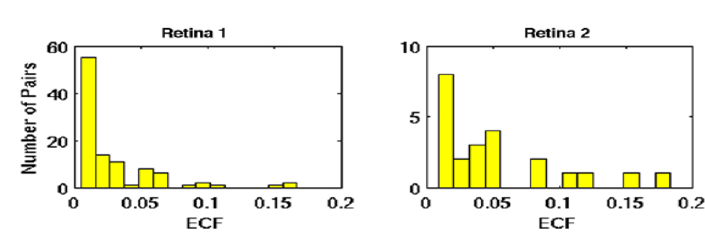

Fig 4. Distribution of Excess Correlated Fractions (ECFs) for all cell pairs. The ECF is the number of correlated spikes divided by the total number of spikes fired by the pair [5]. The ECF for 2 retinas are shown. The degree of correlation is in the same range as reported for other species: up to 27% for cat [4], up to 28% for rabbit [2], up to 34% previously reported for mouse [5], up to 5% for monkey [8]. Note, through, that the majority of ECF's in the mouse are less than 5%.

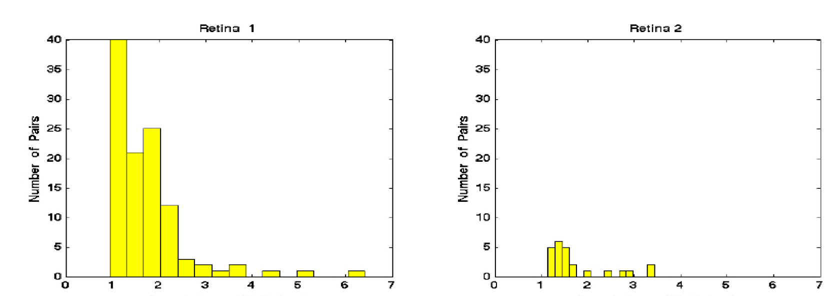

Fig 5. Distribution of correlation timescales (from 2 retinas), as measured by the width of the cross-correlerogram, for cell pairs with ECFs above 0.5% . Widths were computed by measuring the width at half-height of the noise cross-correlerogram for each cell pair. This is similar to cat [4], rabbit [2] and monkey [8], but extends to shorter values . Short time scale correlations have been reported in cat LGN [1].

Modeling the Correlations:

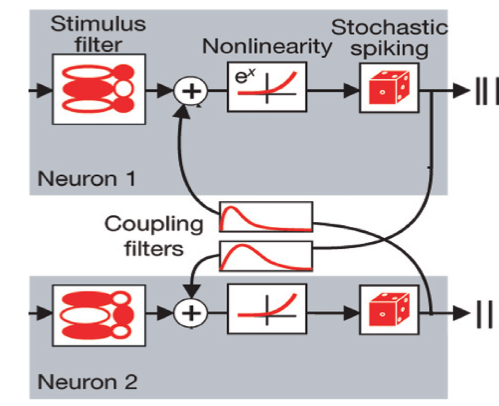

Fig 6. A diagram of the multi-neuron encoding model for two coupled neurons (modified from [8]). Each neuron has a stimulus filter and coupling filters that capture dependencies on spiking in other neurons. Summed filter output passes through an exponential nonlinearity to produce the instantaneous spike rate.

Figures 7 demonstrates that including the coupling both improves the encoding model. Figure 8 shows, as expected, that the correlation peaks are now captured in the simulated responses.

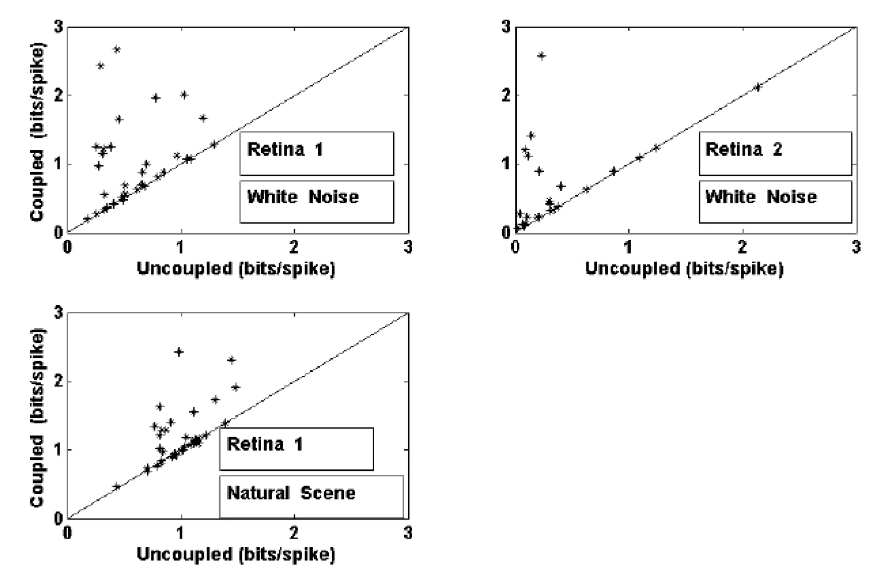

Fig 7. The quality of the fits from 2 retinas was evaluated by comparing the log likelihood of the true spike trains under coupled and uncoupled models; the coupled model achieves higher accuracy, predicting multi-neuronal spike responses on a single trial.

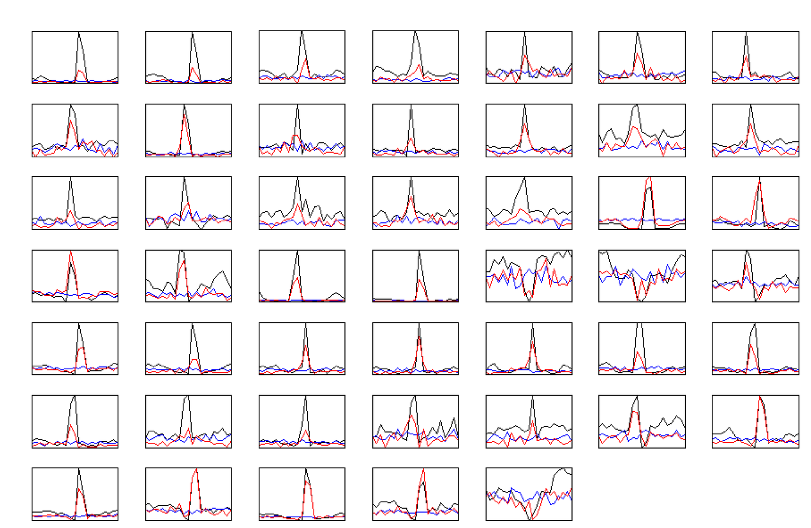

Fig 8. Example of cross-correlation functions of retinal responses from Retina 1. Black, the raw cross-correlerogram; red, the coupled simulated cross-correlerogram; blue, the uncoupled simulated cross-correlerogram (plotted -10 to 10 ms). It is clear that the coupled model is capturing correlations in the data while the uncoupled model is not.

The coupled model accurately captures dependencies in the activity of neurons; however, this does not tell us whether this extra component is important for conveying visual information to the rest of the brain. In other words, if we decode spike trains using the coupled model, will we capture more information about the visual stimulus than if we decode with the uncoupled model (i.e. the independent model)?

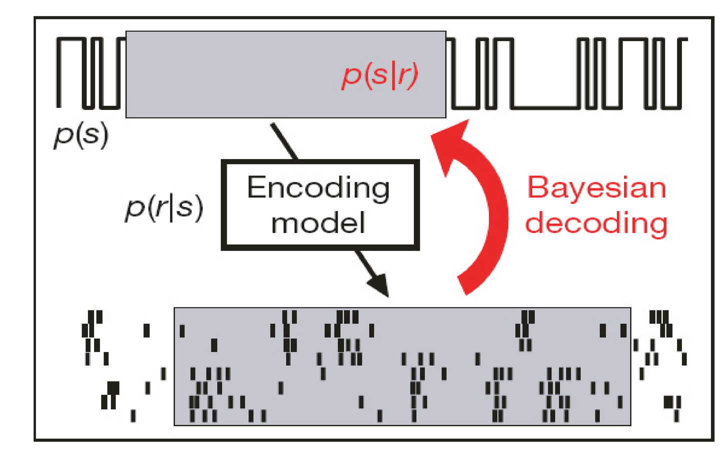

Fig 9. Shown is a Baysian decoding schematic [8] to estimate an unknown stimulus segment from a set of observed spike times (highlighted in boxes). The posterior mean is the Bayes' least-squares stimulus estimate.

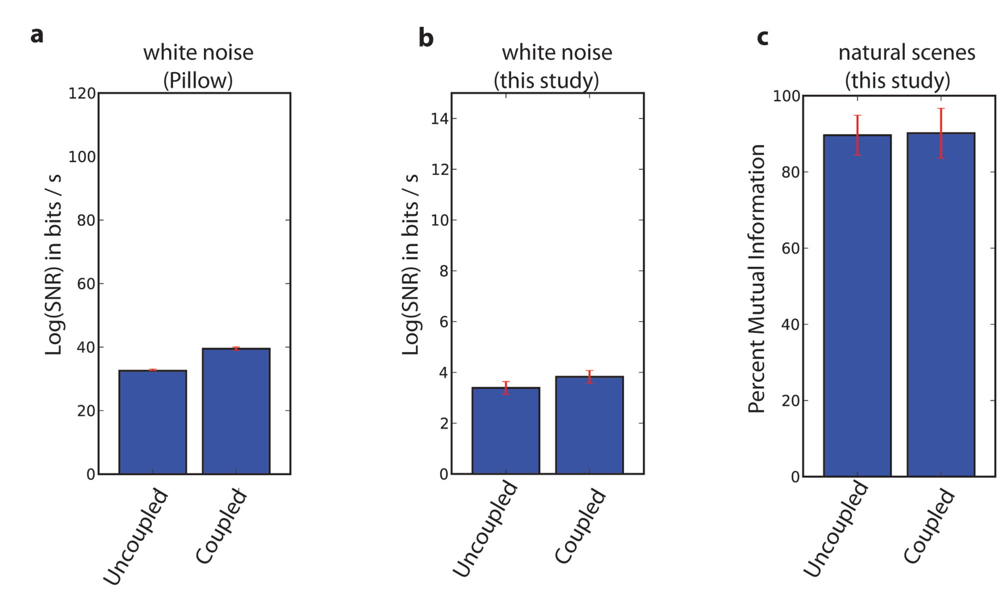

Fig 10. Comparison of decoding performance with and without coupling. **a.** White noise decoding results using the log signal-to-noise ratio (log SNR) of Bayesian decoding for a previously reported macaque retina. Height of y-axis indicates stimulus entropy. **b.** Average white noise decoding results for mouse. Height of y-axis indicates stimulus entropy. Error bars show 95% confidence intervals, based on 2000 bootstrap resamplings of 3000 decoded stimulus segments (primate) and 1000 bootstrap resamplings of 200 decoded stimulus segments (mouse). **c.** Decoding performances for a mouse retina on a natural scene stimulus. For the natural scenes, information was calculated by directly estimating discrete entropy across a fixed natural scene library of 200 segments, rather than taking the log(SNR). Error bars show 95% confidence intervals, based on 1000 bootstrap resamplings of 50 decoded stimulus segments.

Discussion

Previous work has shown that correlations among mouse retinal ganglion cells add little information above what can be obtained from the independent responses [5]. However, this work was done with pairs of neurons. Now, with the aid of a neuronal population model [8] we were able to address this question for much larger populations. We tested this with both binary checkerboard and natural scenes. The results show that, for the white noise stimulus, there was only a small information increase, and, for the natural scenes, there was no clearly detectable increase.

Some caveats should be taken into account when interpreting this result. First, the analysis was done with a model's output rather than direct measurements (although the model was clearly capturing the correlations as shown in Figures 8 and 9). Second, for the white noise stimulus, information was measured using a Gaussian assumption, although a binary stimulus was used. Third, the natural scene decoding performance was estimated using a discrete entropy calculation with a lower stimulus entropy than the white noise, and hence may not be directly comparable.

References

1. Alonso, J., Usrey, W. & Reid, R. (1996) Precisely correlated firing in cells of the lateral genicualte nucleus. Nature 383: 815-819.
2. Devries, S. (1999) Correlated firing in rabbit retinal ganglion cells. J Neurophysiol 81: 908-920.
3. Gawne and Richmond (1993) How independent are the messages carried by adjacent inferior temporal cortical neurons. J Neurosci. 13: 2758-2771.
4. Mastronarde D. (1983) Correlated firing of cat retinal ganglion cells. II Spontaneously active inputs to X- and Y-cells. J. Neurophysiol 49: 303-324.
5. Nirenberg et al. (2001) Retinal ganglion cells act largely as independent encoders. Nature. 411:698-701.
6. Oram et al. (2001) Excess synchrony in motor cortical neurons provides redundant direction information with that from coarse temporal measures. J Neurophysiol 86:1700-1716.
7. Rolls et al., (2003) An Information theoretic approach to the contributions of the firing rates and the correlations between the firing of neurons. J Neurophysiol. 89:2810-2822.
8. Pillow et al., (2008) Spatio-temporal correlations and visual signalling in a complete neuronal population. Nature 454:995-999.

Acknowledgements

This work was supported by National Institute of Health and National Eye Institute Grant -- NIH/NEI T32 EY07138-15 and the Tri-Institutional Training Program in Vision Research, and NEI R01EY12978 (to S.N.).