RESPONSE VARIABILITY IN CAT VISUAL CORTEX

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INTRODUCTION

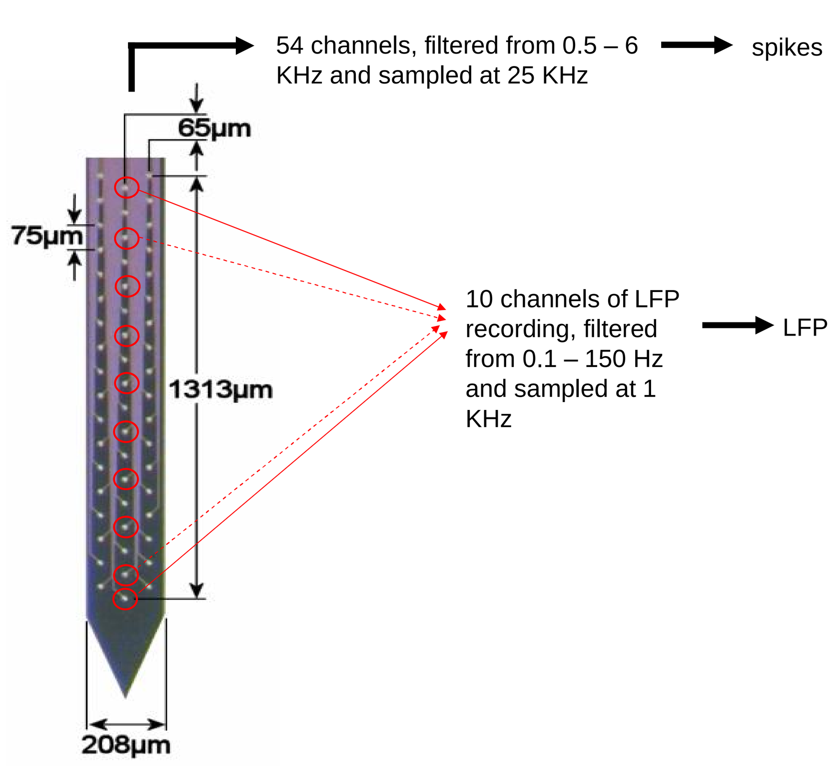
When recording from visual cortex in anaesthetized cats it is common to observe that responses wax and wane over periods of several minutes. Relatively little attention has been paid to these fluctuations. We have studied them using polytrode electrodes which are able to isolate the responses of many simultaneously responding neurons (Blanche et al., 2005). We studied fluctuations in spontaneous as well as visually evoked firing rates.

OUR FINDINGS

- fluctuations are correlated with changes in the frequency content in the local field potential (LFP);
- the response rates of most, but not all, cells tend to fluctuate in the same way;
- fluctuations reflect changes in response gain and spontaneous activity;
- fluctuations are not accompanied by changes in stimulus selectivity.

METHODS

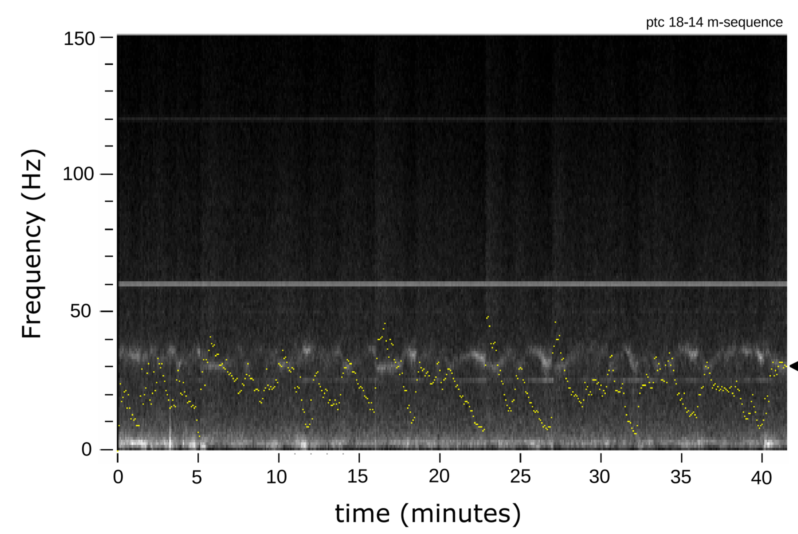
We used 54-channel Michigan polytrodes to record from cat visual cortex

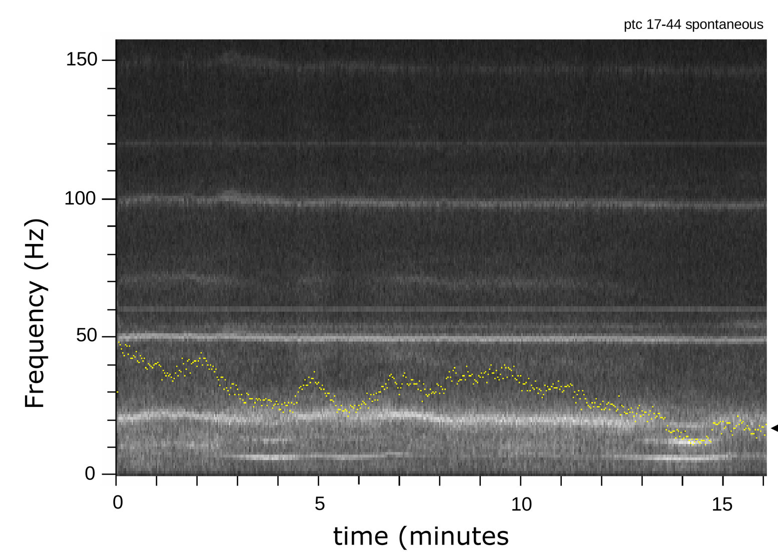


Cats were anesthetized with isoflurane/N_2O_2 or with a propofol/fentanyl mixture. A subset of 10 of the polytrode channels provided parallel recordings of the LFP. Moving bars, or white-noise m-sequence patterns presented on a CRT at 200 Hz refresh rate were used as stimuli. Spike sorting was done using Gradient Ascent Clustering (Swindale & Spacek, submitted) and typically yielded 50 – 100 units per penetration.

FIRING RATE & THE LFP

LFP spectra and net firing rate show correlated changes

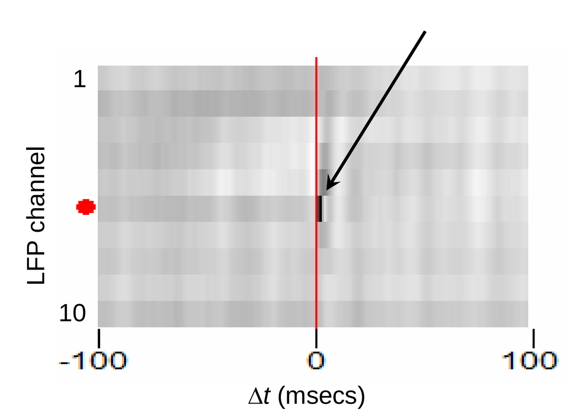




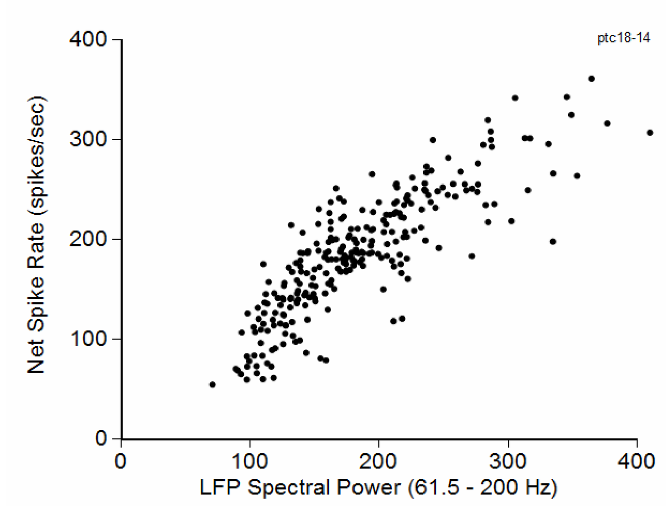
Time-varying LFP spectra. Yellow dots show the summed firing rate of all the isolated units. Firing rate changes are of two kinds: slow drifts up and down, and sudden jumps upward. The jumps are accompanied by sudden changes in the LFP spectra and, often, the drifts seem to be related to changes in dominant frequencies in the LFP. We have been unable to determine a systematic relationship between specific frequencies in the LFP and firing rate. Frequencies <10 Hz sometimes inhibit firing, but not always.

Spikes contribute directly to broadband energy in the LFP

A section of spike-triggered average LFP signal showing a sharp transient (arrow) in the averaged LFP record 0 – 2 ms after the spike, on the LFP channel that was closest to the unit (red dot). Such signals are frequently observed.

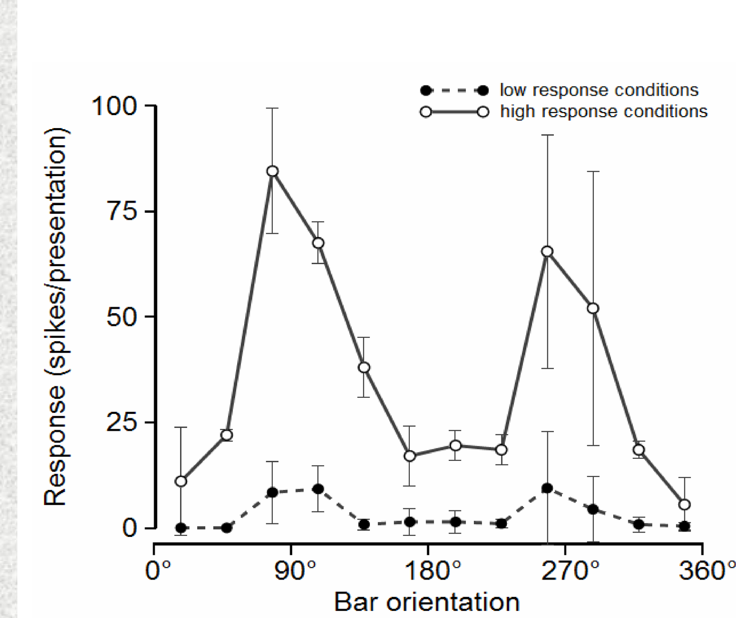


There is a strong correlation between broadband energy in the LFP (e.g. > 60 Hz) and firing rate. This probably reflects a direct contribution of spikes to LFP signals. From the point of view of the LFP, spikes are delta functions with energy spread over a range of frequencies, including those > 60 Hz.

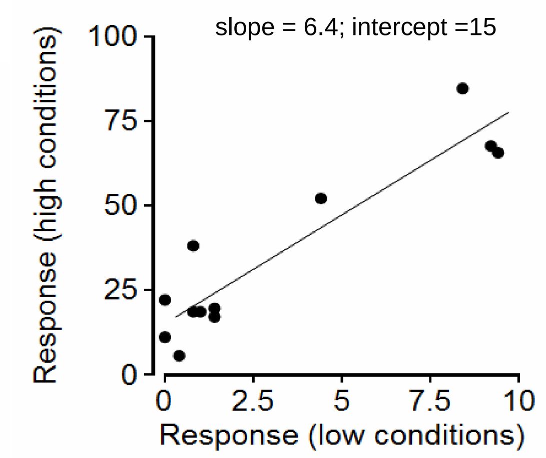


ORIENTATION RESPONSE VARIABILITY

Fluctuations in responses to moving bars result from changes in cells' response gain plus smaller changes in spontaneous activity.



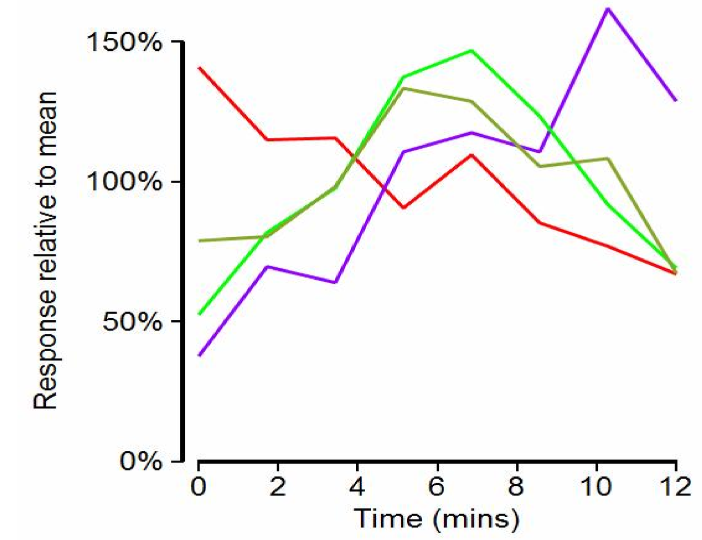
Orientation tuning curves in low vs. high response conditions obtained about 5 minutes apart.



A plot of the responses in the high-response conditions *vs.* the low-response conditions. Most of the difference between the two curves is accounted for by a change in response gain plus a small increase in spontaneous firing.

The responses of most cells fluctuate up and down with a similar timecourse. However not all cells follow the majority pattern.

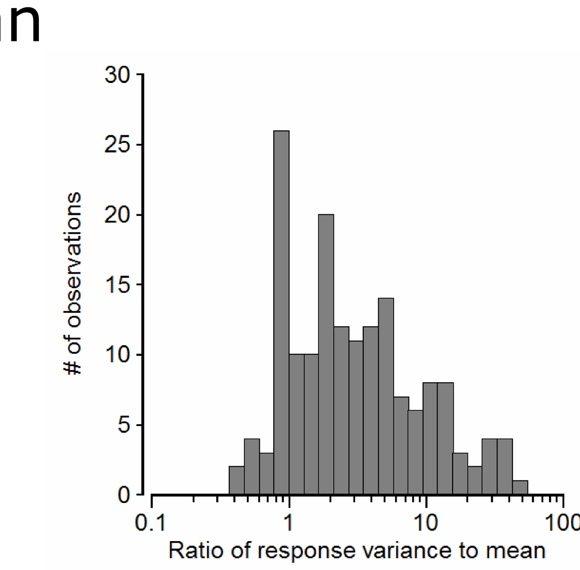
Response rates (total spikes summed over a single complete set of moving bar stimuli) for 4 different, simultaneously recorded cells. Two of them (green curves) follow the overall trend, however the red and purple neurons behave differently.



SUPER-POISSON STATISTICS

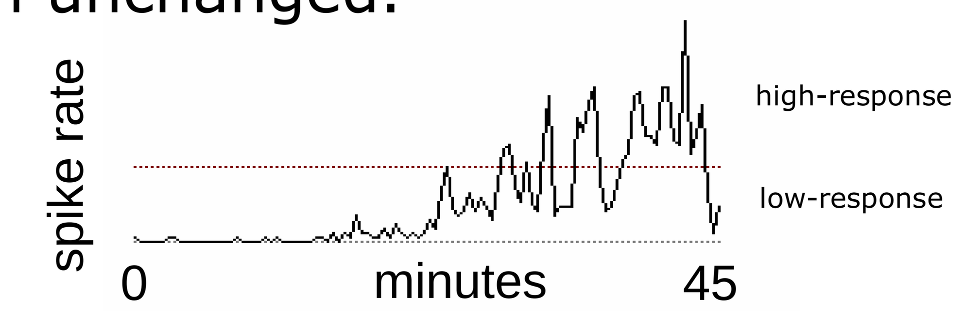
The variance of spike rate can be much greater than the mean

Response fluctuations add to the variability of spike counts with the result that counts often vary much more than predicted by Poisson statistics. The histogram shows a distribution of ratios of response variances to the corresponding means for a sample of orientation tuning curves (biased towards those with variable responses).

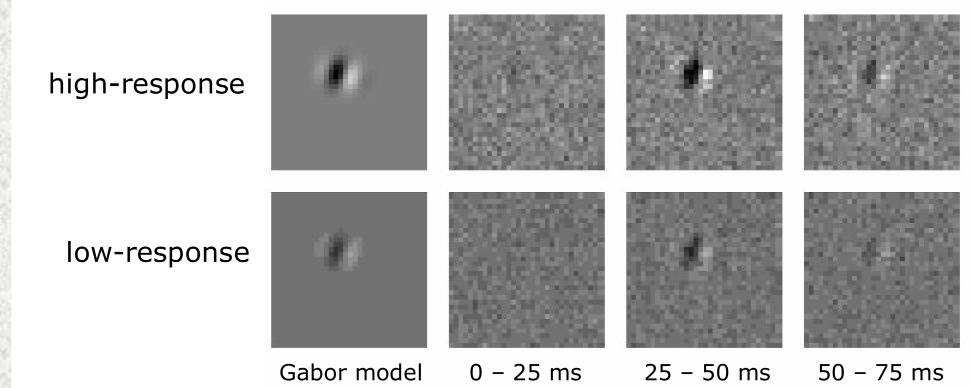


M-SEQUENCE RESPONSE VARIABILITY

Fluctuations in responses to m-sequence stimuli result from changes in response gain. Other receptive field properties remain unchanged.



Response rate of a neuron during an m-sequence experiment. The dashed line is used to divide the recording into periods of low vs. high rate.



Receptive fields from the high- and low-response rate conditions. The contrast of the low-response fields has been increased to make them visible.

THE GOOD NEWS

Changes in response gain have little impact on measurements of basic receptive field properties. The sum of lots of tuning functions scaled by different factors is just the same tuning function times the average of the gains.

THE BAD NEWS

Predictions based on matches of response rate (e.g. predicting the response of a simple cell to a movie) may go wrong because of gain fluctuations.

If the unanaesthetised brain is similarly variable, having firing rates vary in different ways within populations of simultaneously responding cells will interfere with rate-based population coding.

TAKE HOME MESSAGE

Factors other than the stimulus determine much of the variation in firing rates among cells.

ACKNOWLEDGEMENTS

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