Transformation of stimulus correlations by the retina

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Goals

Redundancies and correlations in the responses of sensory neurons may seem to waste neural resources. A longstanding hypothesis is that retina “should” fully decorrelate its inputs.

But correlations can carry cues about structured stimuli, and may help the brain to correct for response errors.

**Does the retina fully decorrelate its inputs? Does it dynamically adjust its coding strategy to represent different classes of stimuli efficiently?**

To investigate the effect of stimulus structure on redundancy in retina, we measured simultaneous responses from *populations* of retinal ganglion cells presented with *natural and artificial stimuli* that varied greatly in correlation *structure*.

Recording from an entire population allowed us to measure the spike-train correlation of a particular pair of ganglion (output) cells with one kind of input, then compare to that obtained from the *same cells* with a different input, then repeat with many pairs of cells.
Cavia porcellus.
OK, mammals are harder than amphibians. But not that much harder.
Cf Meister, Pine, and Baylor 1994. Incredibly, one can keep a mammalian retina alive in a dish for over 6 hours while presenting it stimuli and recording its activity.
67 ms of data, viewed as a movie.
[data taken at 10kHz have been smoothed. Biggest spikes about 400µV.]

Some spikes move across the array:

Mostly we are hearing retinal ganglion cells, as desired, because they’re the ones that spike.

The **spike-sorting problem** is: Given raw data like these, convert to a list of discrete events (which cells fired at what times).

*Classic: Gerstein+Clark 1964; Abeles+Goldstein 1977; Schmidt 1984.*
Superposing 50 traces chosen from 284 in this cluster shows that they really do all resemble each other.

Occasional events in which this event collides with another don’t affect the “archetype waveform” (template) (next slide).

Although the shape of each instance of the template is quite constant, still its amplitude has significant variation.

*JS Prentice, J Homann, KD Simmons, G Tkacik, V Balasubramanian, PCN, PLoS ONE 6(7): e19884 (2011).*
We scaled each instance of each template to get best agreement with the others, then took the median at each time point to find our best estimate of the consensus waveform (blue). As a check, the pointwise mean waveform looks the same (red).
1. Experiment
2. Clustering
3. Fitting
4. Performance

Get data ➔ Cluster ➔ Fit ➔ Interpret
Suppose we measure some experimental data, and wish to make an inference about some situation that we cannot directly observe. That is, we imagine a variety of worlds with different values of $X$, and ask which is most probable given the observed data.

If we know the probability that those data would have arisen in a world with a particular value of $X$, then the Bayes formula gives us what we actually want:

$$ P(X|\text{observed data}) = P(\text{data}|X) \frac{P(X)}{P(\text{data})} $$

We can ignore the denominator, if all we want is to compare two hypotheses (e.g. maximize over $X$).

For our application, we’d like $P(\text{spikes} \mid \text{data})$, where “data” is an observed waveform and “spikes” refers to a collection of spike templates $\mu_1, \ldots$ occurring at times $t_1, \ldots$ with amplitudes $A_1, \ldots$ relative to the amplitude of the corresponding template (neuron). Bayes’s formula gives what we want as:

$$ K \times (\text{likelihood}) \times (\text{prior}) = KP(\text{data} \mid \text{spikes})P(\text{spikes}) $$
Vanilla least-squares fitting is not appropriate for time series, because it assumes that every sample is independent of all others--whereas actually, successive samples are correlated.

Here is the covariance of one channel with nearby channels (after doing an initial spatial filter, which we also obtained from data).

We see that the selected channel is correlated only with itself, and it has a simple covariance matrix that is easy to invert. The inverse covariance thus obtained defines our correlated Gaussian model of the noise.

[Again: The covariance is not a delta function, contrary to what is assumed in naive least-squares fitting.]

*JS Prentice, J Homann, KD Simmons, G Tkacik, V Balasubramanian, PCN, PLoS ONE 6(7): e19884 (2011).*
Closeup of four channels, showing four fit templates found by the algorithm.

Sum of those fits (color) versus actual data (black).
Many authors say **bursts** are a big problem, but here is a nice fit that we obtained with no special effort.

We even handle overlapping spikes, which some algorithms do not attempt.

Even though successive spikes in a burst have different amplitudes, the algorithm fit them.
The receptive fields of individual ganglion cells tile the whole visual field. MEA recording is **high throughput**: We got dozens of cells all at once. Here are cells from just one functional group, “on cells.” Each putative receptive field is a single connected region of image space, and they really do tile the region we studied.

Once you’ve got the spike trains, you can find receptive fields etc. Here’s a typical spike-triggered average.

Interesting--guinea pig retina has a lot of these highly anisotropic receptive fields. Moreover, many of the receptive fields are time-dependent (motion-sensitive).
The mammalian retina dynamically adjusts its signal processing in response to statistical properties of recently-viewed scenes, as predicted on information-theoretic grounds.

Here a particular OFF ganglion cell maintains a constant amount of temporal correlation in its output, regardless of the amount of correlation in its visual stimulus.

Also at the multi-cell level, after adaptation the degree of correlation between any two ganglion cells is nearly unchanged when we change the correlation strength in the stimulus.

Goals revisited

**Does the retina fully decorrelate its inputs?**

No, contrary to Barlow hypothesis. Even our least correlated stimuli resulted in correlations between pairs of output ganglion cells.

**Does it dynamically adjust its coding strategy to represent different classes of stimuli efficiently?**

Yes. Natural scenes (highly correlated) and random checkerboard patterns (highly uncorrelated) gave almost the same (nonzero) level of correlation in output. Specifically, the differences in output correlations were much less than those predicted by a non-adapting linear- nonlinear functional model responding to these stimuli.

**How is that adjustment implemented?**

This is a model-dependent question. In the context of standard linear-nonlinear models, we found that for correlated input, the spacetime receptive field (obtained by likelihood maximization) had a faster temporal kernel, slightly stronger surround inhibition, and less gain than the ones for uncorrelated input.
Thanks

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