UNEXPECTED SPATIO-TEMPORAL STRUCTURE IN V1 SIMPLE AND COMPLEX CELLS REVEALED BY SPIKE-TRIGGERED COVARIANCE

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V1 neurons are commonly classed as simple and complex based upon their responses to drifting sinusoidal gratings. The periodic response of a simple cell is typically modeled using a single linear filter followed by a half-squaring nonlinearity. Phase-insensitivity in complex cells arises in the motion-energy model by squaring the output of two linear filters in quadrature. In fact, one observes a continuum of response patterns to sinusoidal gratings in V1 cells. We performed a spike-triggered characterization of macaque V1 cells with a range of phase-sensitivities to estimate the number and type of linear filters involved in the generation of these cell's responses.

We stimulated neurons with a dense, random, binary bar stimulus confined to the classical receptive field. For each cell, we recovered a set of linear filters describing the generation of the neuron's response by calculating the spike-triggered average (STA) and significant axes revealed by applying a principal components analysis to the spike-triggered covariance matrix (STC). Assuming a linear-nonlinear-poisson (LNP) model, the number of recovered filters in this analysis sets a lower bound on the number of filters the cell uses in performing its computations.

The results revealed by this analysis predict the continuum of modulation in response to gratings across the population of V1 neurons. In simple cells we recovered an STA with clear spatio-temporal structure in addition to at least one additional filter. The additional filter tended to differ from the STA by a phase shift and decreased the modulation of the cell's response. However, in the more modulated simple cells, the weight of this filter was weak relative to the STA and thus had only a small effect on response. For less modulated simple cells, the weight of this additional filter increased. For complex cells, the STA weakened and two full-rectified, quaderature phase filters were revealed by the STC, as predicted by the energy model.

In complex cells, our analysis often recovered more than one filter pair. While the first pair of filters always had clear spatio-temporal structure in the middle of the receptive field, additional filter pairs tended to have more structure near the receptive field's edges. These additional pairs thus describe the spatio-temporal tuning along the receptive field fringe. These filters were not the product of eye movements, deviations from Poisson spiking, or the particular stimulus used for the characterization. In the context of the LNP model, the presence of additional filter pairs beyond the first suggests the existence of multiple spatially-shifted subunits in complex cells.