Got a moment or two? Neural models and linear dimensionality reduction

Il Memming Park, Evan Archer, Nicholas Priebe, and Jonathan Pillow

A popular approach for investigating the neural code is via dimensionality reduction (DR): identifying a low-dimensional subspace of stimuli that modulate a neuron's response. The two most popular DR methods for spike train response involve first and second moments of the spike-triggered stimulus distribution: the spike-triggered average (STA) and the eigenvectors of the spike-triggered covariance (STC). In many cases, these methods provide a set of filters which span the space to which a neuron is sensitive. However, their efficacy depends upon the choice of the stimulus distribution. It is well known that for radially symmetric stimuli, STA is a consistent estimator of the filter in the LNP model. Recently, Park and Pillow[6] proposed an analogous model-based interpretation of both STA and STC analysis based on a quantity called the *expected log-likelihood* (ELL). Here, building upon the previous work[6], we present a novel model class—the generalized quadratic model (GQM)—which bridges a conceptual and methodological gap between moment-based dimensionality reduction on one hand and likelihood-based generative models on the other. The resulting theory generalizes spike-triggered covariance analysis to both analog and binary response data, and provides a framework enabling us to derive asymptotically-optimal moment-based estimators for a variety of non-Gaussian stimulus distributions. This extends prior work on the conditions of validity for moment-based estimators and associated dimensionality reduction techniques[1;5;7]. The GQM is also a probabilistic model of neural responses, and as such generalizes several widely-used models including the LNP, the GLM, and the 2nd-order Volterra series. Finally, the GQM extends generalized linear models (GLMs) to allow multi-dimensional dependence on spike history. We apply these methods to simulated and real neural data from retina (spiking) and V1 (membrane potential).

Additional detail:

GQM consists of a low-rank quadratic form Q, a nonlinear inverse link function f, and an exponential-family distribution $\mathbf{P}$. GQM extends several popular nonlinear neural encoding models including the 2nd-order Volterra model (with linear f and Gaussian $\mathbf{P}$)[4;3], the elliptical-LNP model (with arbitrary f and Poisson $\mathbf{P}$)[6], and the quadratic-logistic regression model (for logistic f and Bernoulli $\mathbf{P}$)[2]. Although GQM itself does not provide analytical expression for the maximum likelihood estimate, we show that for "canonical form" GQMs, the first two response-weighted moments yield simplified maximum-likelihood estimators for certain stimulus distributions via ELL[6;8]. Specifically, we derive maximum ELL estimator for axis-symmetric stimuli for the Gaussian likelihood. Moreover, ELL allows fast evaluation of the likelihood by replacing the term that requires computation over the samples. In Fig 2 and 3, we show GQM fit to real data. GQM identifies a low dimensional representation automatically through Empirical Bayes procedure.

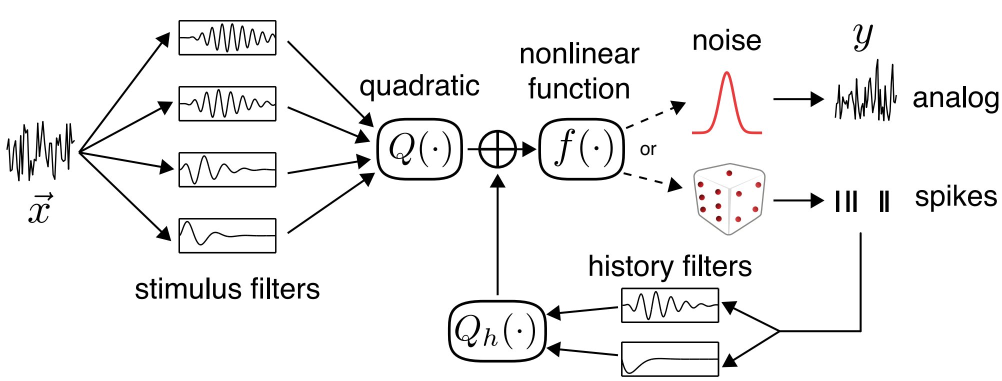

Figure 1: Schematic of GQM. Note that Q contains both linear and quadratic components. For analogue observation, we use Gaussian likelihood, and for spikes we use Poisson likelihood.

Significance: We provide an asymptotic connection between moment based dimensionality reduction techniques and a new model class.
Relevance: Multiple receptive fields can be estimated with GQM for arbitrary stimulus distribution. Moreover, GQM is a flexible model for neural encoding processes applicable to both continuous- and discrete-valued responses as demonstrated.
Originality: We give a novel framework that encompasses many previous models[4;3;6;2], as well as theory on expected log-likelihood and maximum expected log-likelihood estimators.

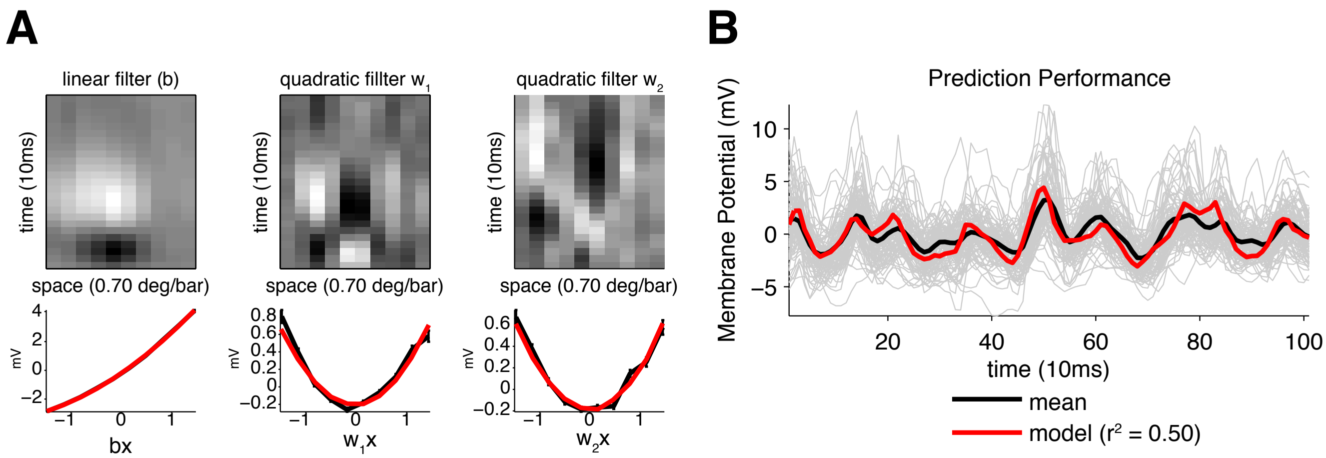

Figure 2: GQM model fit and prediction for intracellular recording in cat V1 with a trinary noise stimulus. **(A)** On top, estimated linear (b) and quadratic (w_1 and w_2) filters for the GQM, lagged by 20ms. On bottom, the empirical marginal nonlinearities along each dimension (black) and model prediction (red). **(B)** Cross-validated model prediction (red) and $n = 94$ recordings with repeats of identical stimulus (light grey) along with their mean (black). Reported performance metric ($r^2 = 0.55$) is for prediction of the mean response.

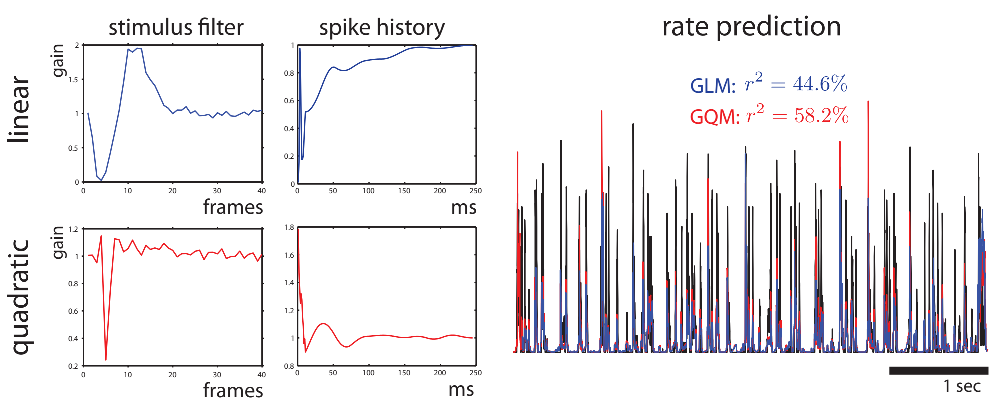

Figure 3: **(left)** GLM and GQM filters fit to spiking response of a retinal ganglion cell under binary full field flicker stimulus at 120 Hz. GLM is composed of only the linear stimulus and spike history filter (blue, top left) while GQM consists of all four filters. Each filter is exponentiated and plotted to represent gain. Both quadratic filters were suppressive. **(right)** Cross-validated rate prediction averaged over repeated trials.

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