Statistical models of visual neurons

Final Presentation

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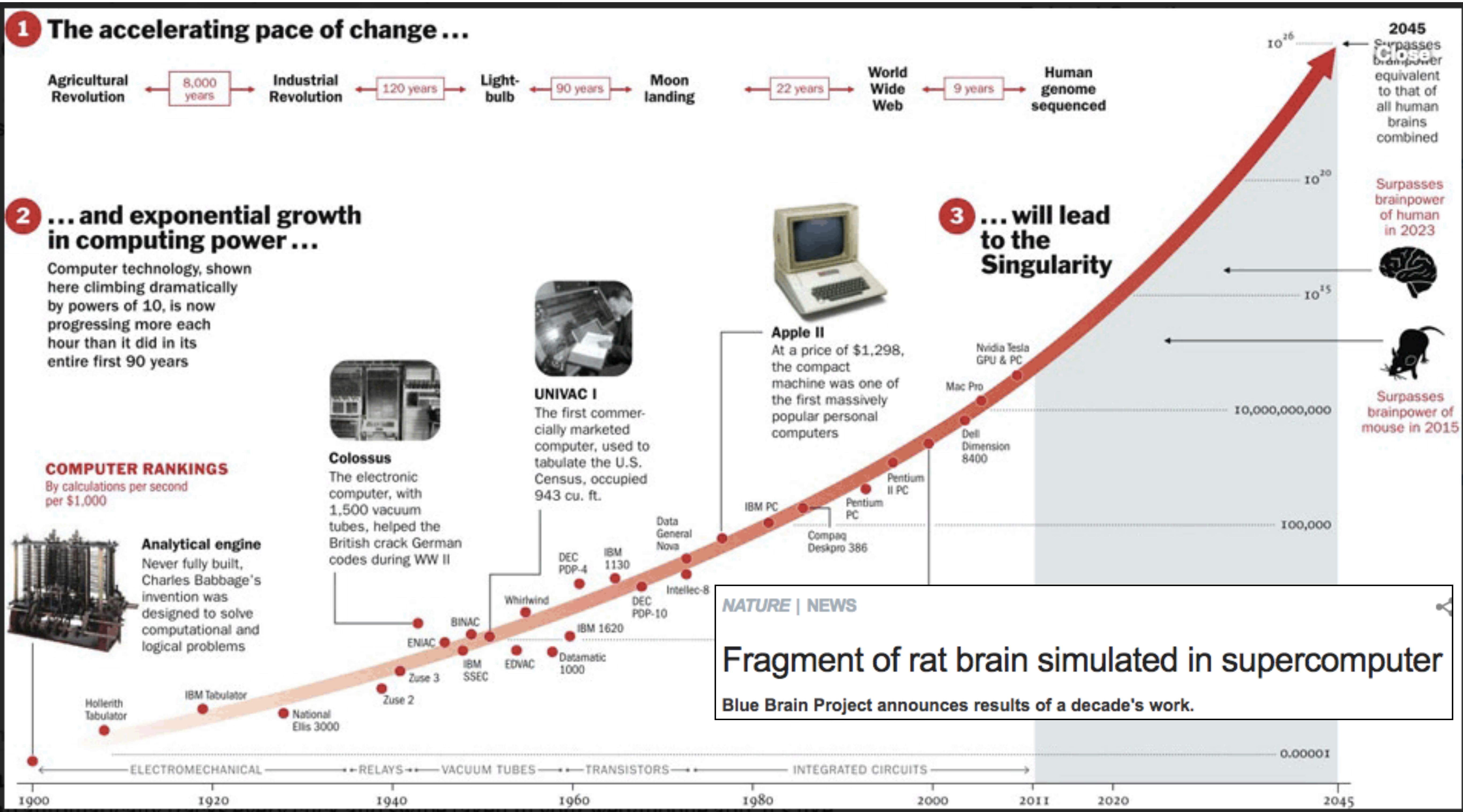
The power of transistor-based computing…

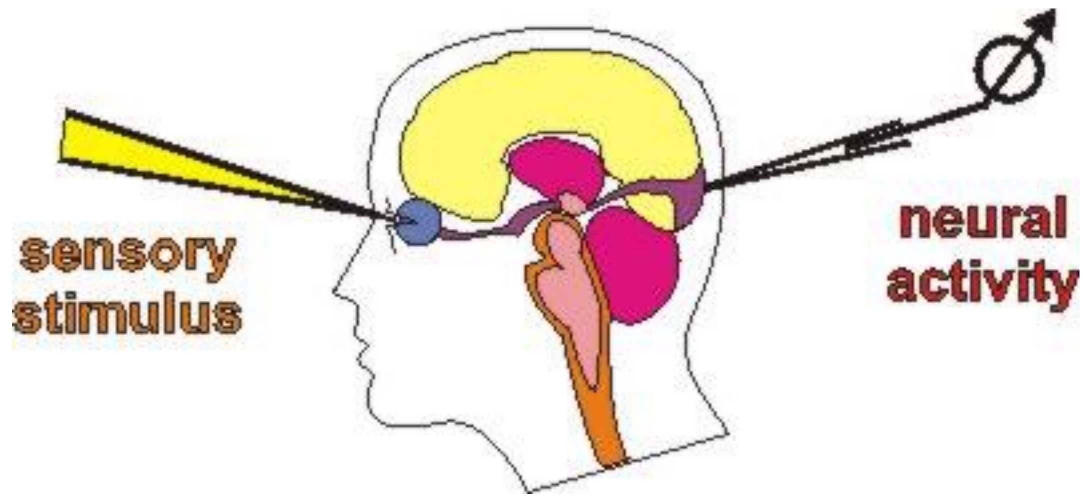


…barely competes with brainpower of a mouse

Inspired by Ray Kurzweil's book 'The Singularity is Near'

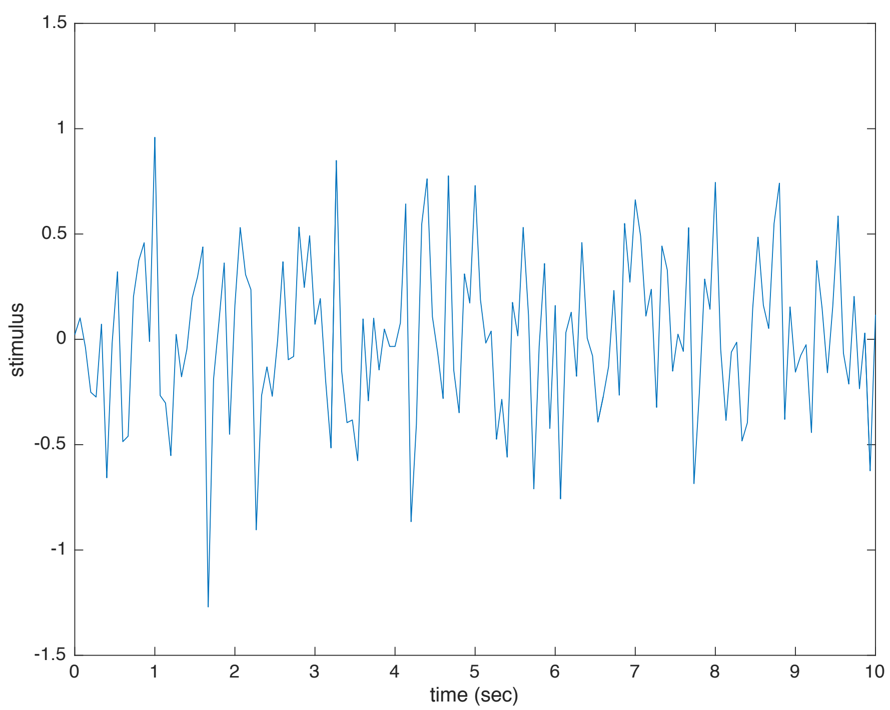
Visual system of a neuron

light



electrical spikes

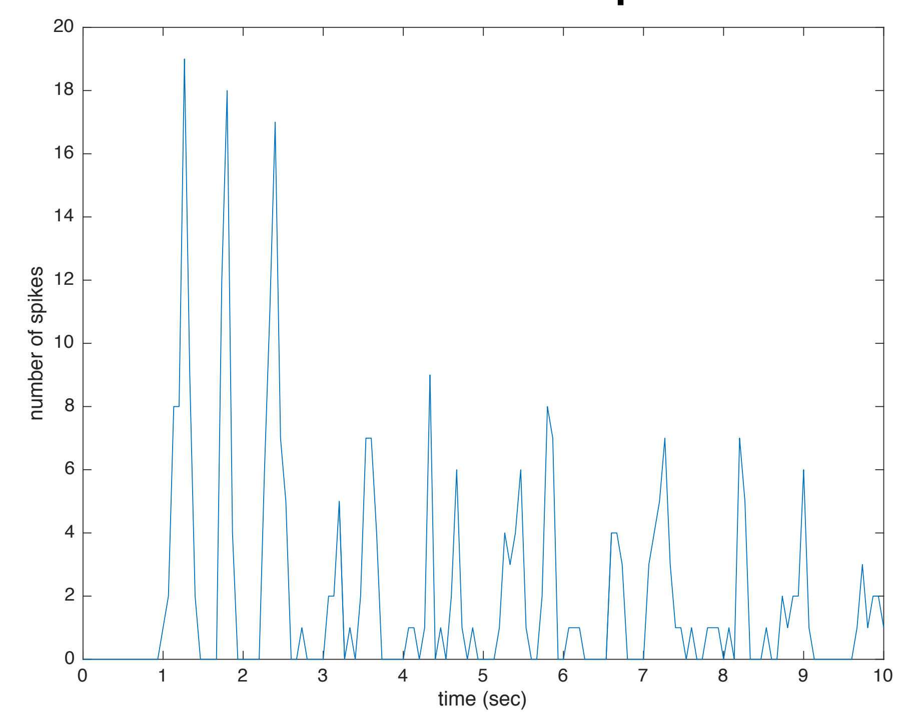
stimulus



time

computation

neural response



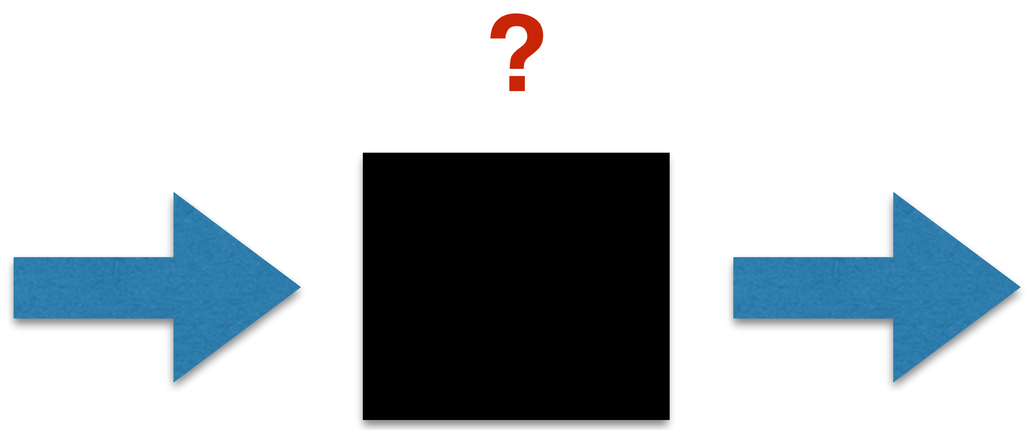
time

General goal: find a functional link between stimulus and response

http://www.pc.rhul.ac.uk/staff/j.zanker/ps1061/l2/ps1061_2.htm

Statistical modeling of a neuron's response

stimulus



$\mathbf{r}(t)$ **firing rate**

Poisson process:
average # of spikes
is given by the firing rate
<n(t)> = r(t)dt

$$Prob(n(t)) = \frac{r(t)^{n(t)}}{n(t)!} exp(-r(t))$$

n(t) - # of spikes between t, t+dt

n(t) 

Identify a model for the firing rate

Project goals

- Implement 5 specific models:

    1. Linear models
        - Spike Triggered Average (STA)
        - Generalized Linear Model (GLM)
    2. Quadratic models
        - Spike Triggered Covariance (STC)
        - Generalized Quadratic Model (GQM)
    3. Cascade model
        - Nonlinear Input Model (NIM)

(Fall semester)

(Spring semester)

- Test models on 3 data sets:
    1. Model-specific **synthetic data** to validate all algorithms
    2. Synthetic Retina ganglion cells (**RGC**) data to test NIM model
    3. Experimental Lateral geniculate body (**LGN**) to test GLM model

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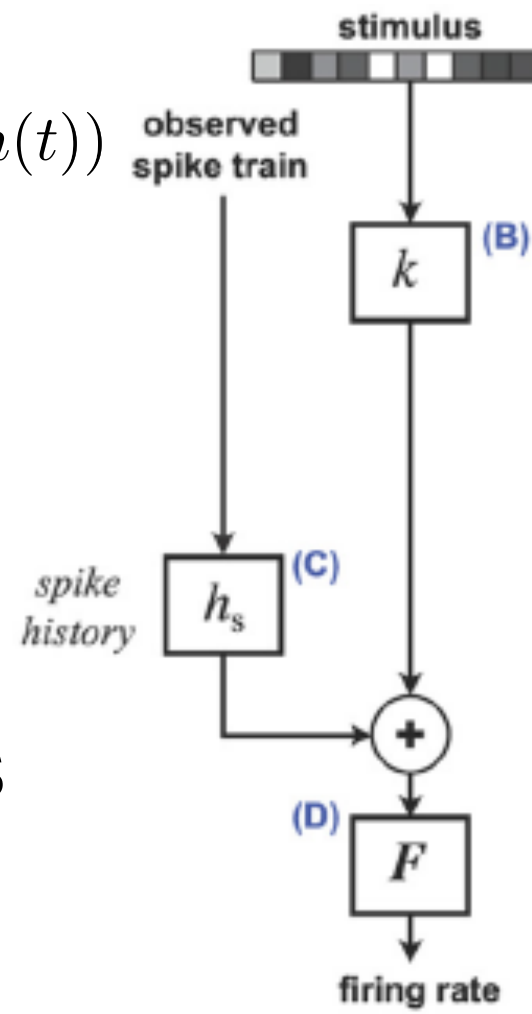
Generalized Linear Model (GLM): a single linear filter (**k**) + history filter (**h**)

$$\mathbf{s}(t,\tau) = (S(t-\tau), ..., S(t))$$

$$\mathbf{n_{obs}}(t,\tau) = (n(t-\tau), ..., n(t))$$



k linear filter: models receptive field of a neuron

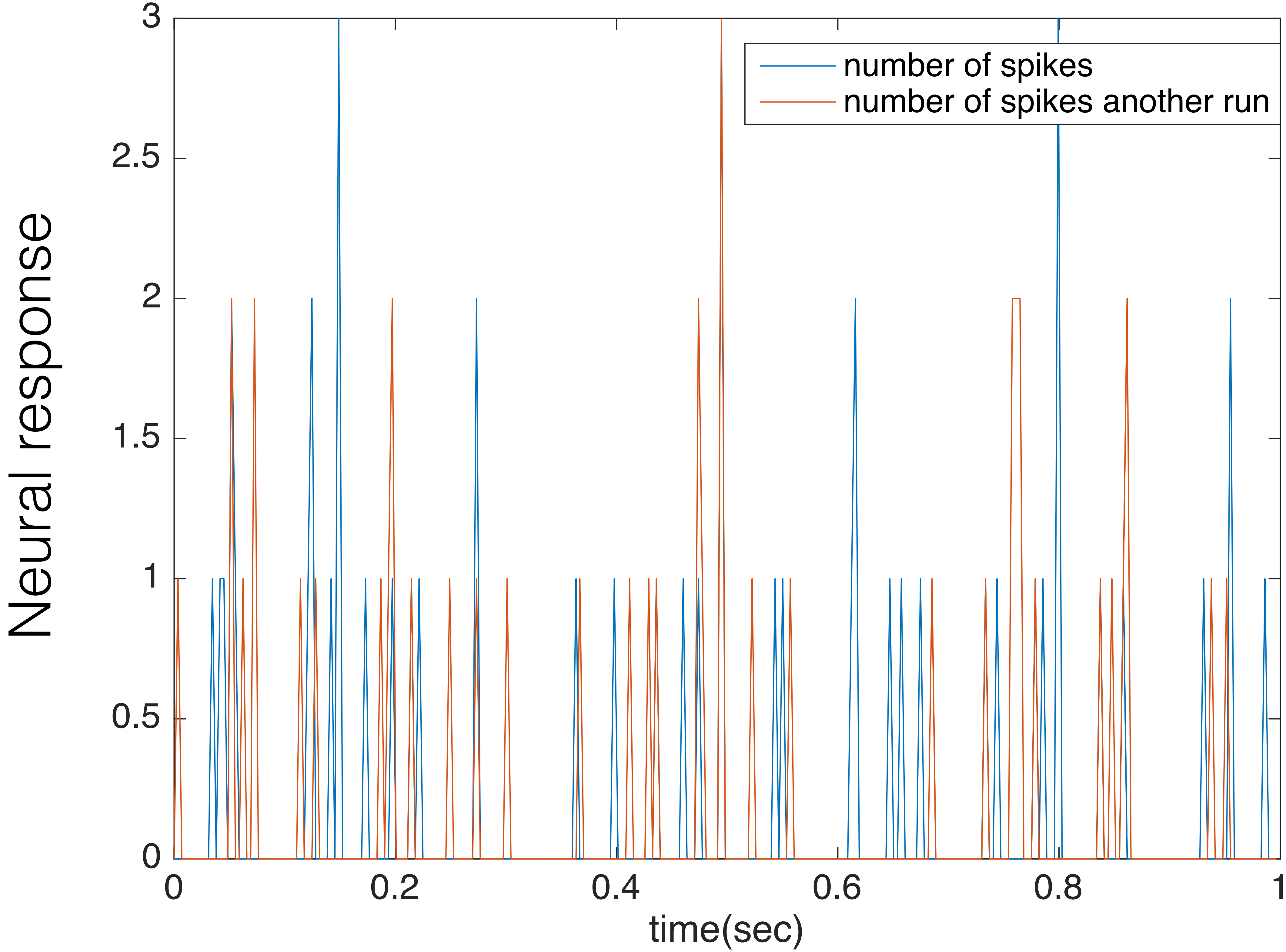
h history filter: models neuron's memory of spikes

Spiking non-linearity: models neuron's non-linear processing

firing rate model	$r(t) = F(\mathbf{k} \cdot \mathbf{s}(t,\tau) + \mathbf{h} \cdot \mathbf{n_{obs}}(t,\tau) + b)$

Picture reference: Butts DA, Weng C, Jin JZ, Alonso JM, Paninski L (2011) Temporal precision in the visual pathway through the interplay of excitation and stimulus-driven suppression.

How to fit parameters to a probabilistic data?



Maximum Likelihood estimation

$$P(N|\Theta) = \prod_t \frac{(r(t))^{n(t)}}{n(t)!} exp(-r(t))$$ ← Poisson distribution

$$N = \{n(t)\} \quad \Theta = \{r(t)\}$$

$$LL(\Theta) = log(P(N|\Theta)) = \sum_t n(t) log(r(t)) - \sum_t r(t)$$

GLM model specifically:

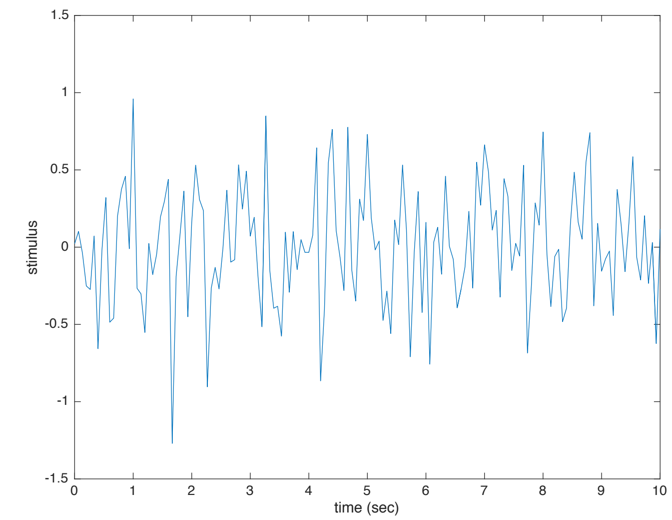
$$r(t) = F(\mathbf{k} \cdot \mathbf{s}(t,\tau) + \mathbf{h} \cdot \mathbf{n_{obs}}(t,\tau) + b) \qquad \Theta = \{\mathbf{k}, \mathbf{h}, b\} \qquad F() = exp()$$

Maximize log-likelihood using gradient ascent method

$$LL(\Theta) = \sum_t n(t)(\mathbf{k} \cdot \mathbf{s}(t) + \mathbf{h} \cdot \mathbf{n}_{obs}(t) + b) - \sum_t exp(\mathbf{k} \cdot \mathbf{s}(t) + \mathbf{h} \cdot \mathbf{n}_{obs}(t) + b)$$

Synthetic data for GLM algorithm validation

Step 1: generate white noise stimulus s(t)

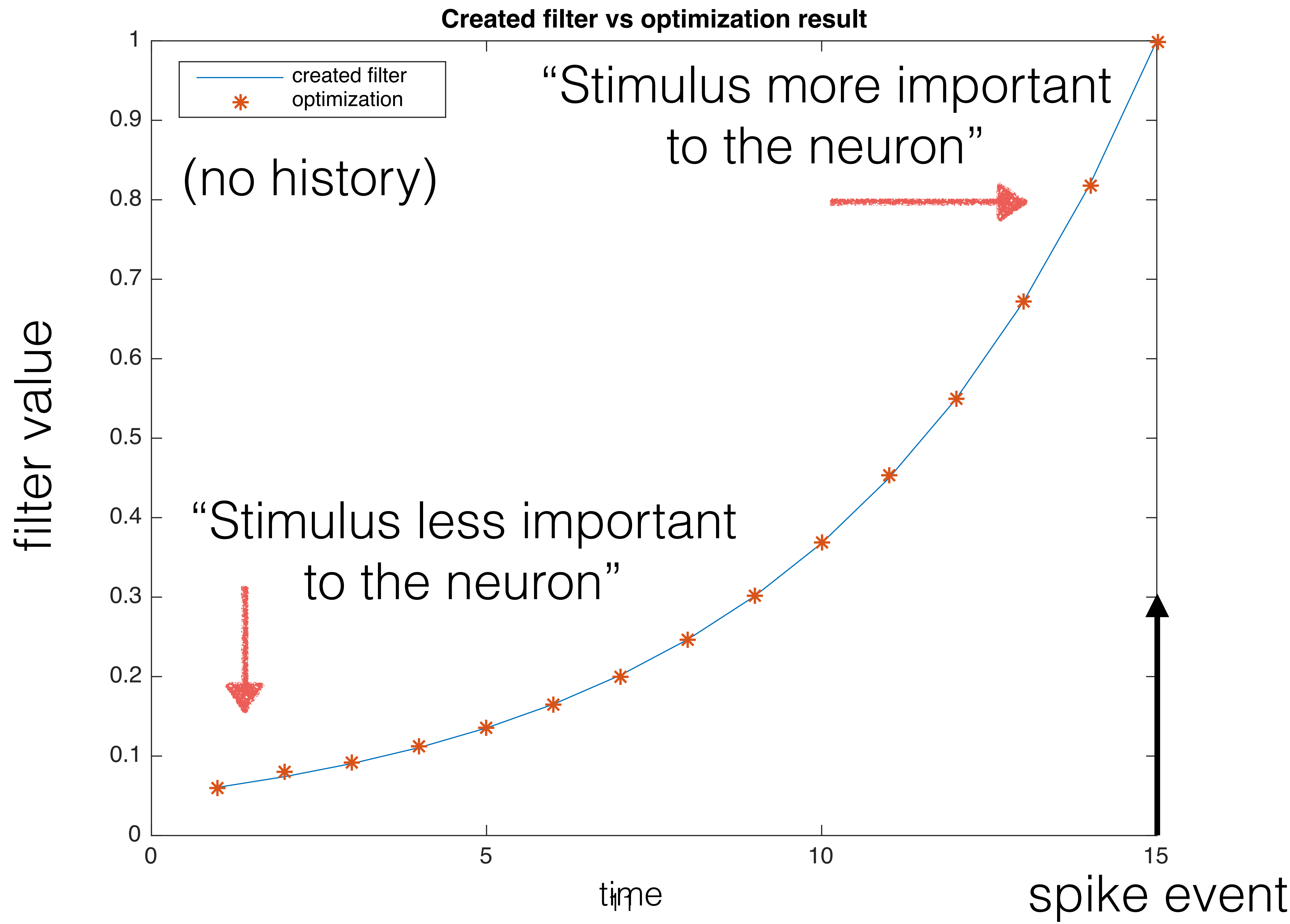


Step 2: calculate r(t) using test filters and test function F:

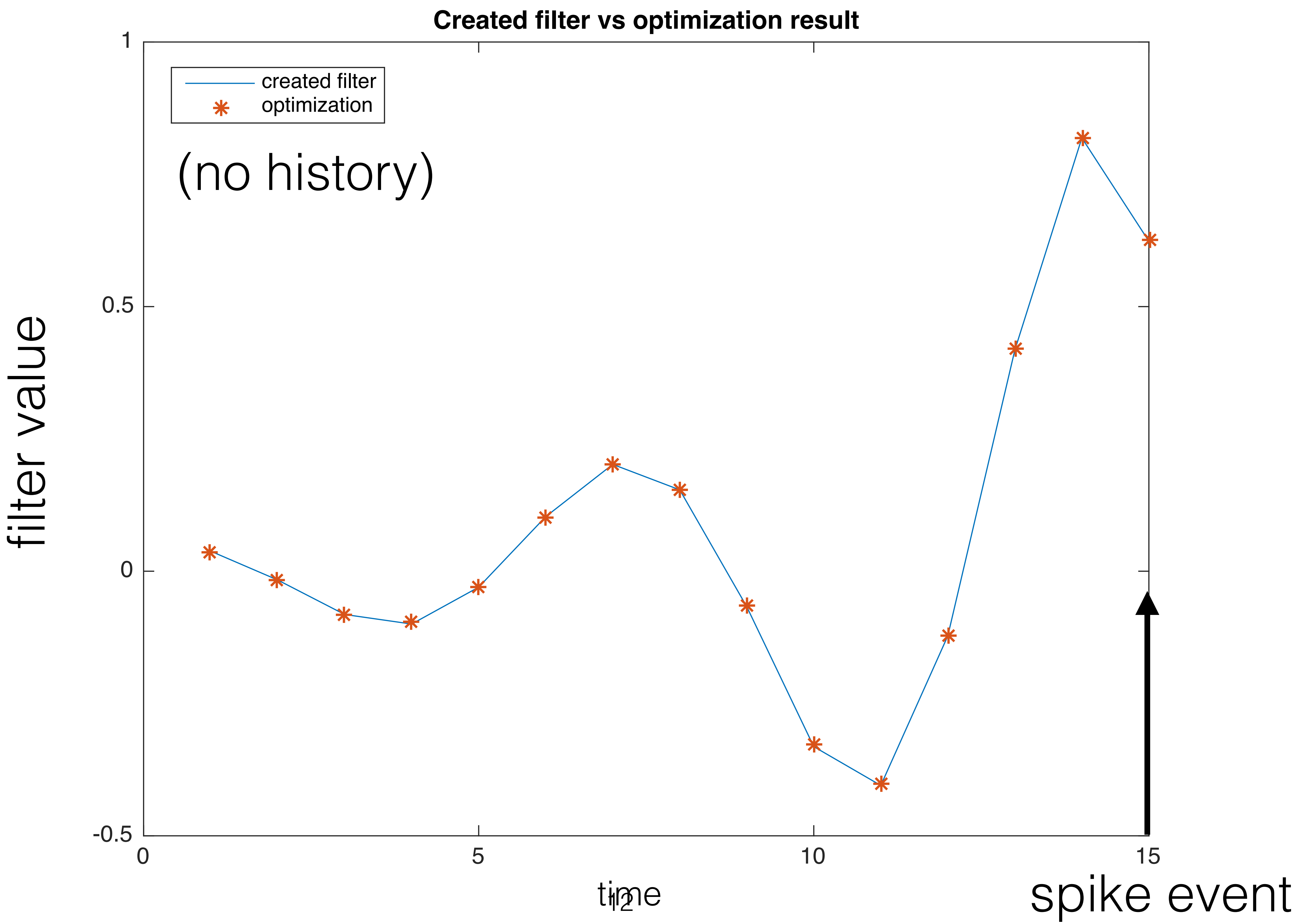
F(x) = Exp(x)

Step 3: generate Poisson spikes n(t) using calculated r(t)

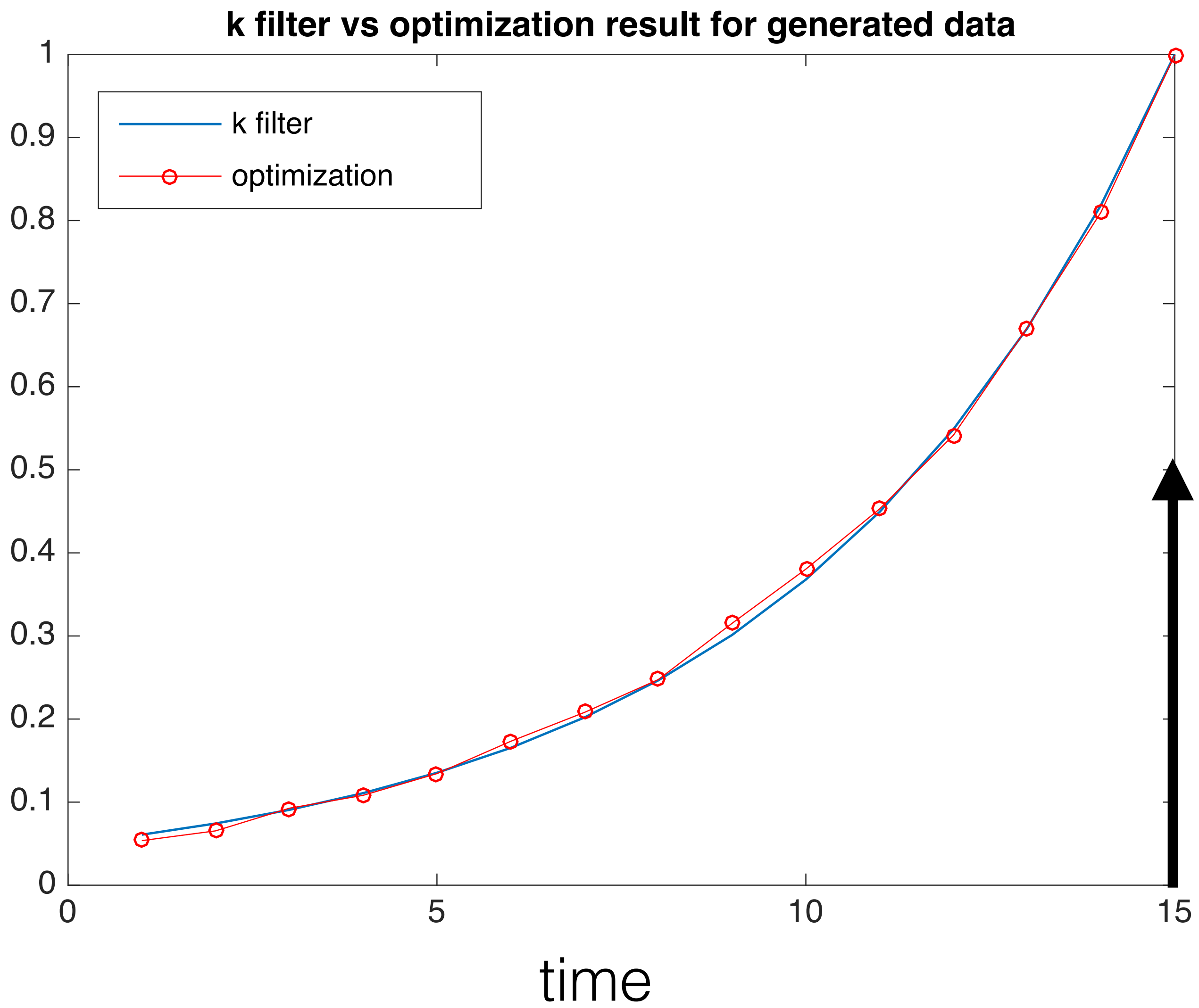
Use synthetic GLM data without history to recover a *decaying* linear k-filter



Use synthetic GLM data without history to recover *oscillating* linear k-filter

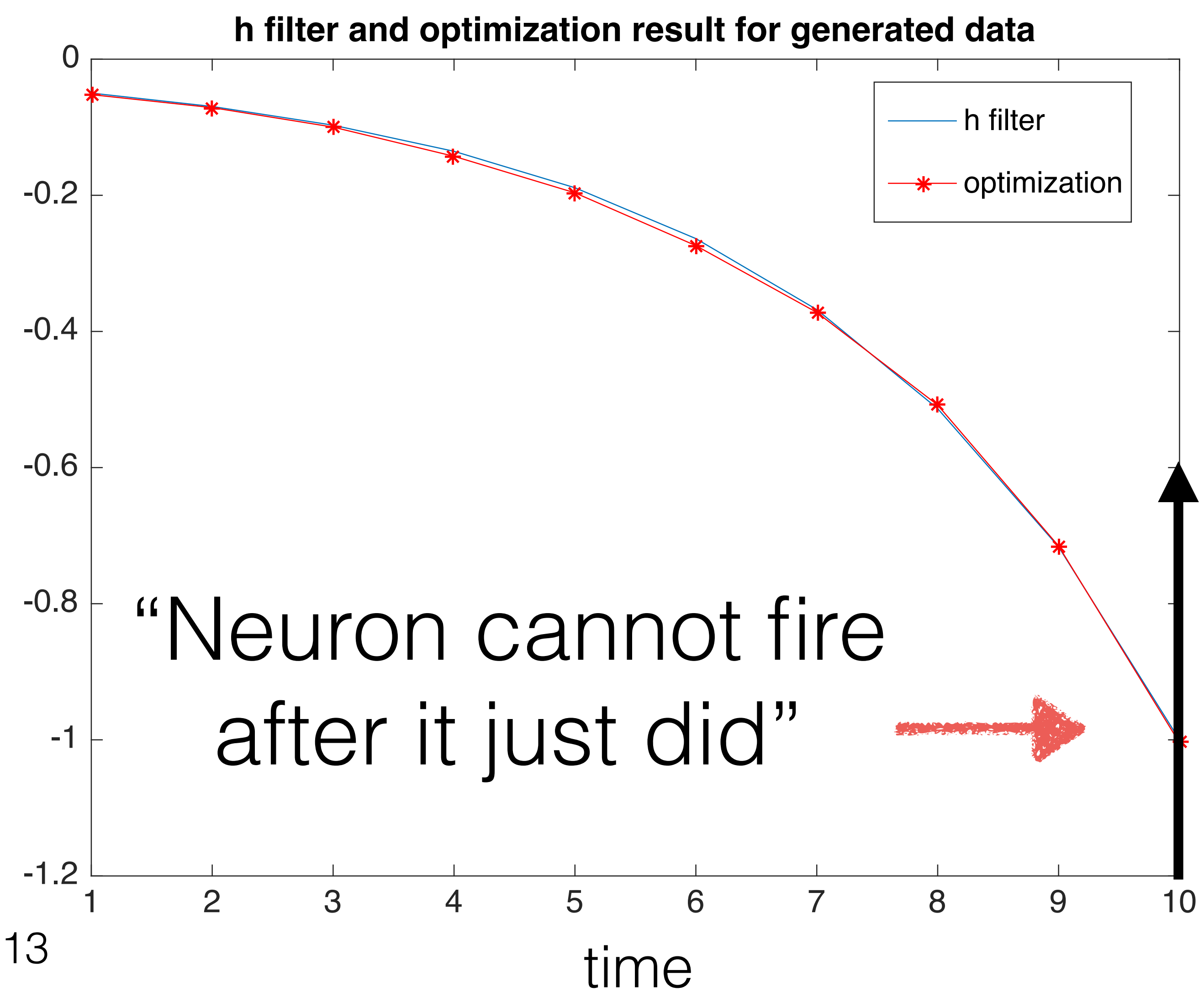


Use synthetic GLM data with history to recover both k (linear) & h (history) filters

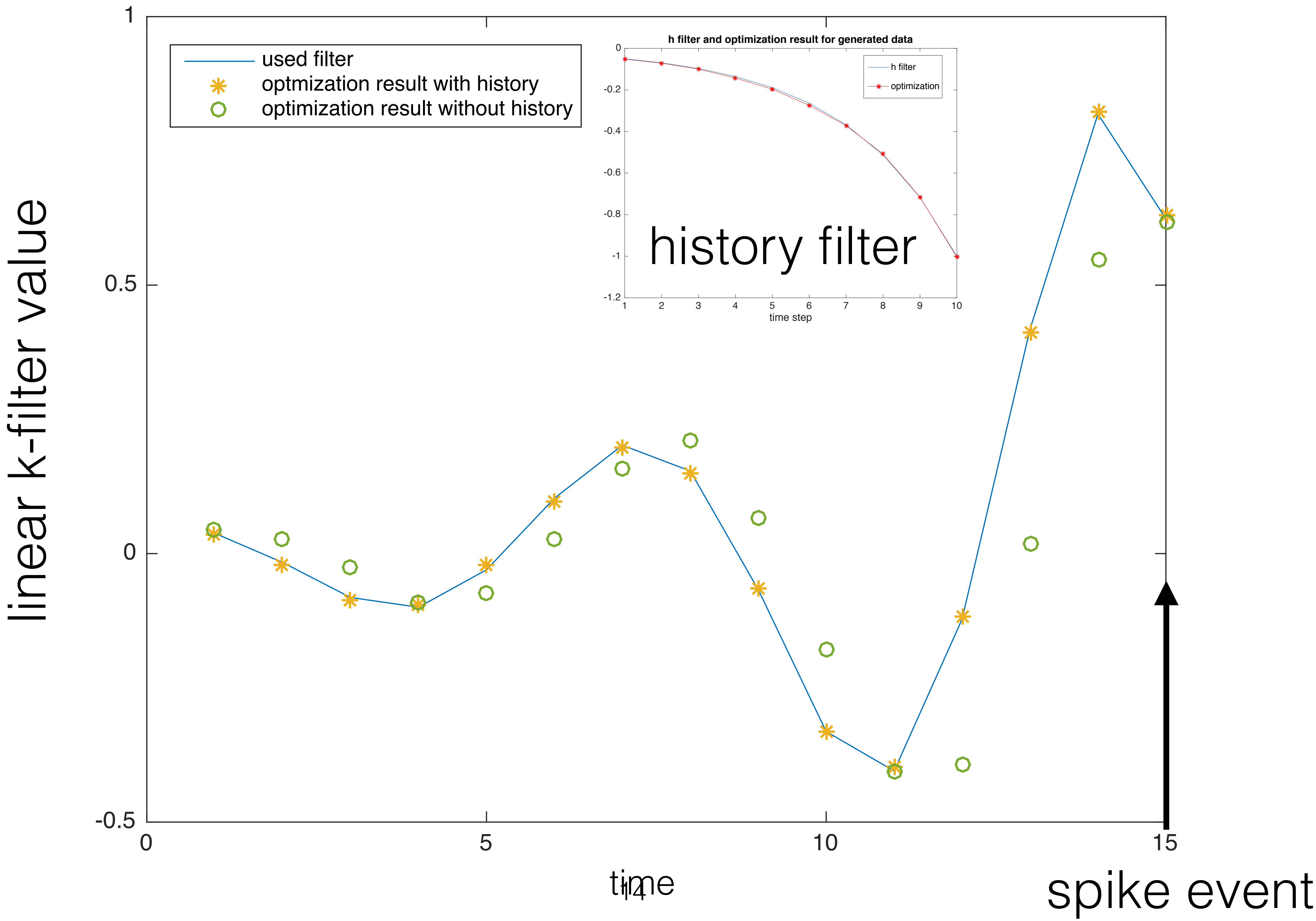


linear filter k

history filter (h<0)

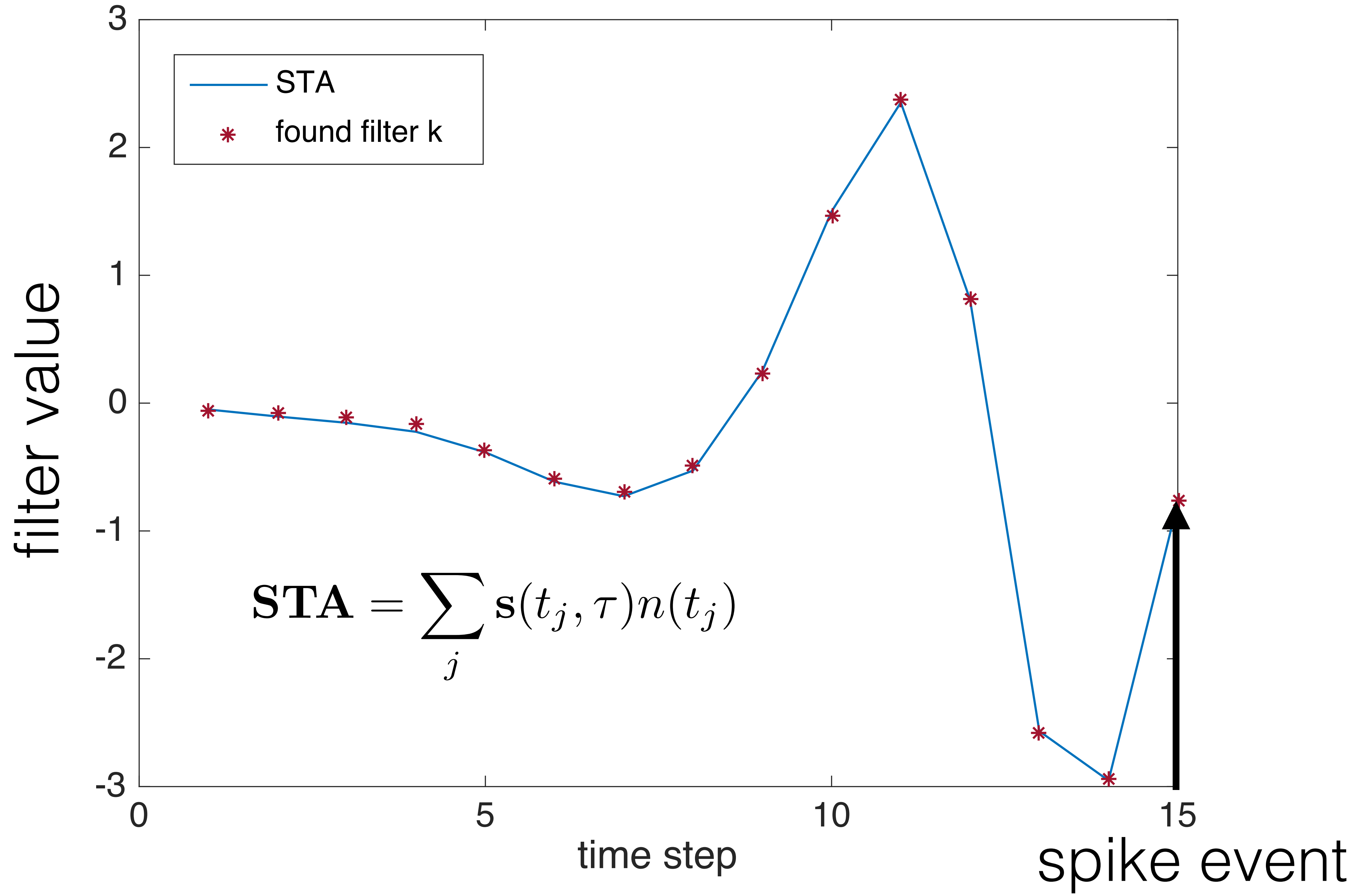


History cannot be ignored!
(synthetic GLM data with exponential history filter)



RGC data (no history): GLM optimal filter matches STA

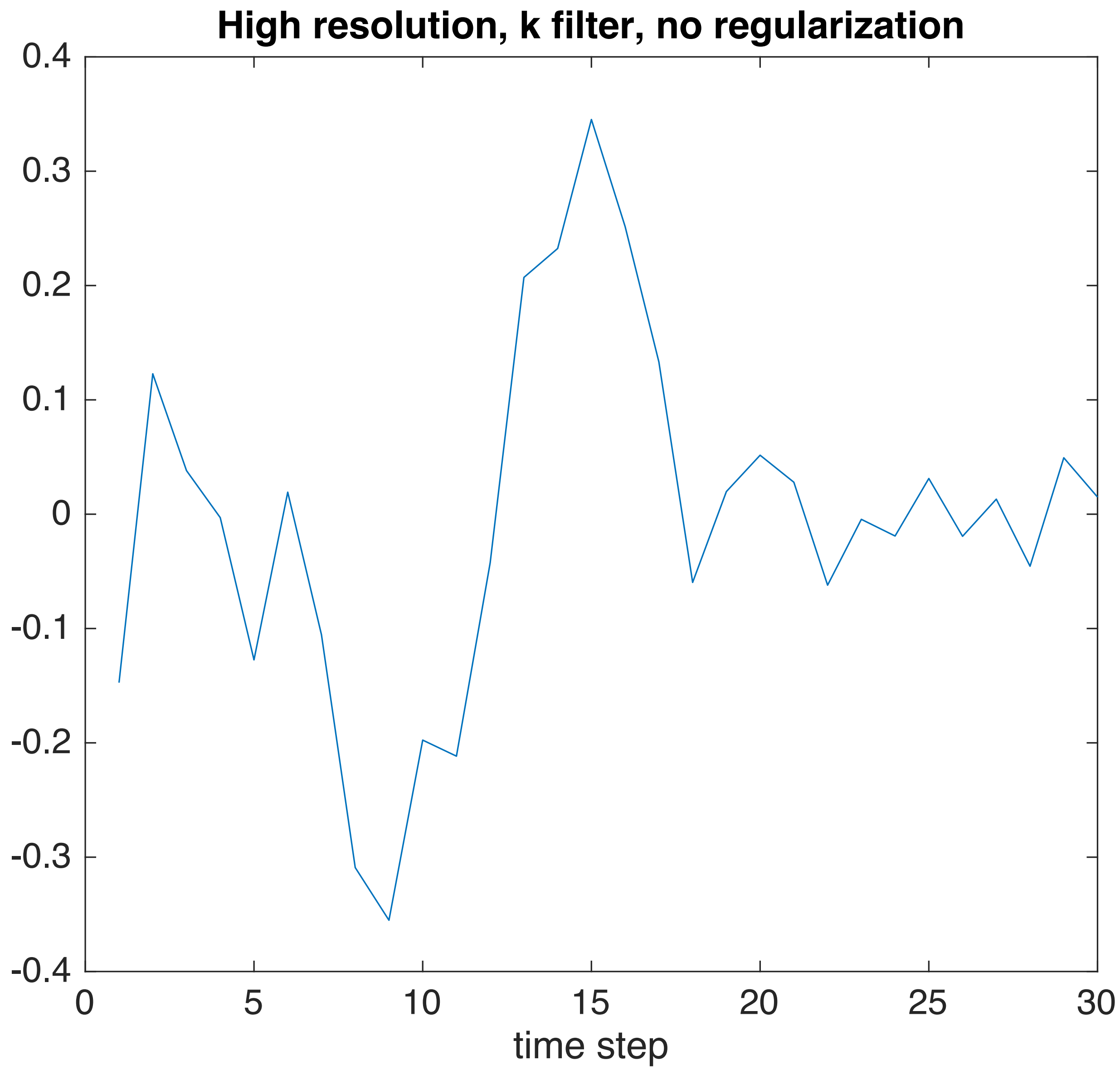
STA = spiked-triggered average stimulus



$$\mathbf{STA} = \sum_j \mathbf{s}(t_j, \tau) n(t_j)$$

True for any Gaussian fluctuating variable (see report for details)

LGN data: regularization of the search algorithm



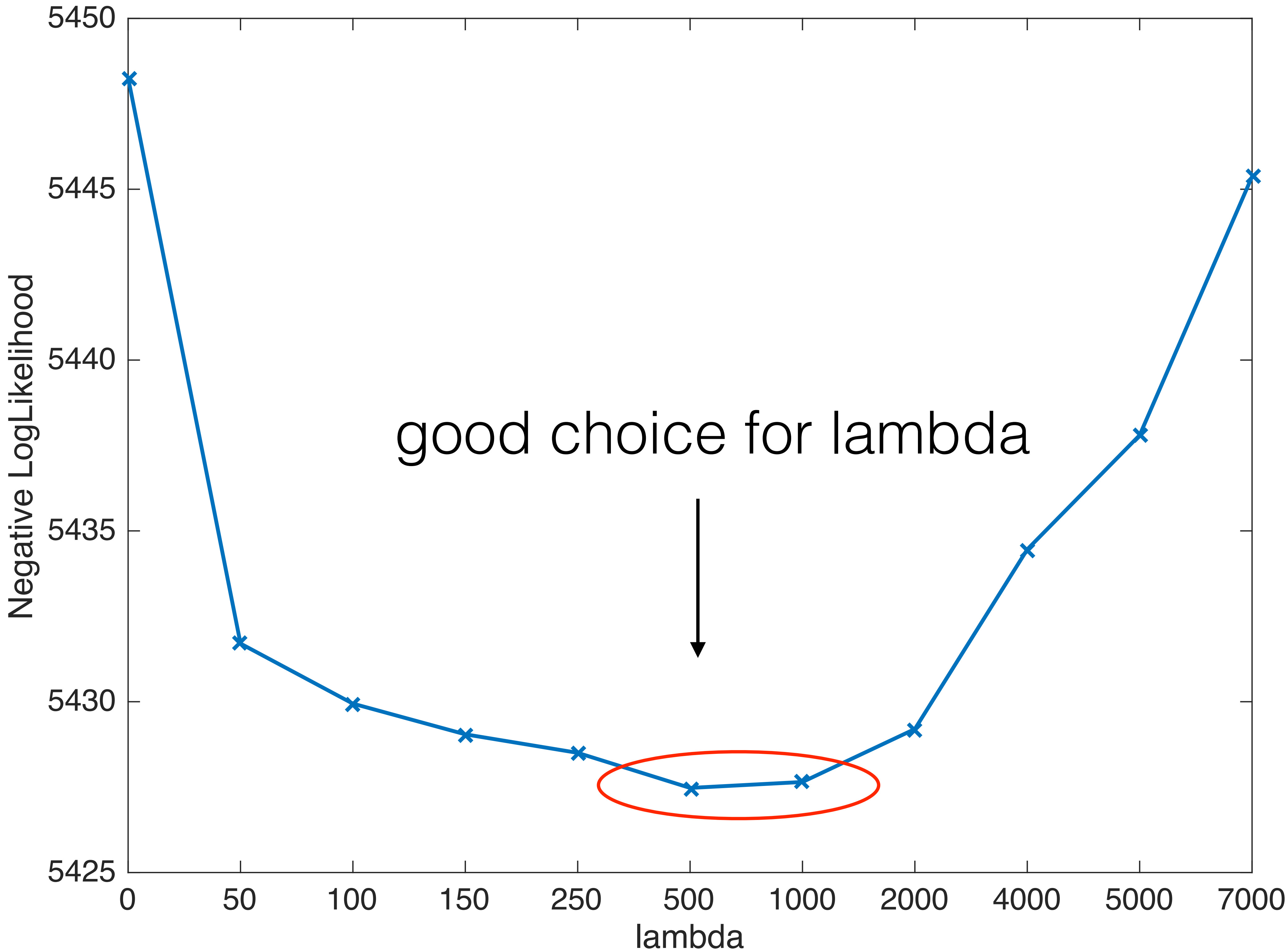
Use a priori information that k-filter must be a smooth filter.

Penalize LL for large gradients

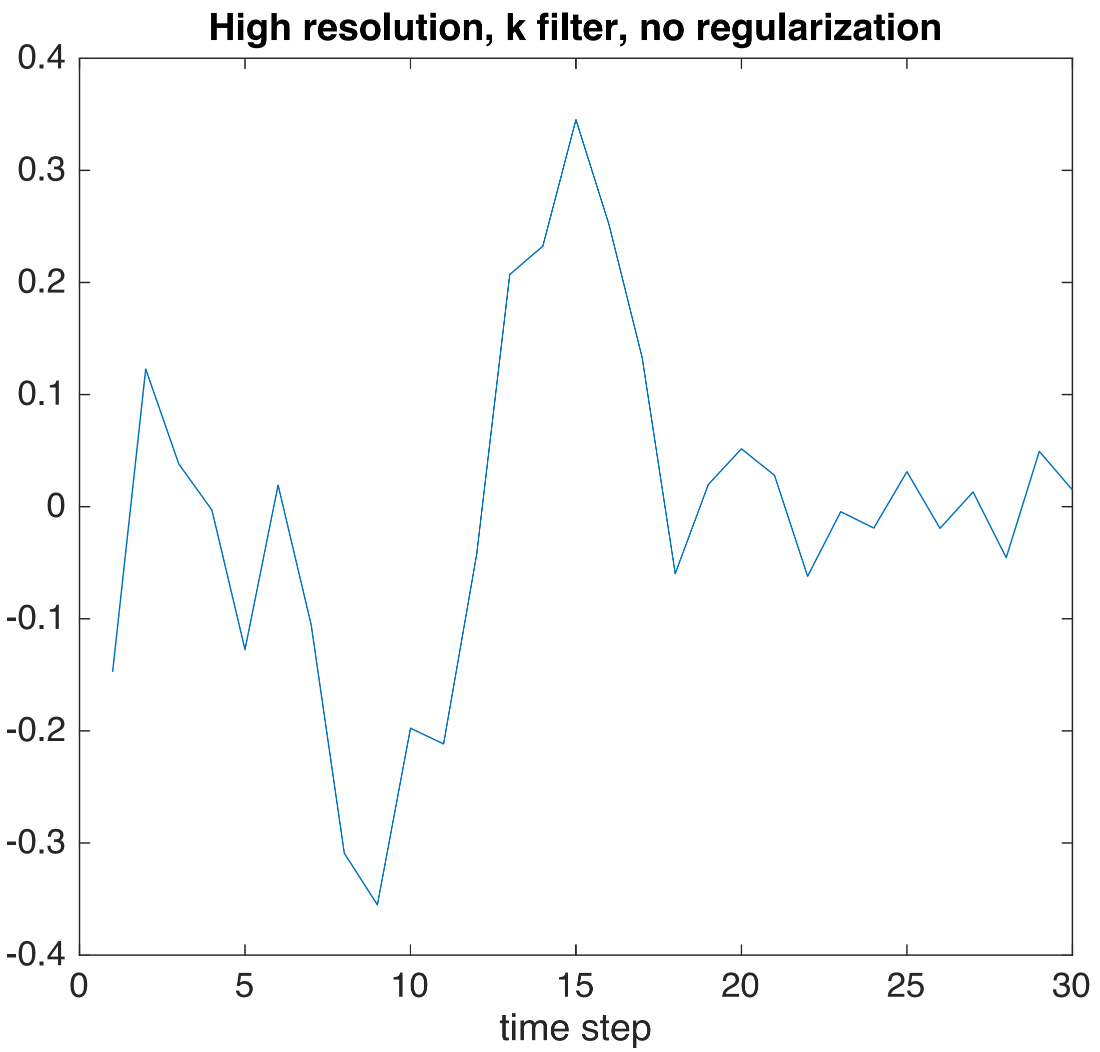
$$RLL(\Theta) = \sum_t n(t)(\mathbf{k}\cdot\mathbf{s}(t) + \mathbf{h}\cdot\mathbf{n}_{obs}(t) + b) - \sum_t exp(\mathbf{k}\cdot\mathbf{s}(t) + \mathbf{h}\cdot\mathbf{n}_{obs}(t) + b) - \lambda\sum_i (k_i - k_{i-1})^2$$

Find optimal lambda by cross validation

LGN data: cross-validation for the choice of regularization parameter

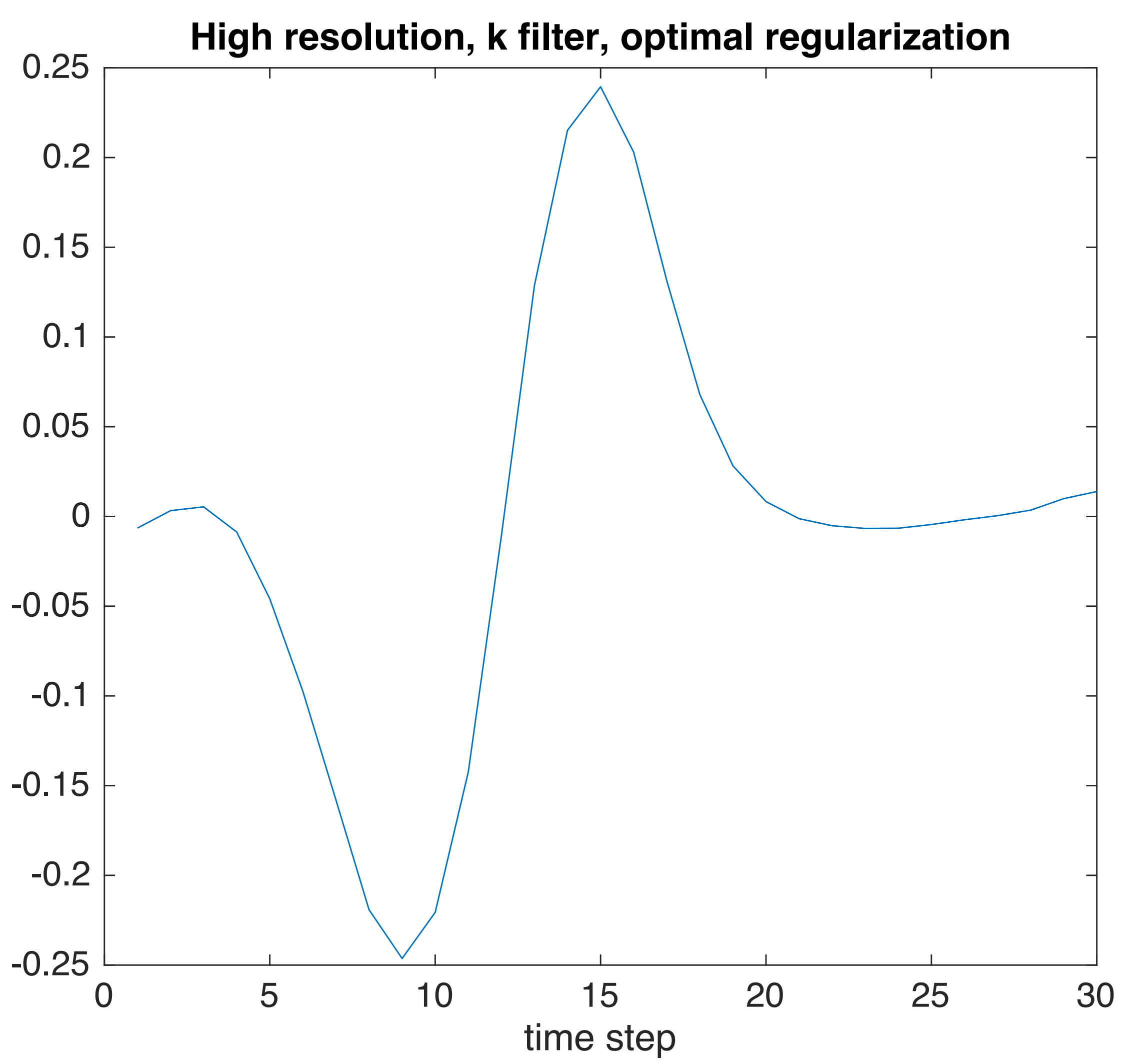


LGN data: GLM implementation with regularization, k filter

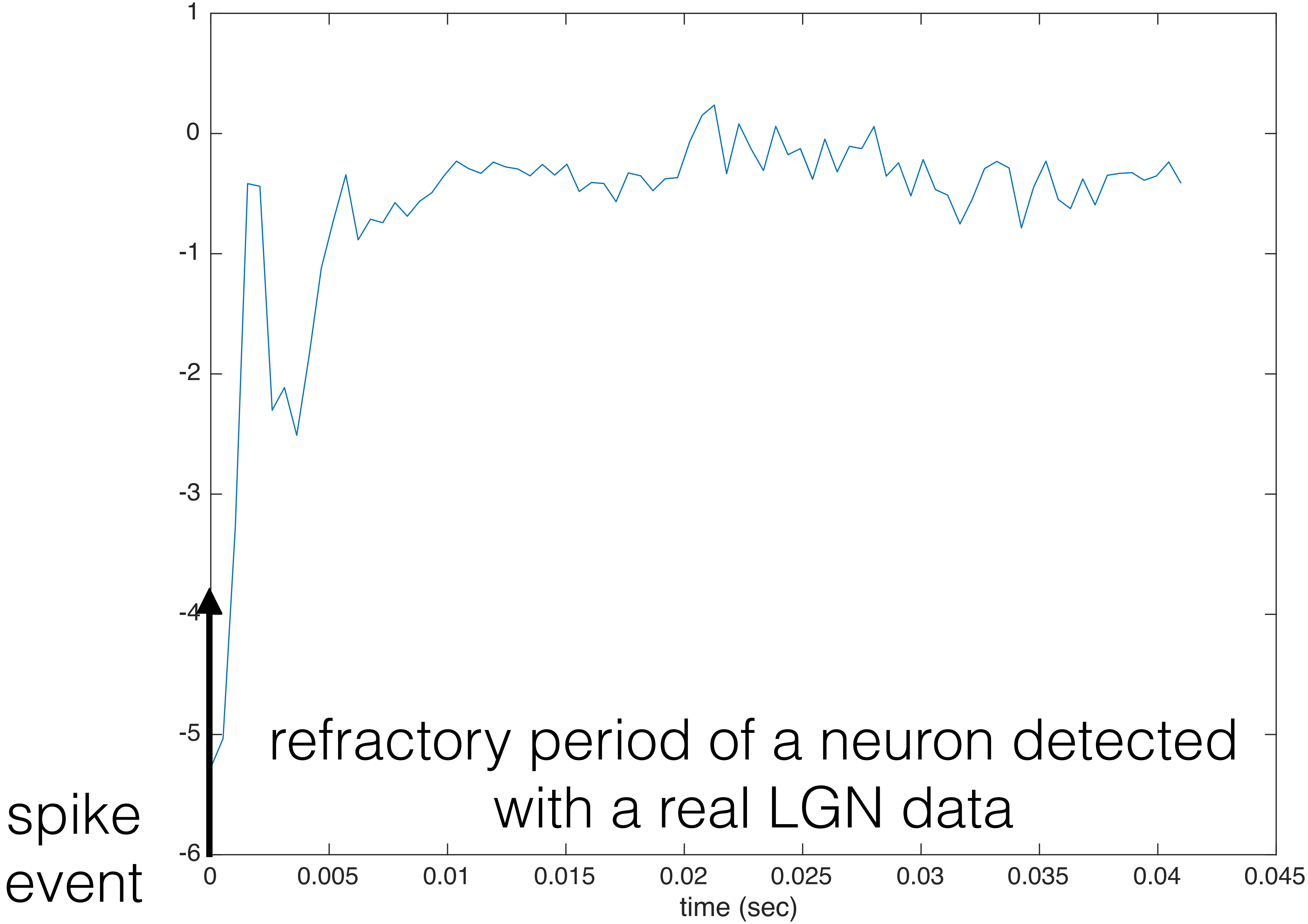


high resolution
no regularization

high resolution
optimal regularization



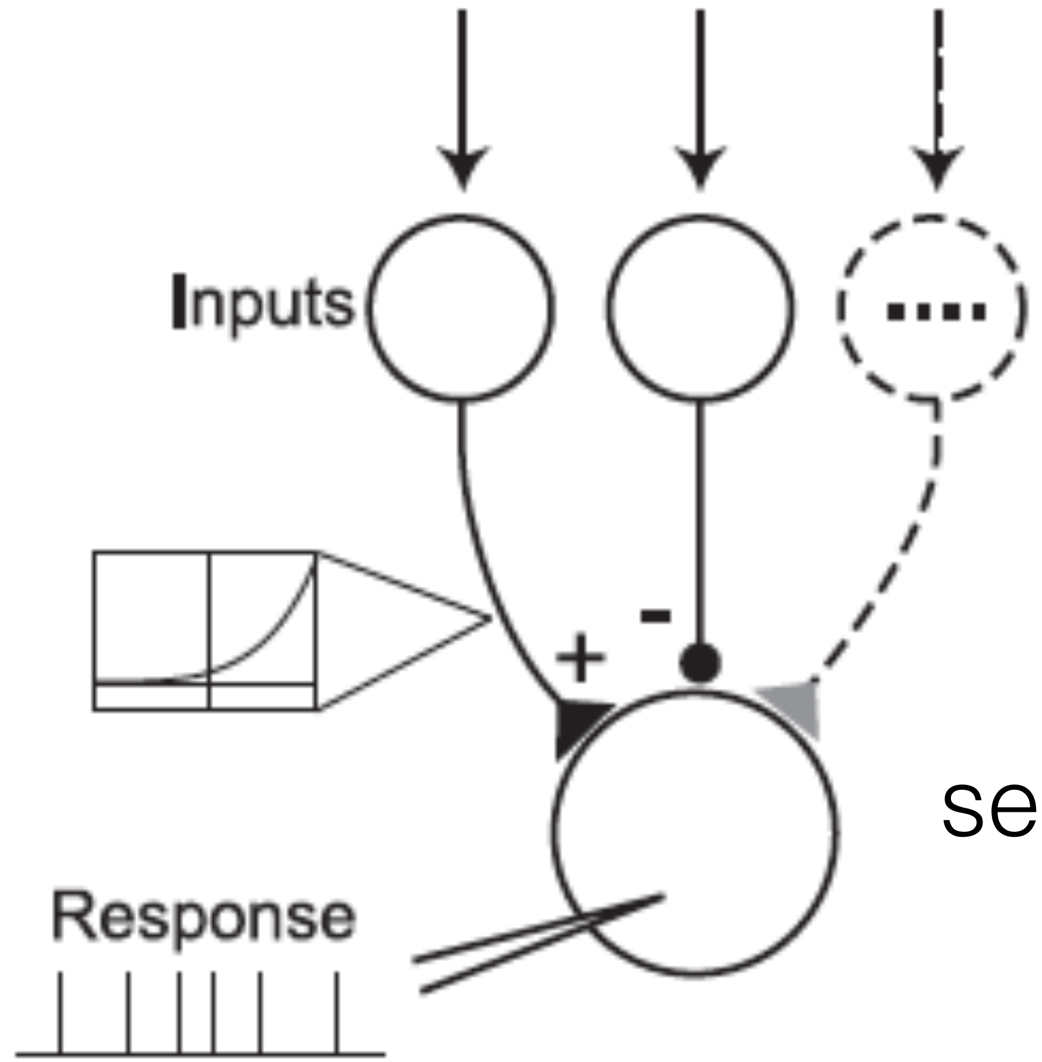
Main result on GLM: recovered history term from LGN data



Picture reference: Butts DA, Weng C, Jin JZ, Alonso JM, Paninski L (2011) Temporal precision in the visual pathway through the interplay of excitation and stimulus-driven suppression.

Non-linear Input Model (NIM)

motivation



primary neurons

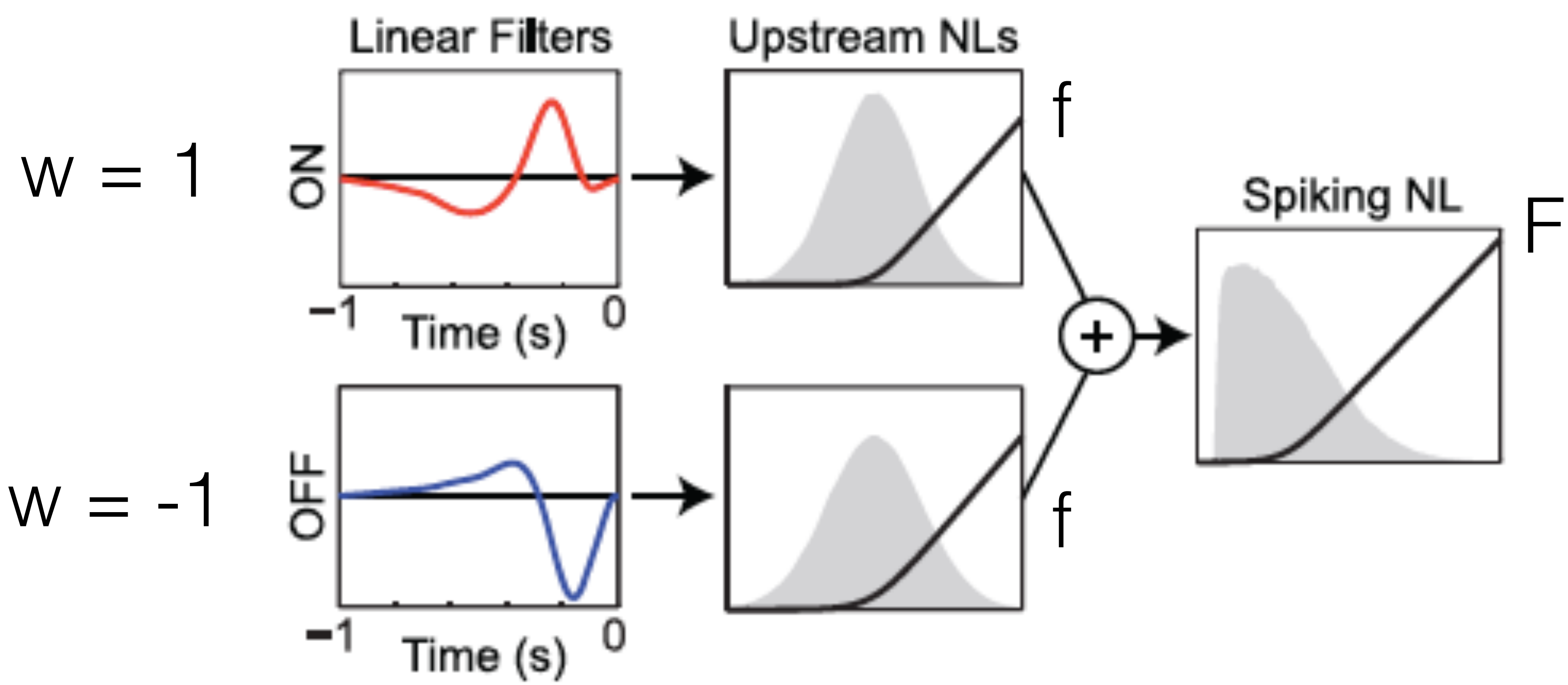
secondary neuron

NIM is based on the hypothesis that the dominant nonlinearities imposed by the physiological mechanisms arise from rectification of neuron's inputs

Picture reference: Butts DA, Weng C, Jin JZ, Alonso JM, Paninski L (2011) Temporal precision in the visual pathway through the interplay of excitation and stimulus-driven suppression.

Non-linear Input Model (NIM)

$$r(t) = F(\sum_i \omega_i f(\mathbf{k}_i \cdot \mathbf{s}(t,\tau)))$$



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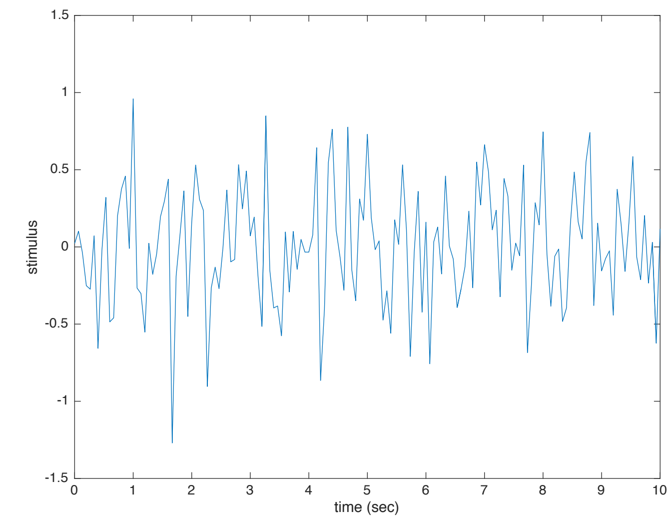
Synthetic data for NIM algorithm validation

Step 1: generate white noise stimulus s(t)

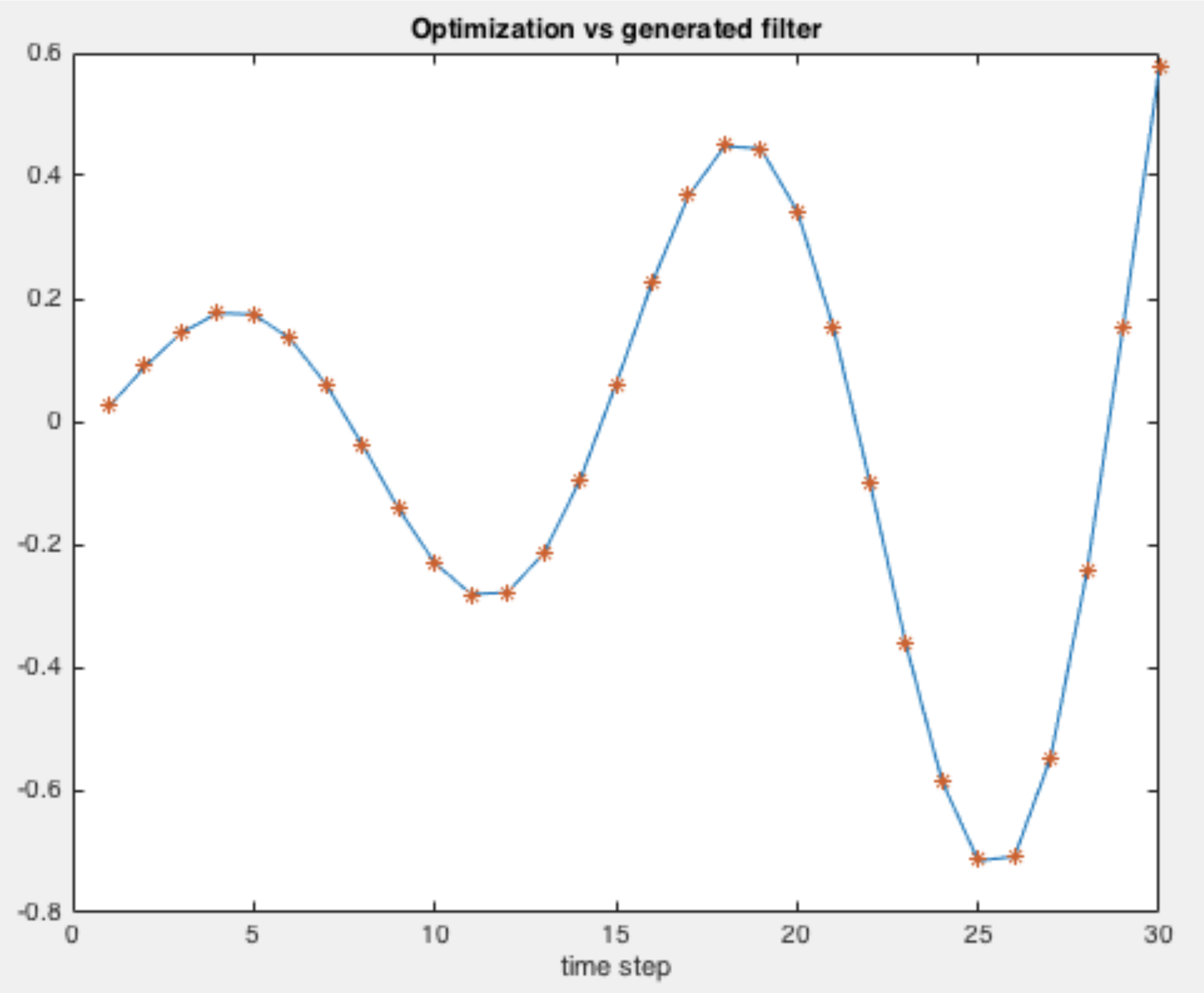


Step 2: calculate r(t) using two test filters k1 & k2 and various combinations for test functions F and f:

F(x) = Exp(x)
f(x) = Log(1+Exp(x))
f(x) = 0, x<0; x, x>=0

Step 3: generate Poisson spikes n(t) using calculated r(t)

Validation of NIM algorithm using synthetic NIM data

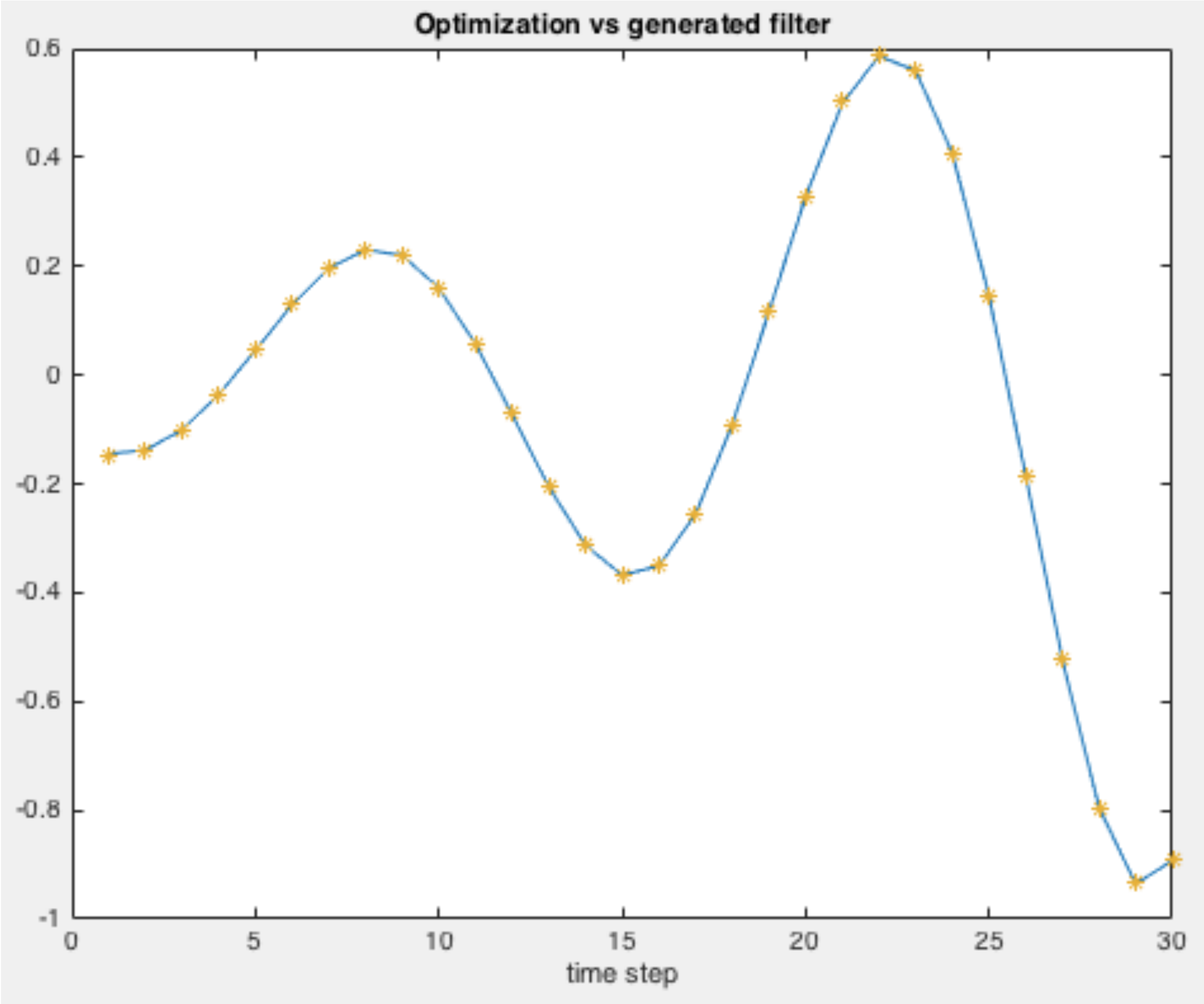


filter 1

$F(x) = Exp(x)$

$f(x) = 0, x<0; x, x>=0$

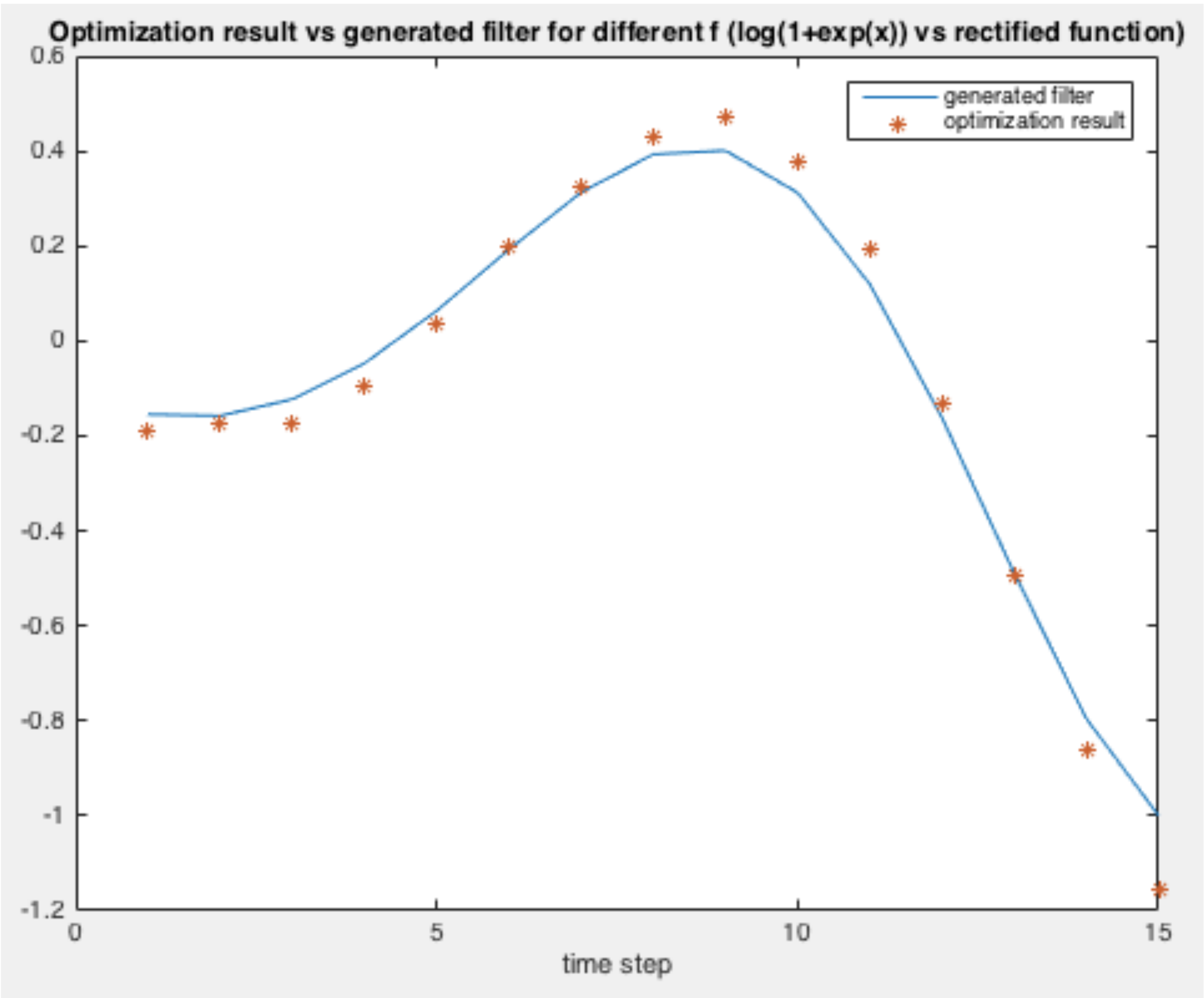
filter 2



Details of rectifying non-linearity are not too important

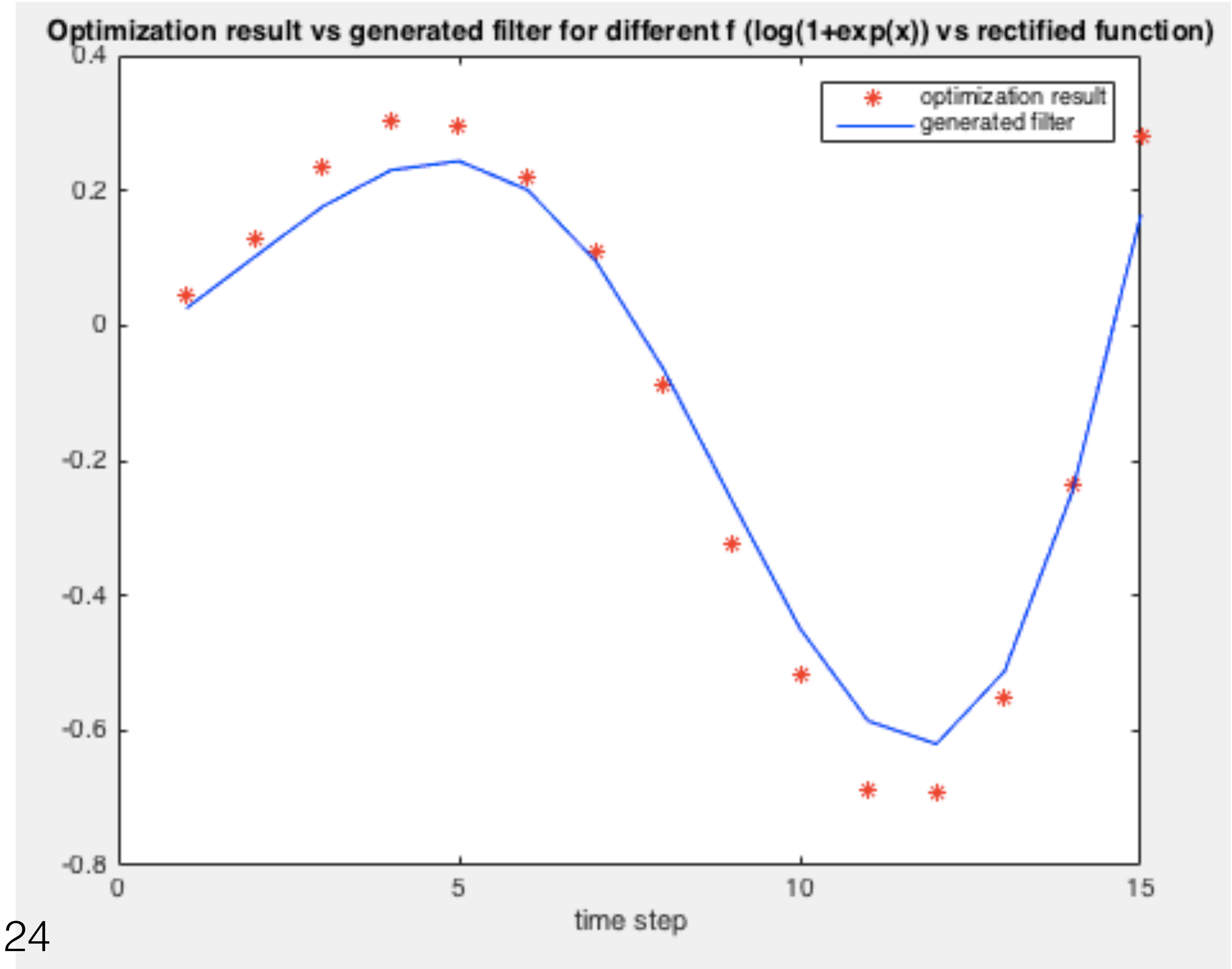
Generate: F(x) = Exp(x)
f(x) = Log (1+Exp(x))

Recover: F(x) = Exp(x)
f(x) = 0, x<0; x, x>=0

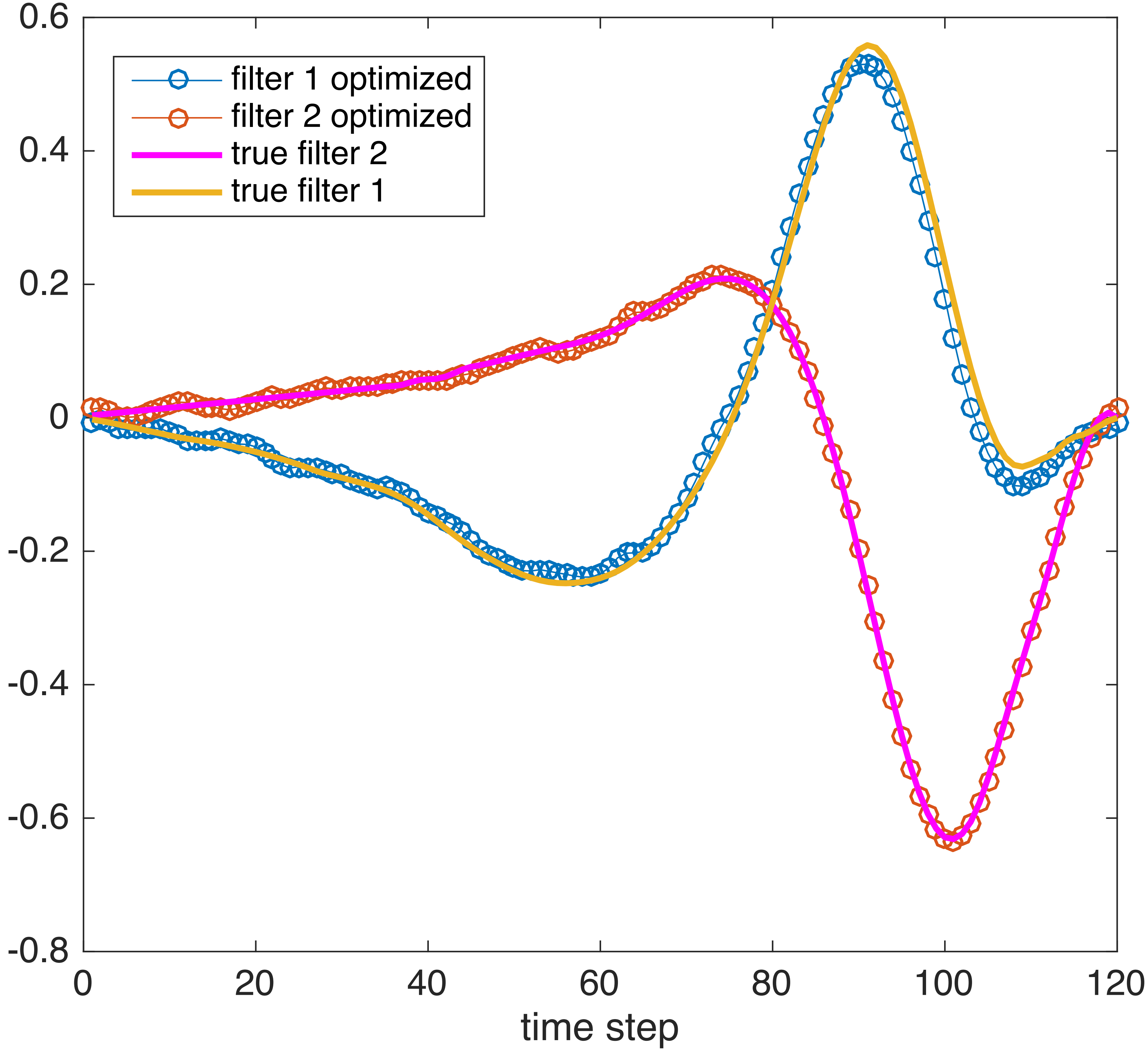


filter 1

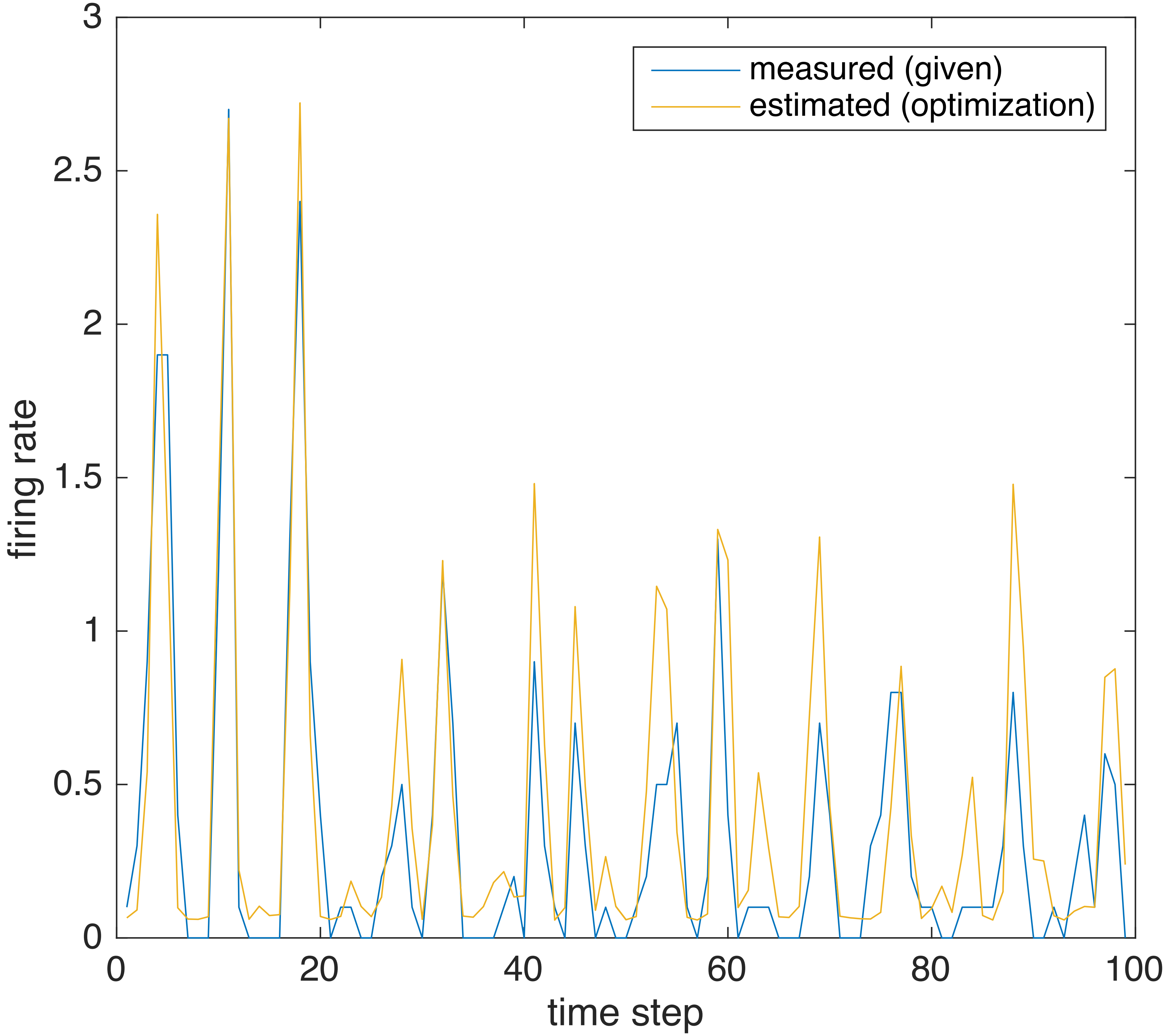
filter 2



Recovering model parameters from RGC synthetic data



RGC spiking output vs NIM-recovered spiking output



Picture reference: Butts DA, Weng C, Jin JZ, Alonso JM, Paninski L (2011) Temporal precision in the visual pathway through the interplay of excitation and stimulus-driven suppression.

Generalized Quadratic Model (GQM)

$$r(t) = F(\mathbf{k}_L \cdot \mathbf{s}(t,\tau) + \sum_i \omega_i (\mathbf{k}_i \cdot \mathbf{s}(t,\tau))^2)$$

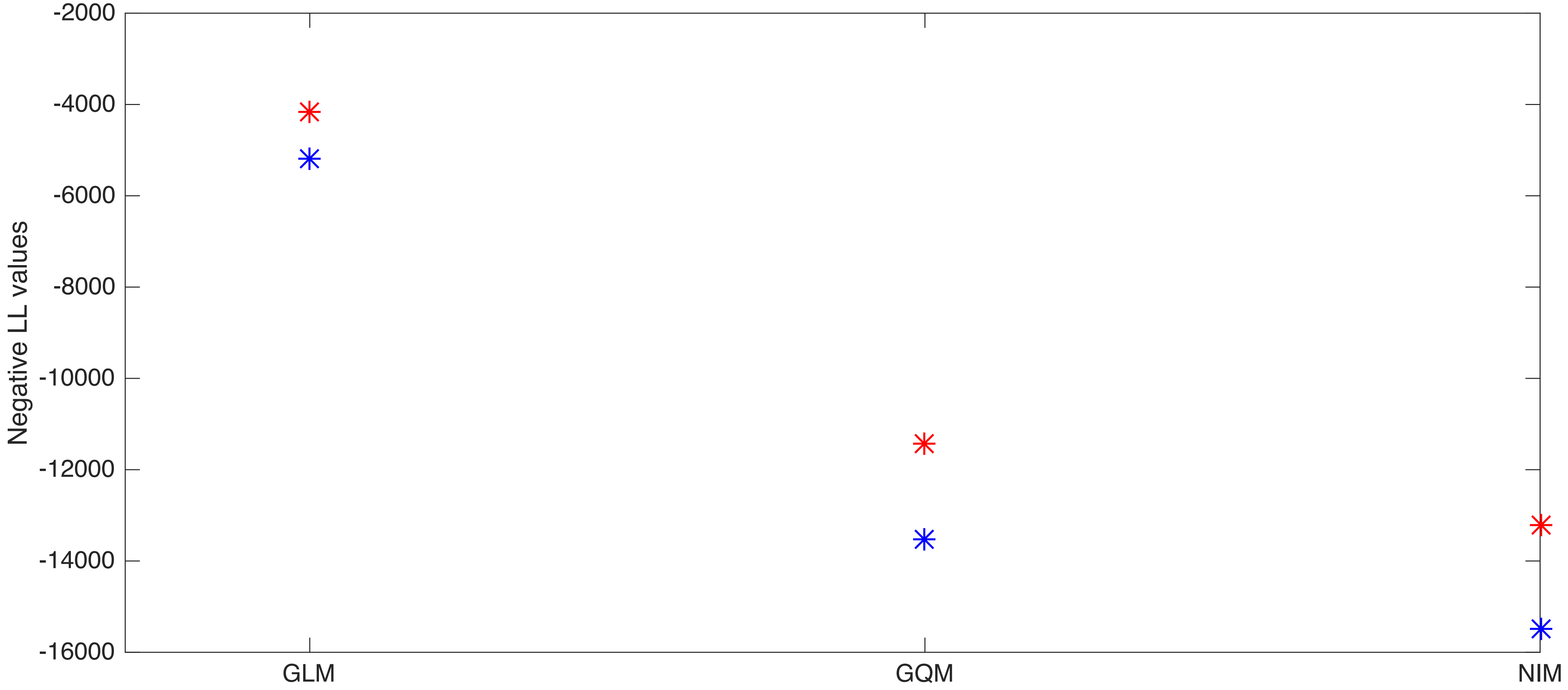
Spiking non-linearity

Linear filter

A set of (a few) quadratic filters
w = +1/-1

A competing model to NIM with minimal (quadratic) modification to simple linear filtering

Comparison of GLM, NIM, GQM for a single RGC data set



Summary

Realized GLM model on both real and synthetic data

- full algorithm validation on synthetic data
- recovered linear filter that matched STA
- detected a short refractory period with a history term
- results matched with the paper: Butts DA, Weng C, Jin JZ, Alonso JM, Paninski L (2011) Temporal precision in the visual pathway through the interplay of excitation and stimulus-driven suppression.

Realized GQM on synthetic data (1 linear/2 quadratic)

Realized NIM model on synthetic data (2 rectified terms)

- GQM does not recover correct NIM filters
- NIM finds correct filters irrespective non-linearity details

Updated project schedule

October - ~~mid November~~ November

- ✓ Implement STA and STC models
- ✓ Test models on synthetic data set and validate models on real data set

~~November - December~~ December - mid February

- ✓ Implement Generalized Linear Model (GLM)
- ✓ Test model on synthetic data set and validate model on LGN data set

~~January - March~~ mid February - mid April

- ✓ Implement Generalized Quadratic Model (GQM) and Nonlinear Input Model (NIM)
- ✓ Test models on synthetic data set and validate models on LGN data set

~~April - May~~ Mid April - May

- ✓ Collect results and prepare final report

Implementation

Hardware

- MacBook Air, 1.4 GHz Intel Core i5, 4 GB 1600 MHz DDR3

Software

- Matlab_R2015b

Deliverables

- Code for STA and STC
- Code for GLM
- Code for GQM
- Code for NIM
- Validation codes for all models
- Reports and presentations

References

1. McFarland JM, Cui Y, Butts DA (2013) Inferring nonlinear neuronal computation based on physiologically plausible inputs. PLoS Computational Biology 9(7): e1003142.

2. Butts DA, Weng C, Jin JZ, Alonso JM, Paninski L (2011) Temporal precision in the visual pathway through the interplay of excitation and stimulus-driven suppression. J. Neurosci. 31: 11313-27.

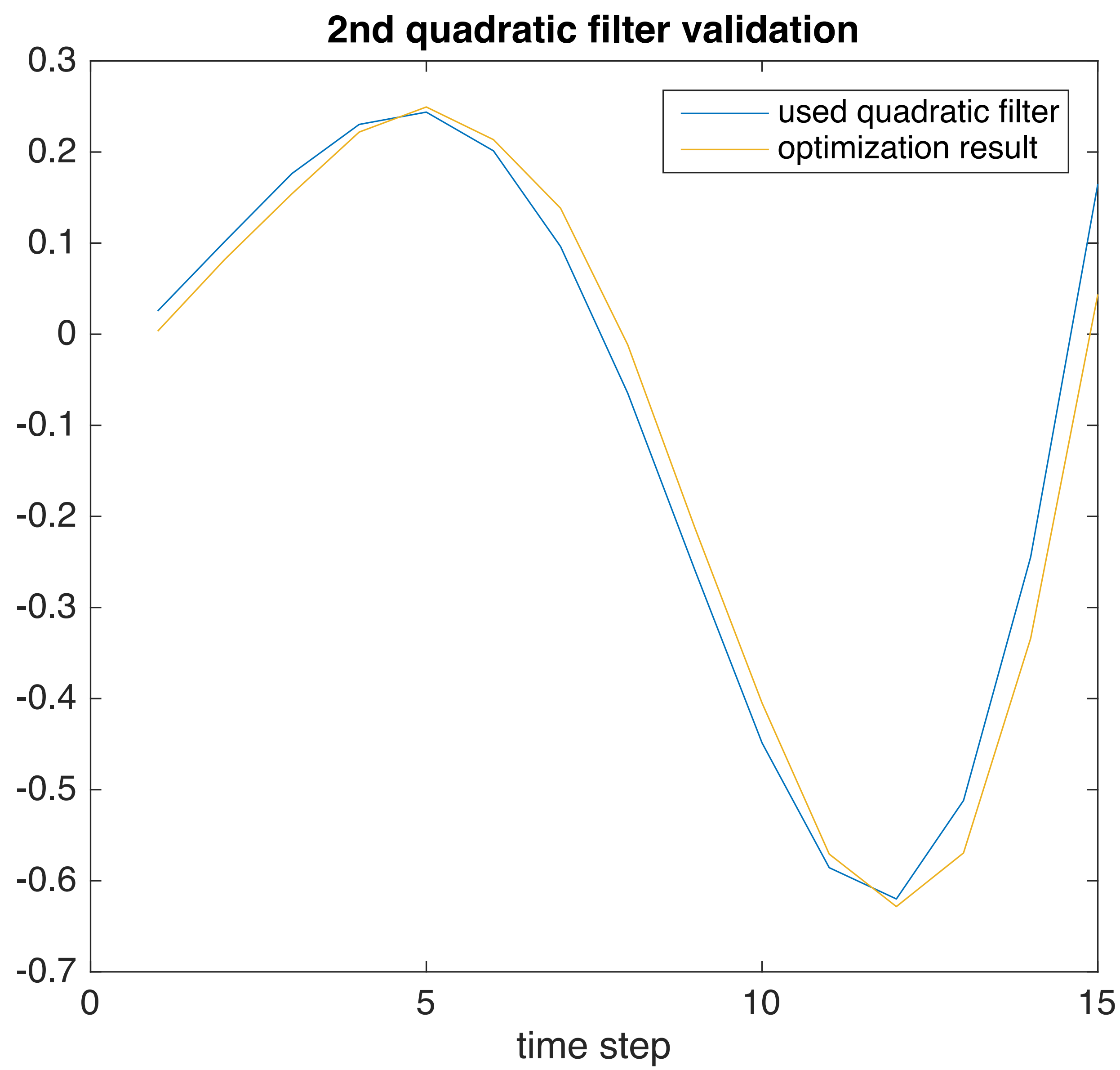
3. Simoncelli EP, Pillow J, Paninski L, Schwartz O (2004) Characterization of neural responses with stochastic stimuli. In: The cognitive neurosciences (Gazzaniga M, ed), pp 327–338. Cambridge, MA: MIT.

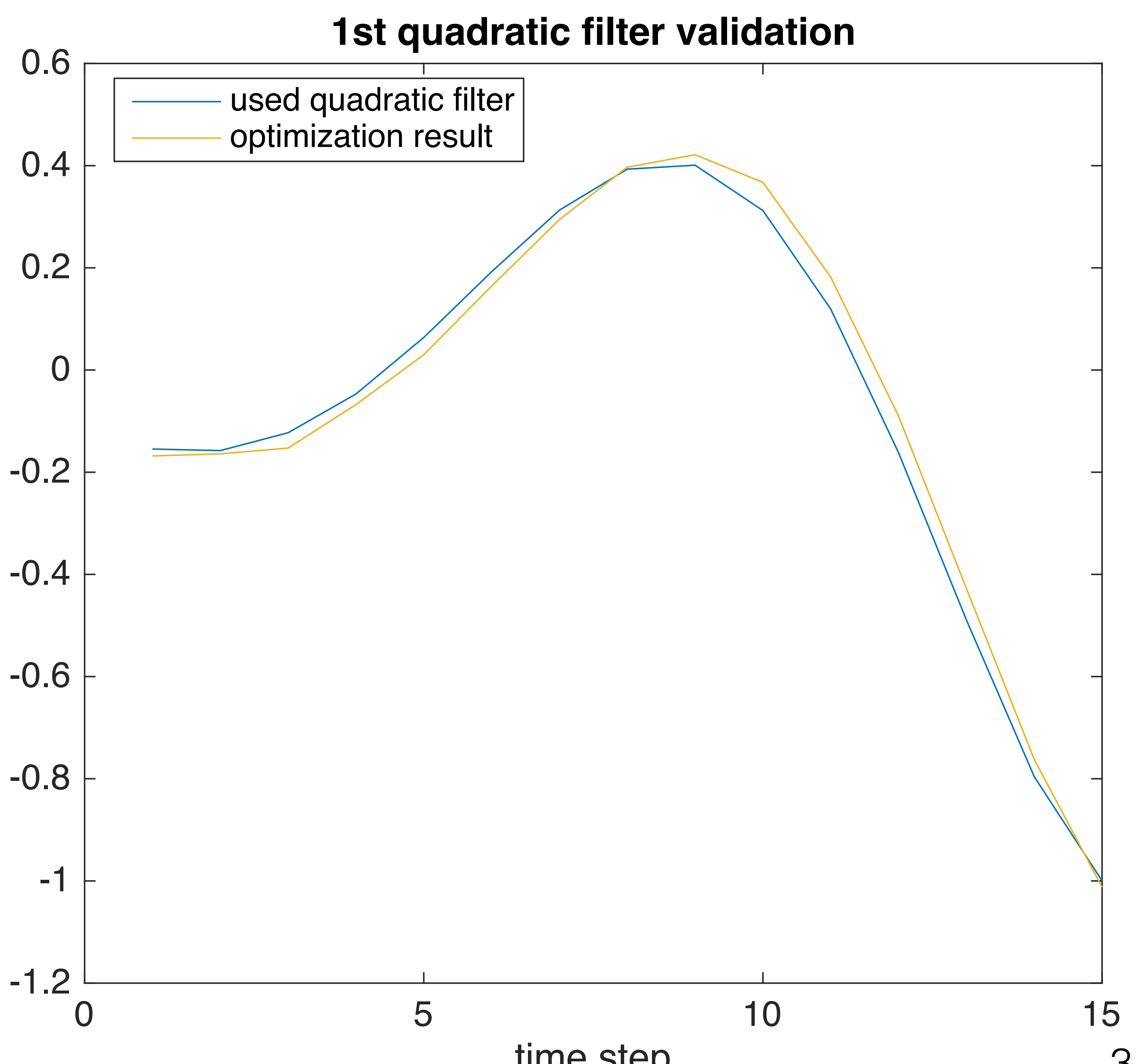
4. Paninski, L., Pillow, J., and Lewi, J. (2006). Statistical models for neural encoding, decoding, and optimal stimulus design.

5. Shlens, J. (2008). Notes on Generalized Linear Models of Neurons.

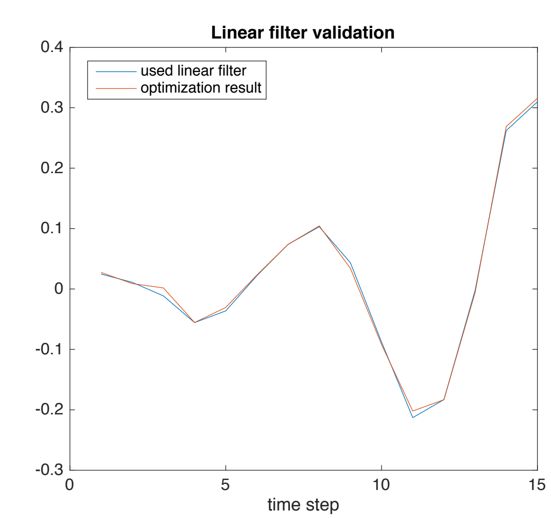
GQM algorithm validation is the same as GLM

synthesize data with 2 (+) quadratic filters
search for 2 (+) quadratic filters



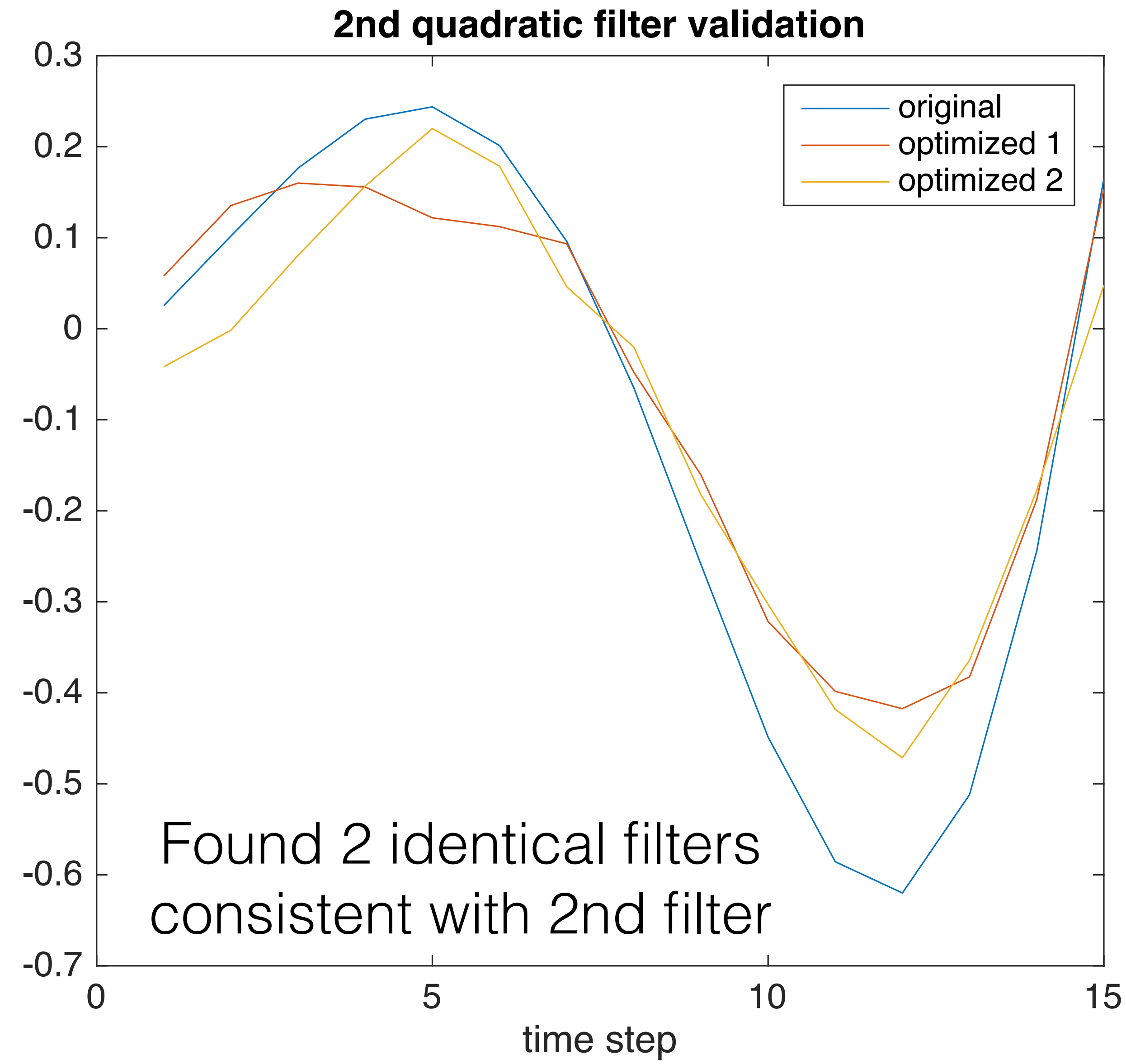


linear filter

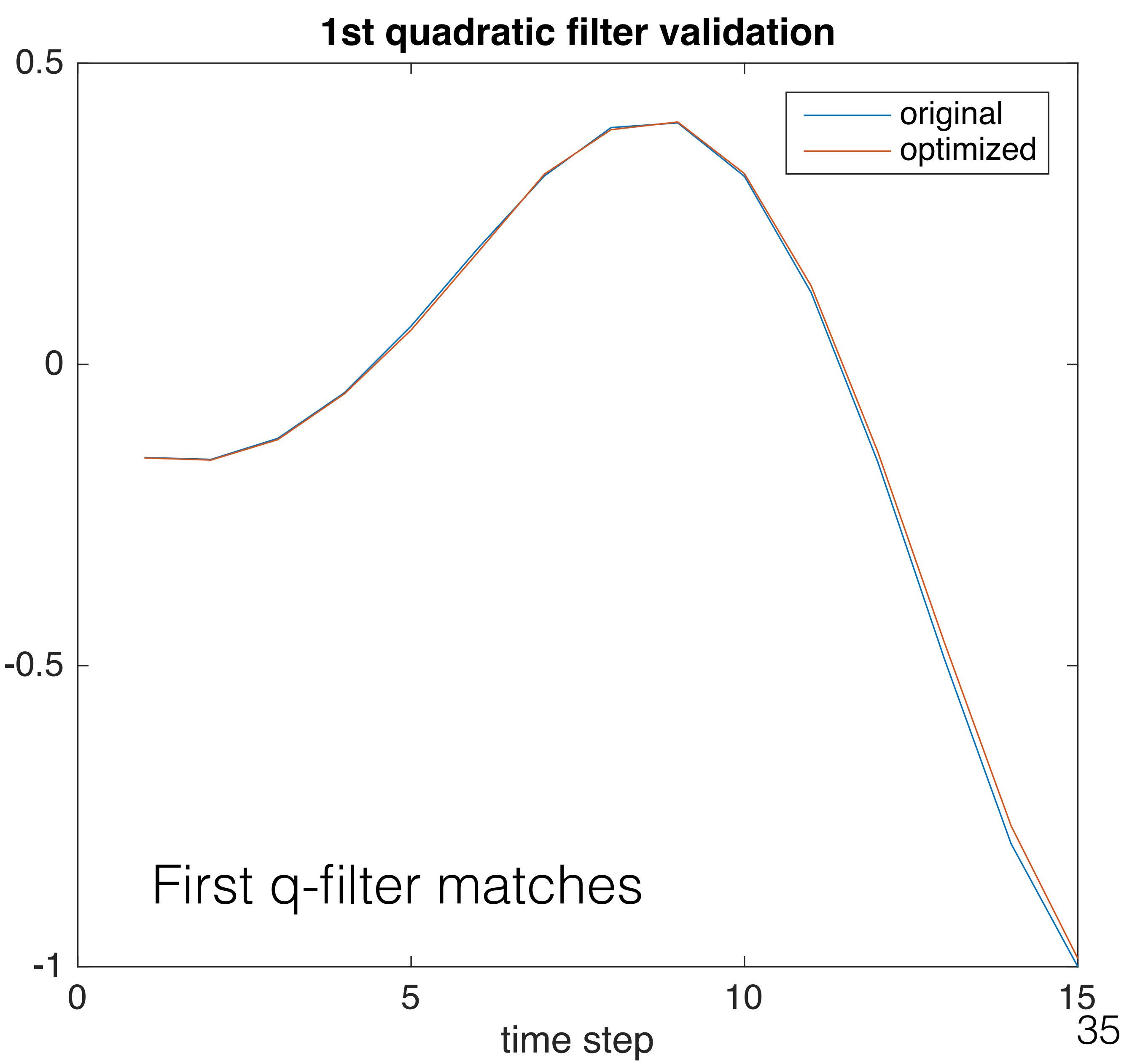


GQM algorithm validation is the same as GLM

synthesize data with 2 (+) quadratic filters
search for **3** (+) quadratic filters



Found 2 identical filters consistent with 2nd filter



First q-filter matches

linear filter matches