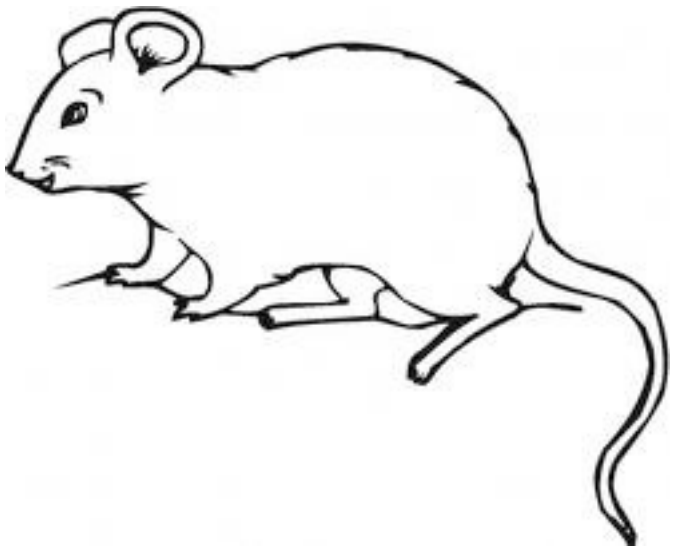
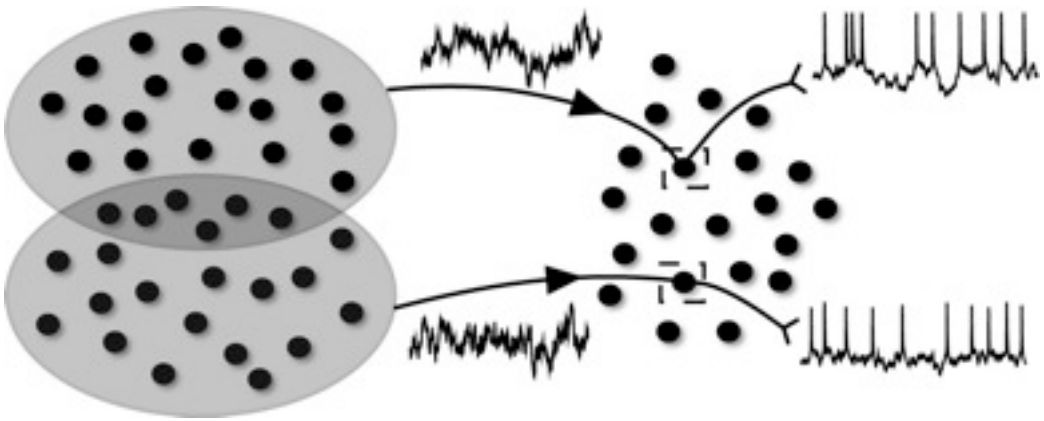
Cellular and circuit mechanisms maintain low spike co-variability and enhance population coding

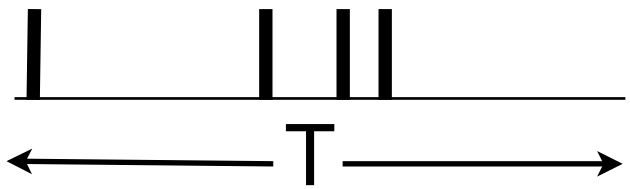




Cheng Ly*^, Jason Middleton#^, Brent Doiron*^

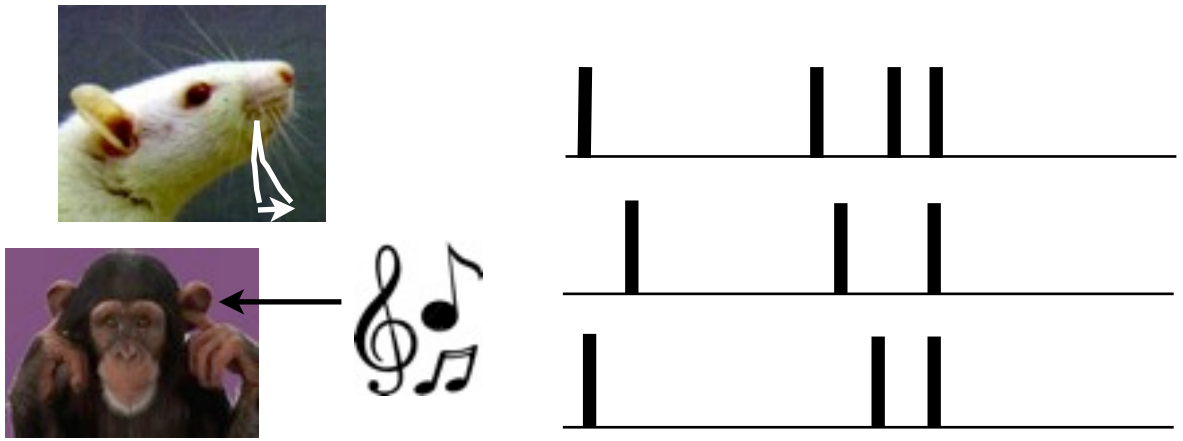
*Department of Mathematics, University of Pittsburgh.
#Department of Otolaryngology, University of Pittsburgh Medical Center.
^Center for the Neural Basis of Cognition, University of Pittsburgh and Carnegie Mellon University.

Quantifying Experimental Data



$$\text{firing rate} = \frac{\#\ \text{spikes}}{T}$$

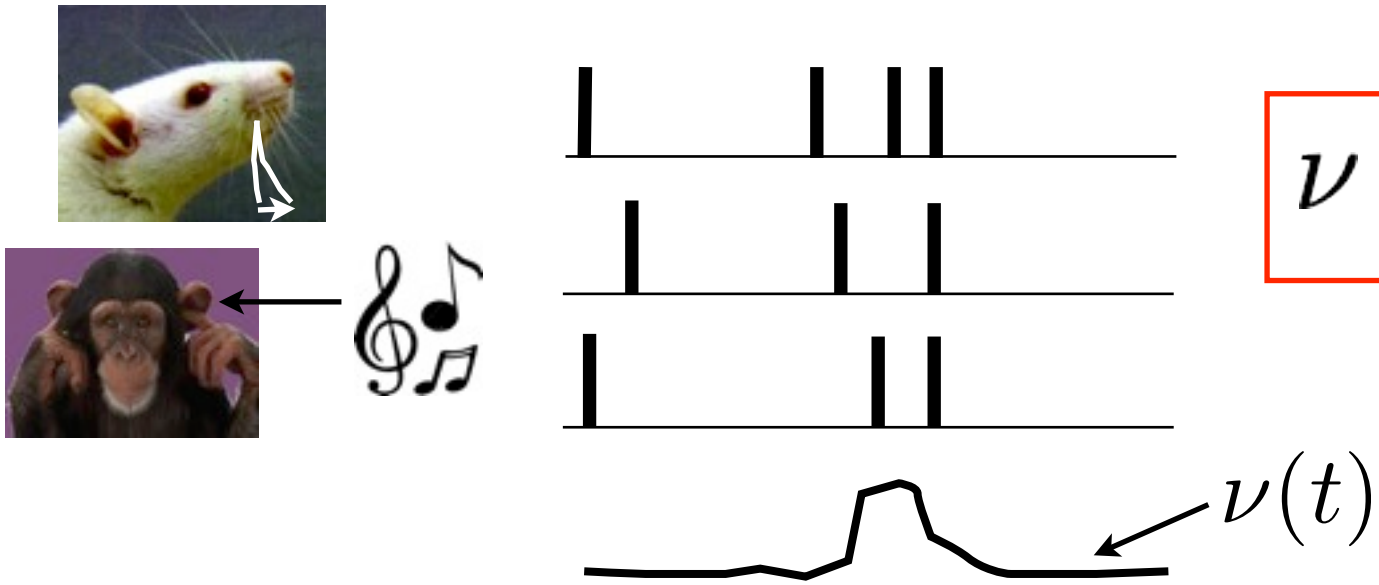
Quantifying Experimental Data



$$\nu = \frac{\text{total \# spikes}}{dt*M}$$

Firing Rate

Quantifying Experimental Data



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Firing Rate

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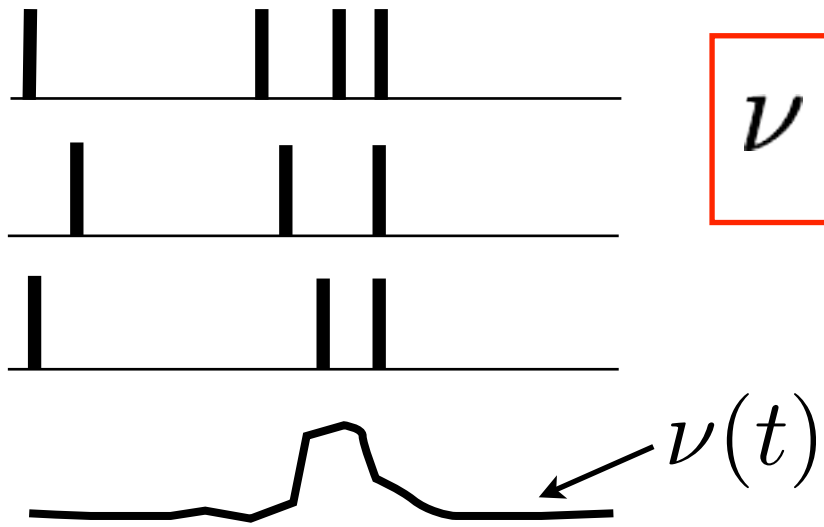

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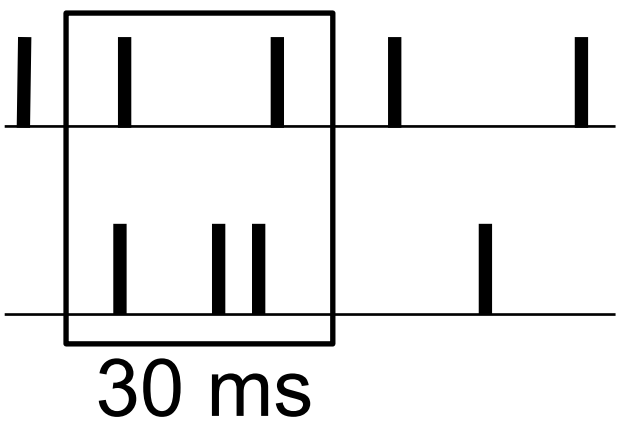

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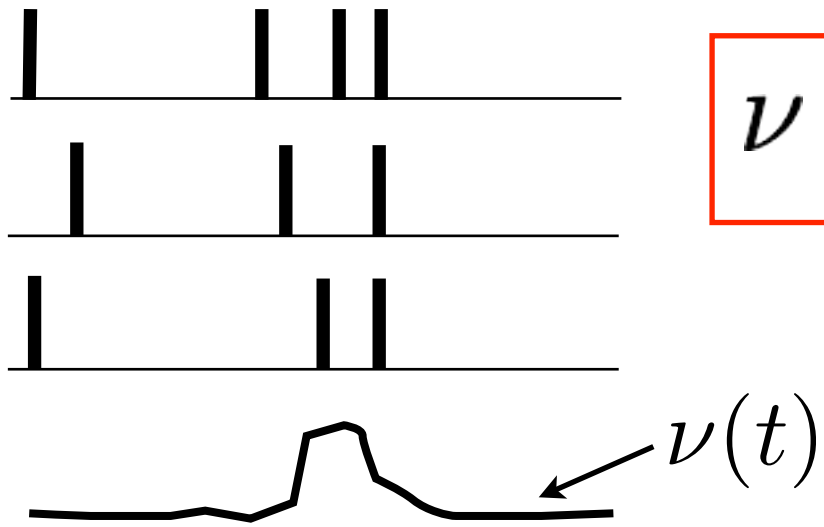

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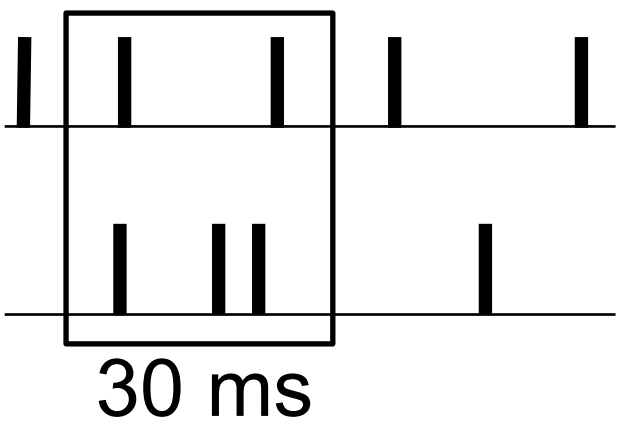
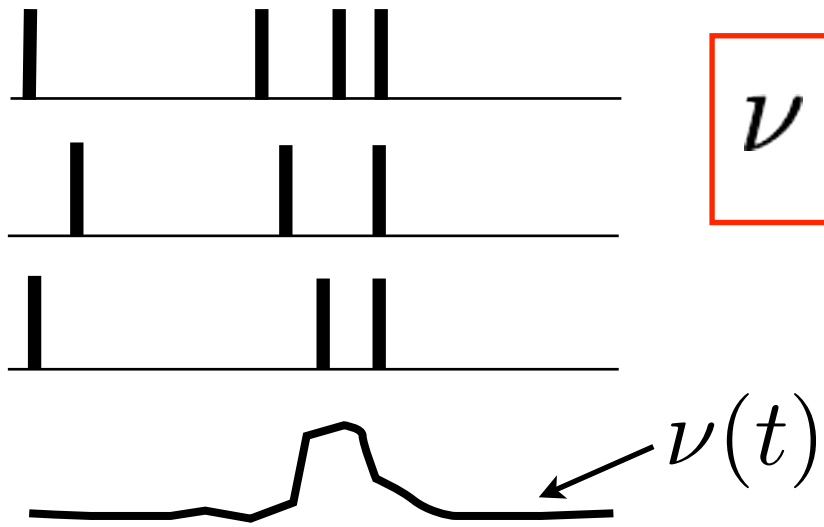


X, Y = random spike counts in a window

Quantifying Experimental Data



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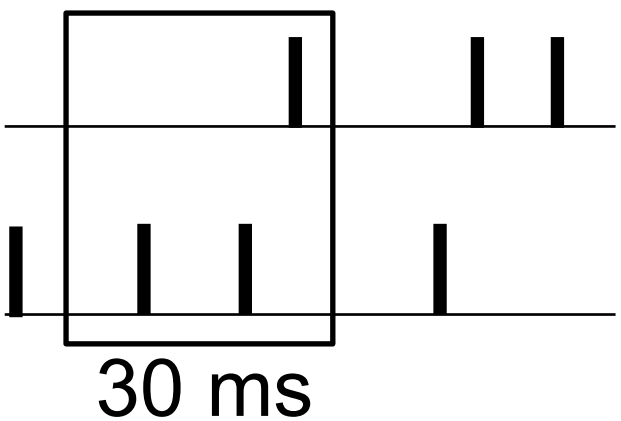

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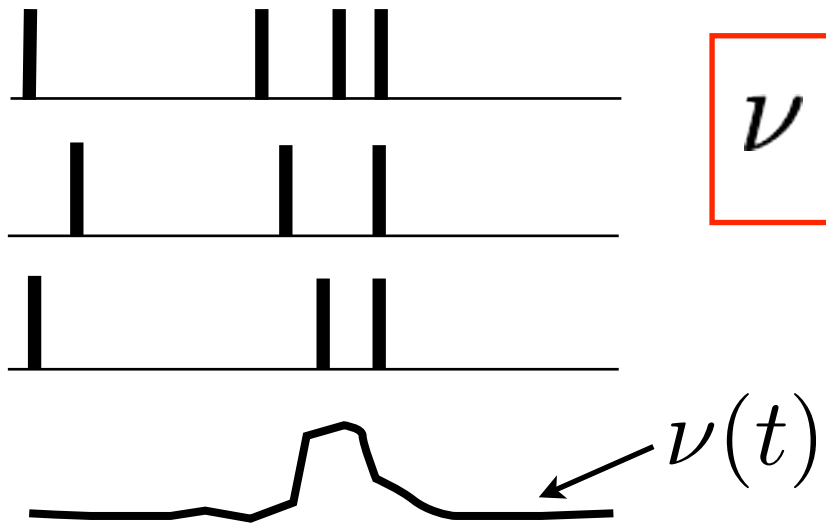

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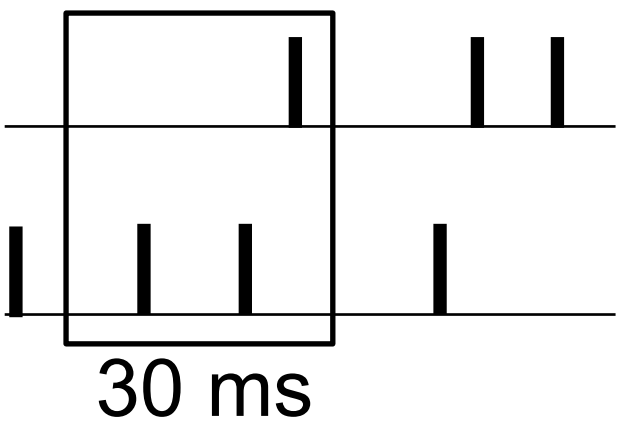
Firing Rate



X, Y = random spike counts in a window

$$\rho = \frac{\mathrm{Cov}(X,Y)}{\sqrt{\mathrm{Var}(X)\mathrm{Var}(Y)}} \in (-1, 1)$$

Correlation

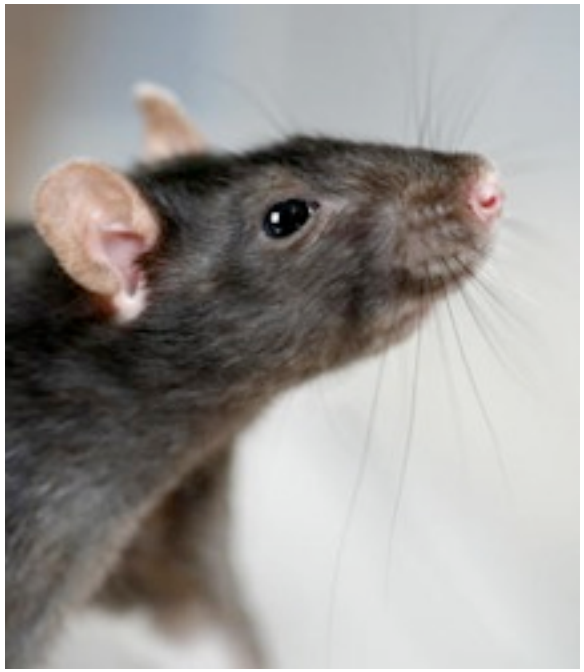
Why is co-variability important?

Table 1 Summary of studies measuring spike count correlations in primates

Reference number	Area	Firing rate (spikes per s)	Duration (ms)	State (task, anesthesia, etc.)	r_{SC}
12*	V1	~25	2,560	Anesthetized	0.2
26*	V1	~8	1,280	Anesthetized	0.16
23	V1		1,894	Anesthetized	0.25
31	V1			Anesthetized	0.26
13*	V1	~50	1,860	Fixation	0.25
28*	V1	~3	500	Fixation	0.01
82	V1		400	Tracing	0.18
83*	V1	30	1,000	Discrimination	0.1
A. Zandvakili and A.K., unpublished data*	V2	5	1,000	Anesthetized	0.11
M. Smith and M. Sommer (University of Pittsburgh), personal communication*	V4	5.2	1,000	Fixation	0.05
7*	V4	21	200	Attention/detection task	0.04
8*	V4	>5, ~20	800	Attention/tracking task	0.05
A.B.G. Graf (New York University), personal communication*	MT	~10	300	Anesthetized	0.09
29*	MT	~20	500	Fixation	0.1
15*	MT	28.5	500	Discrimination	0.13
6/22*	MT	~20	1,000	Discrimination	0.15
84	Perirhinal	~12	200–500	Fixation/matching task	0.02
85	Supp motor area		66 or 200	Serial reaching	0.013
27	Supp motor area	~15	200	Reaching	0.02
86	Premotor areas	~5	400	Grasping/imagery task	0.02
87	M1	~20	600	Reaching	0.1–0.2
25	Motor/parietal; areas 2/5	~5	1,000	Reaching	0.02–0.04
88	Substantia nigra	58	500	Cue matching	0.01–0.04
89	FEF	~50	A few hundred	Visual search	0.05–0.2
90	FEF	~20	~200	Visual search	0.09
24	Prefrontal	~5	3,000	Delayed saccade task	0.08

Cohen & Kohn,
Nature Neurosci. Rev. '11

The somatosensory system



iStockphoto / Peta Curnow

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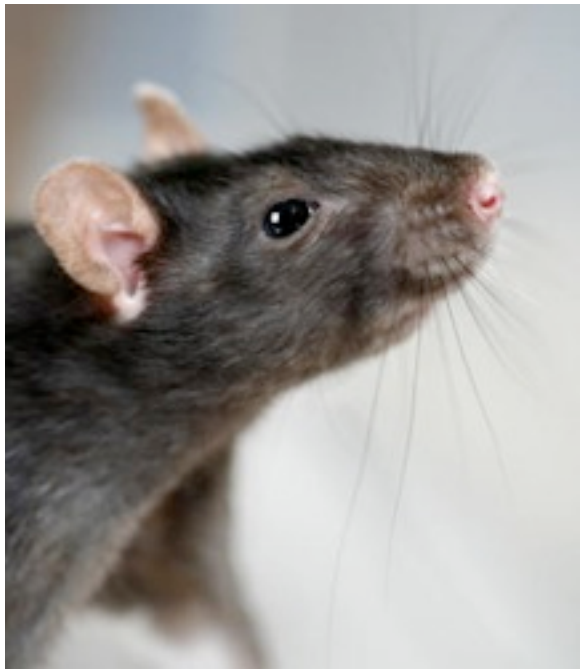

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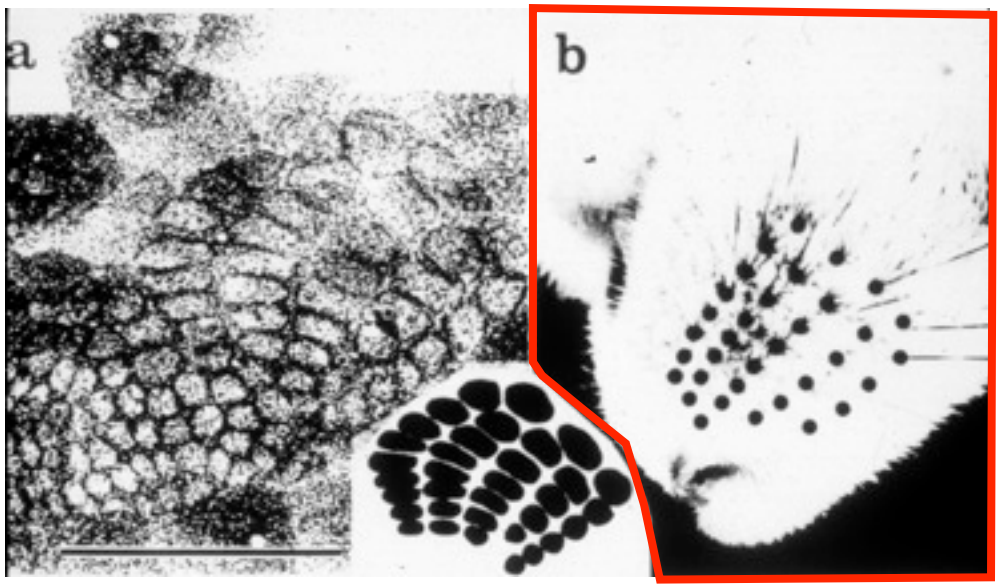
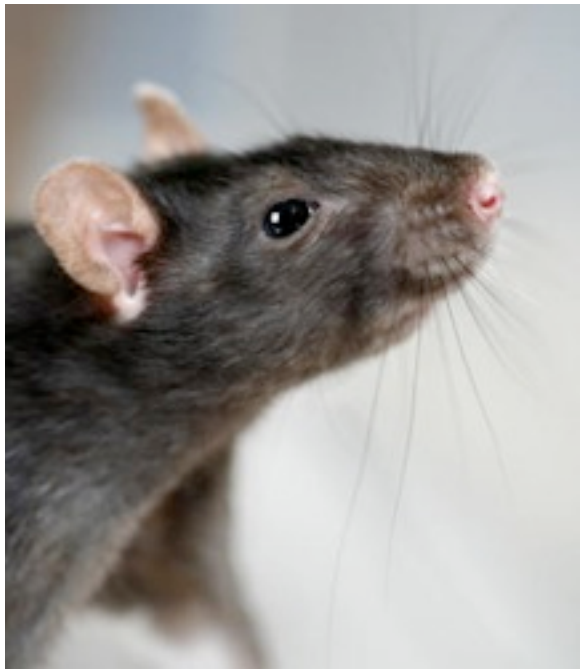


Layer 4

Woolsey & van Der Loos '70

The somatosensory system



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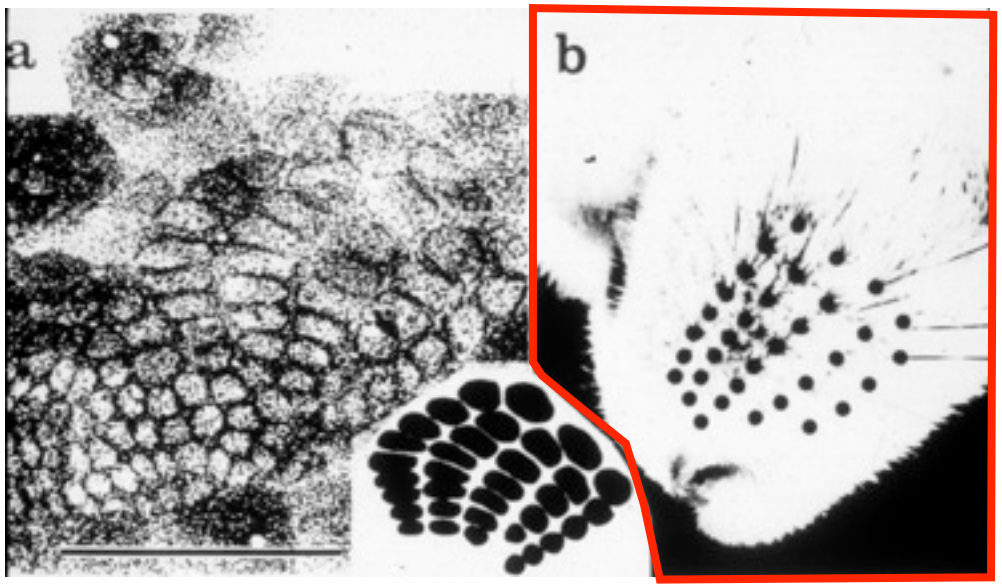

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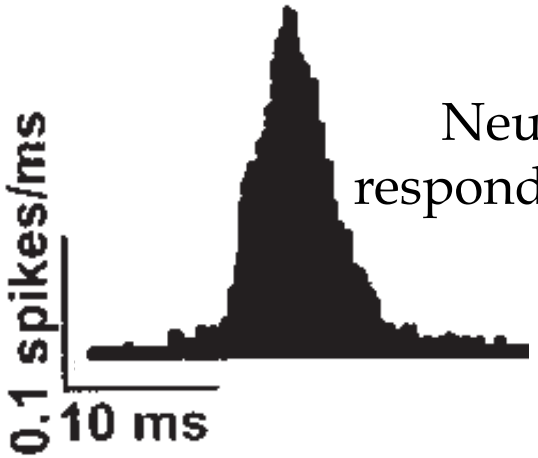
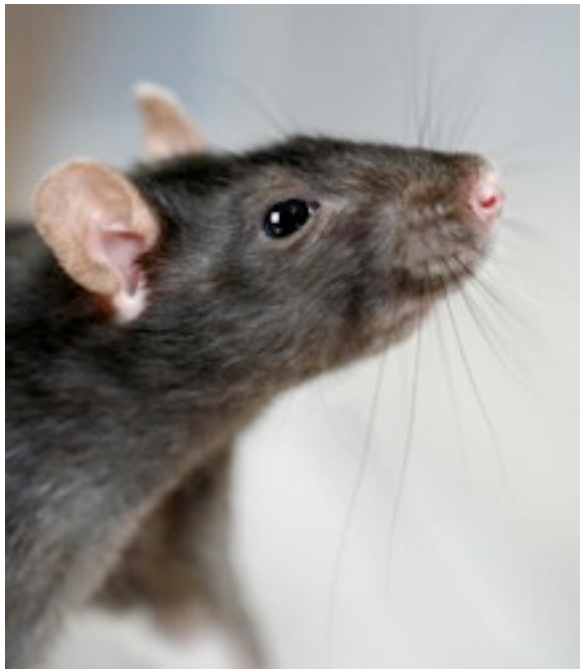
Woolsey & van Der Loos '70



Neurons in a 'barrel' respond to a whisker tweak

Pinto et al. '03

The somatosensory system



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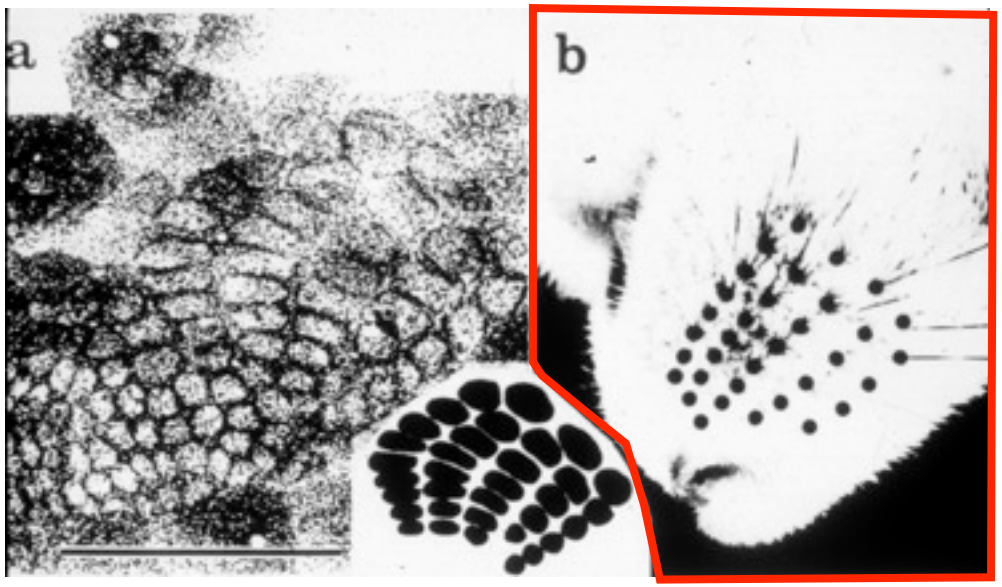
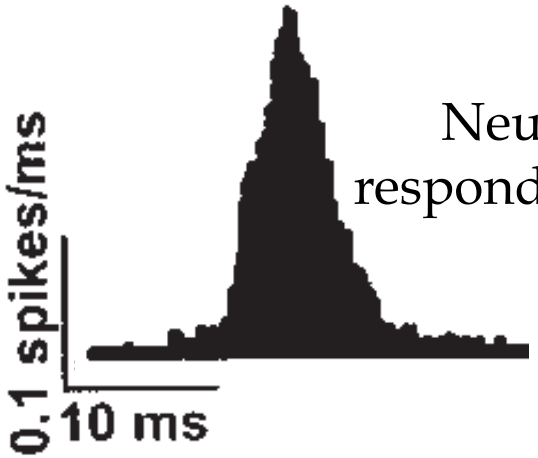


Woolsey & van Der Loos '70

Layer 4

We have paired recordings in layer 2/3
(input from layer 4)



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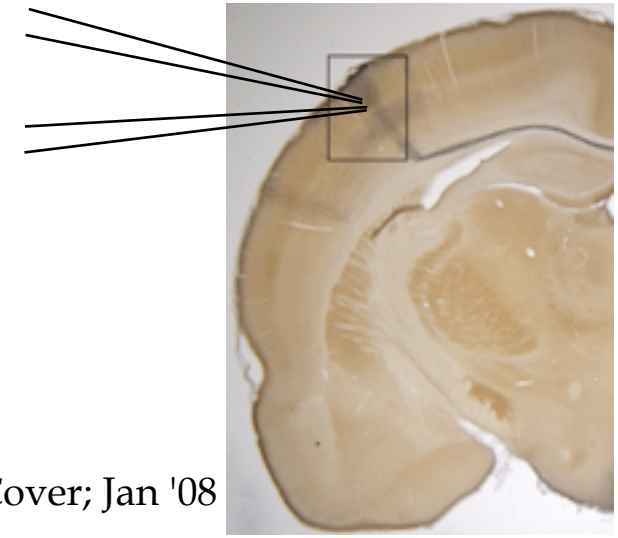
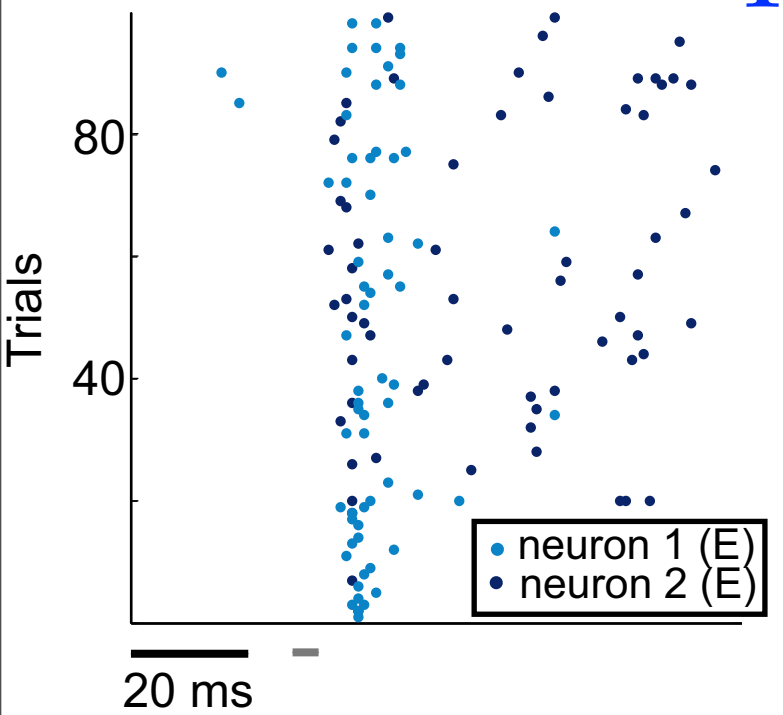


Cerebral Cortex Cover; Jan '08

Our Experimental Results



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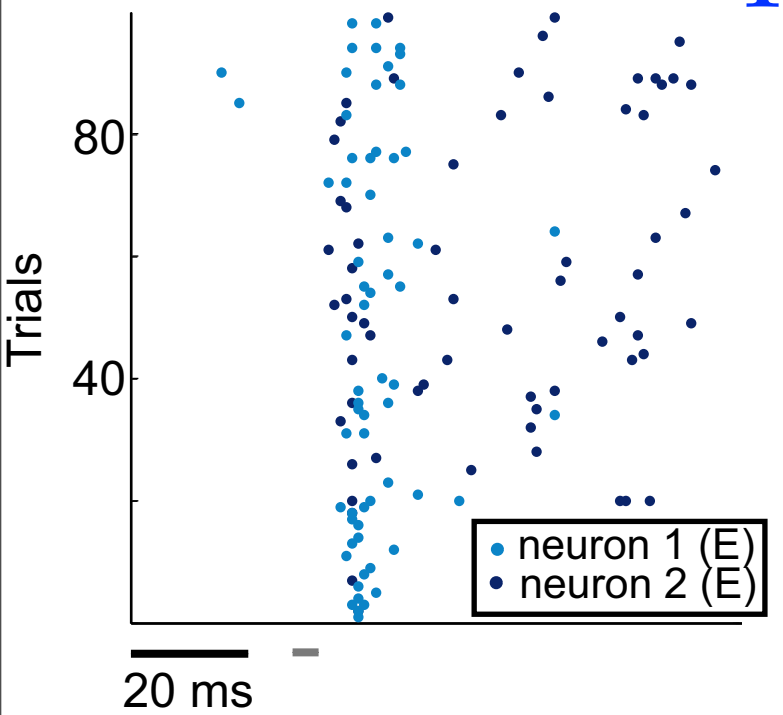

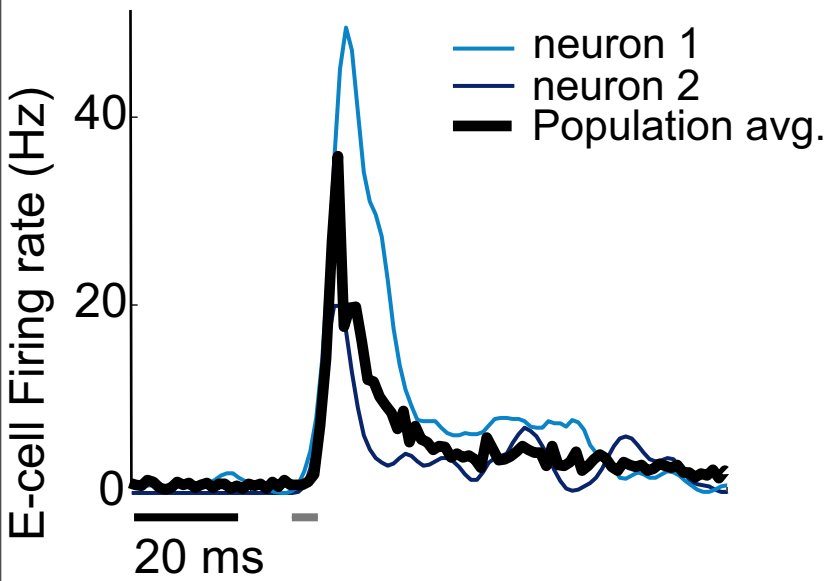

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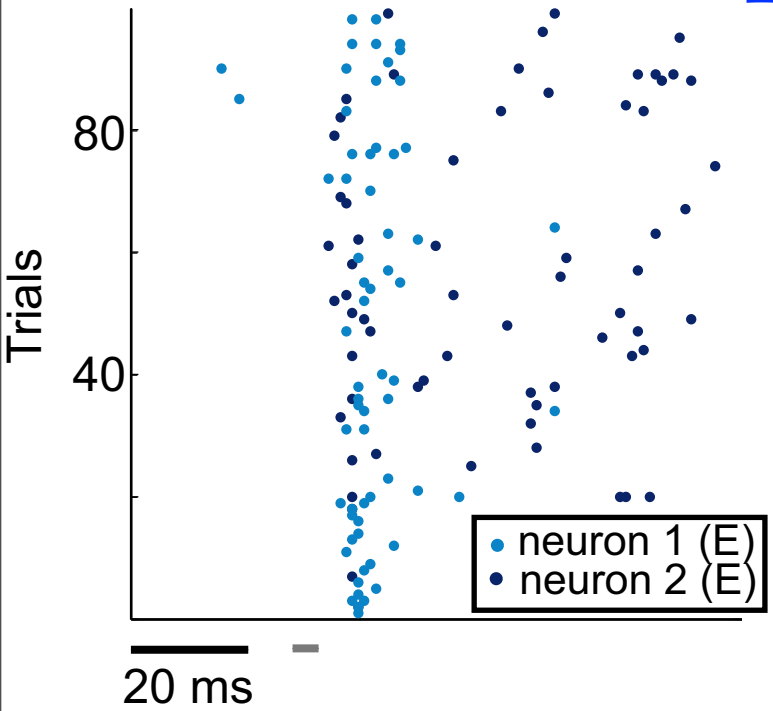

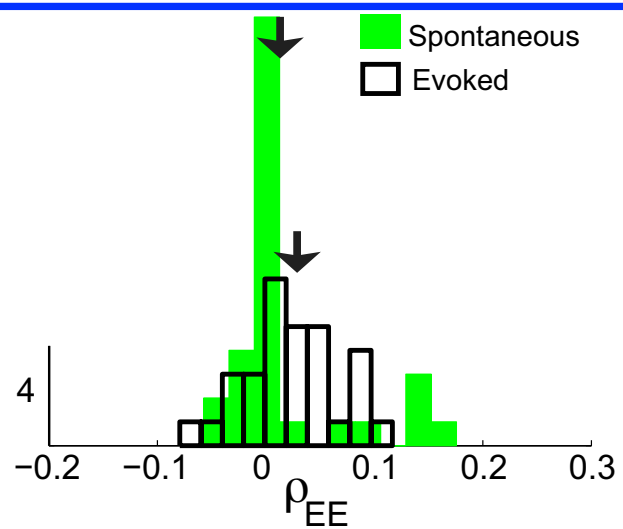

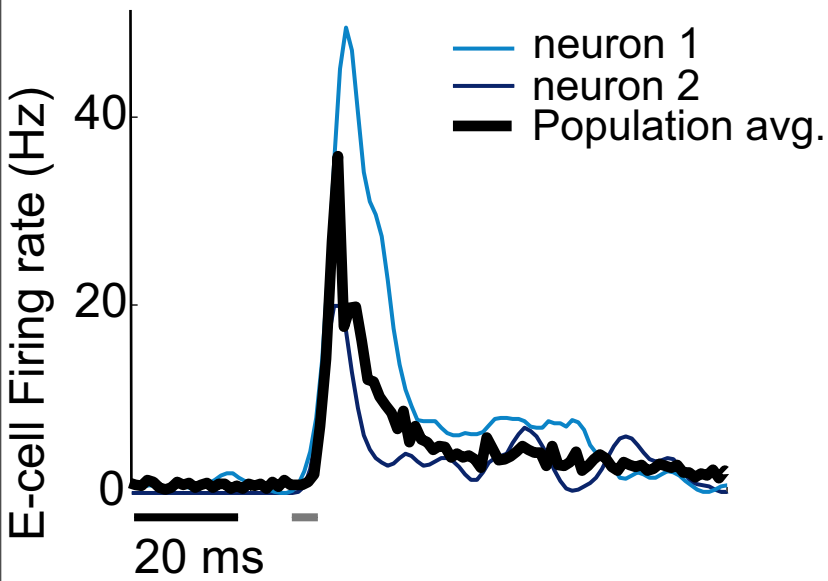

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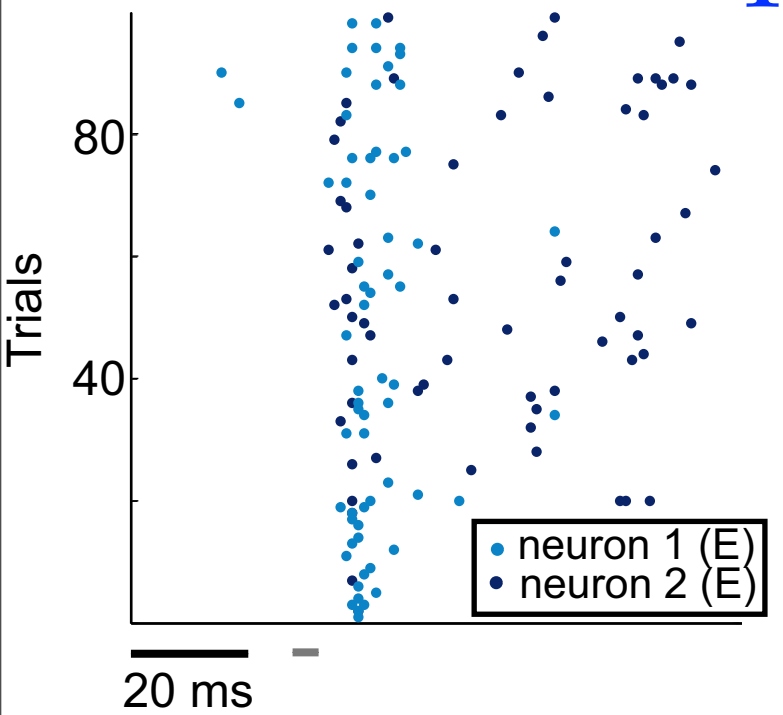
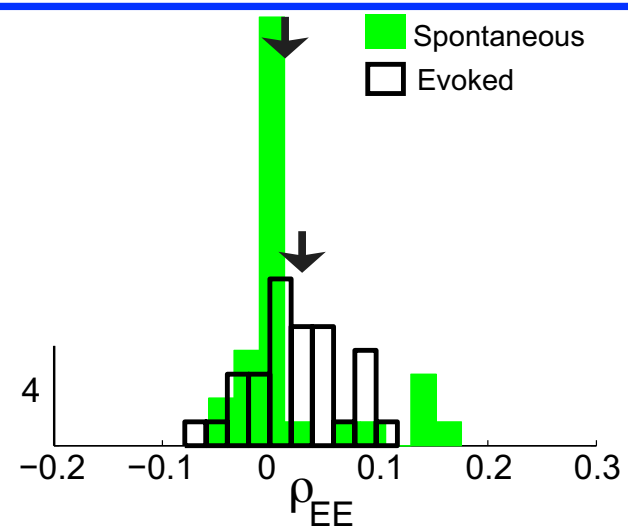
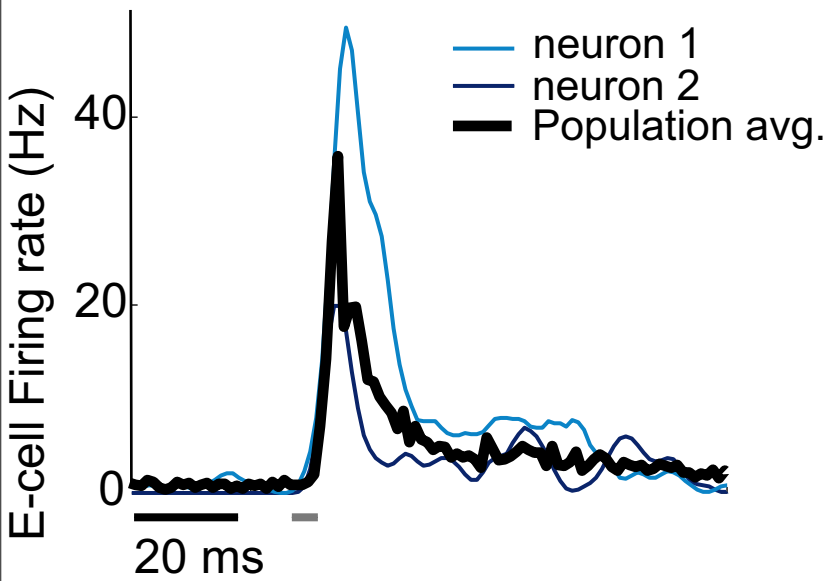




Big change in firing rates,
yet the correlation remains low



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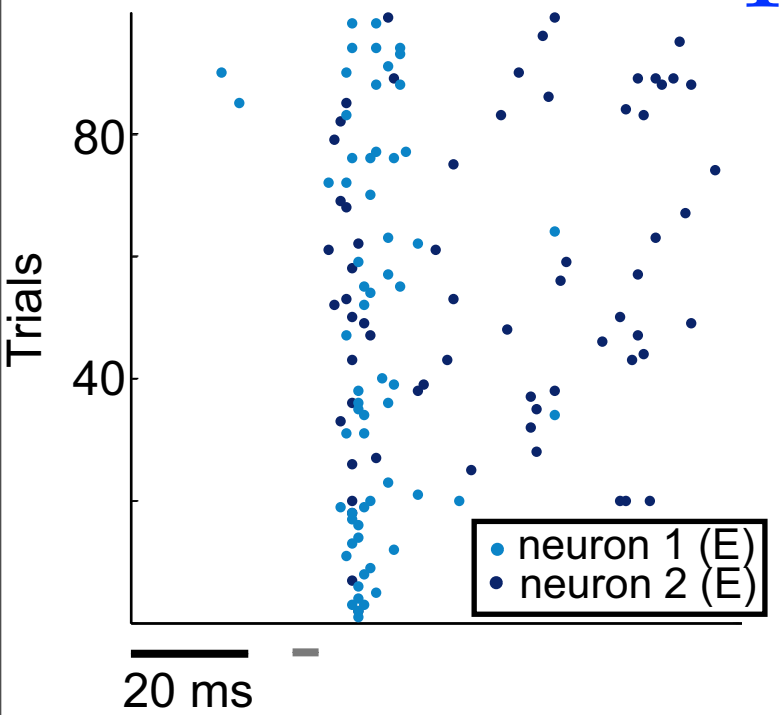

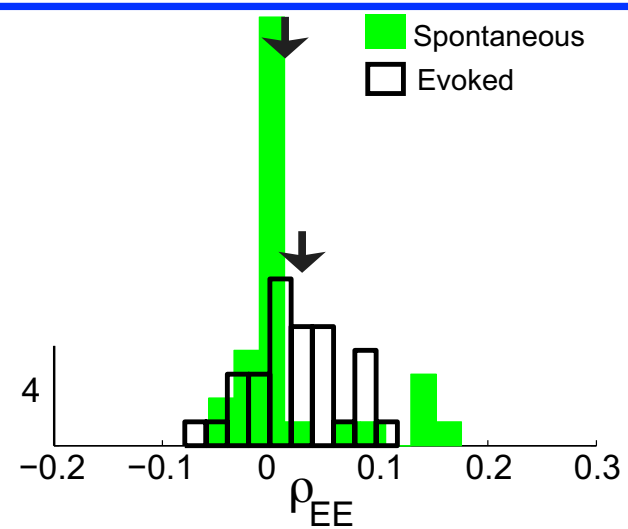

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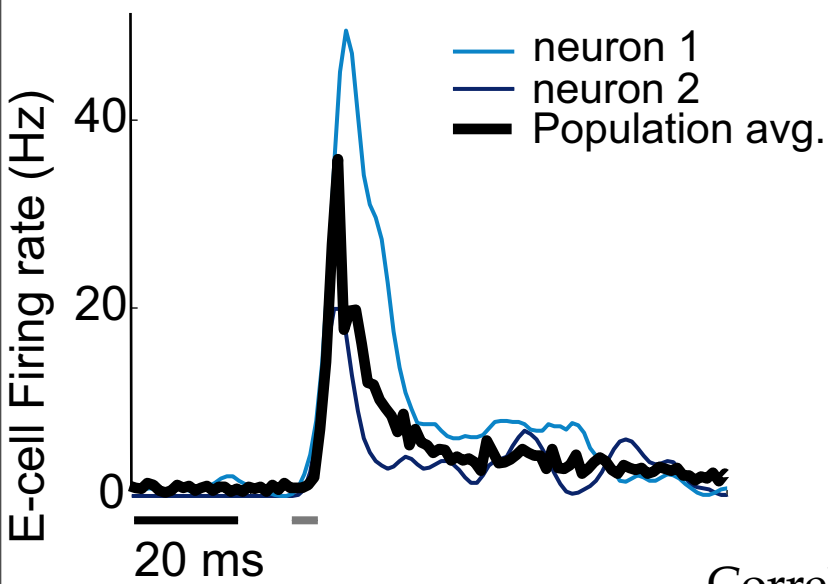
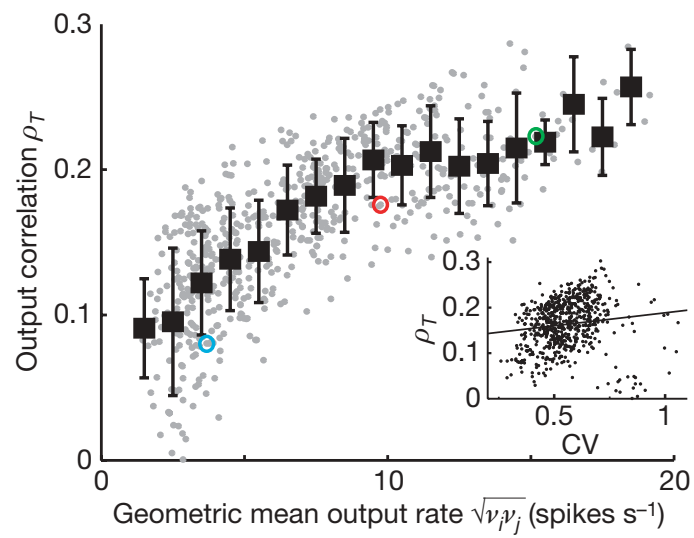


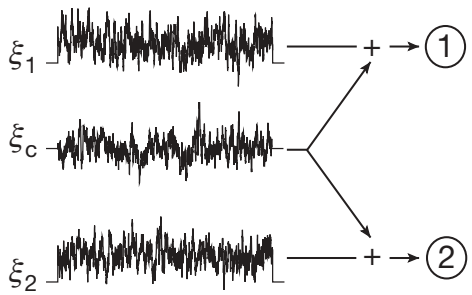


[No coupling]

Correlation between neural spike trains increases with firing rate.

de la Rocha, Doiron, et al., **Nature** 2007.

Previous Results



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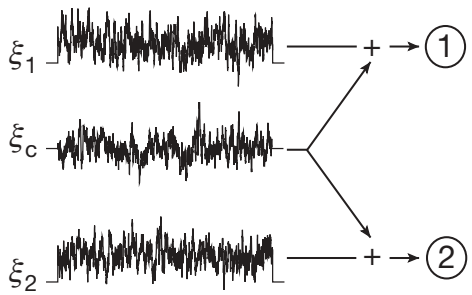

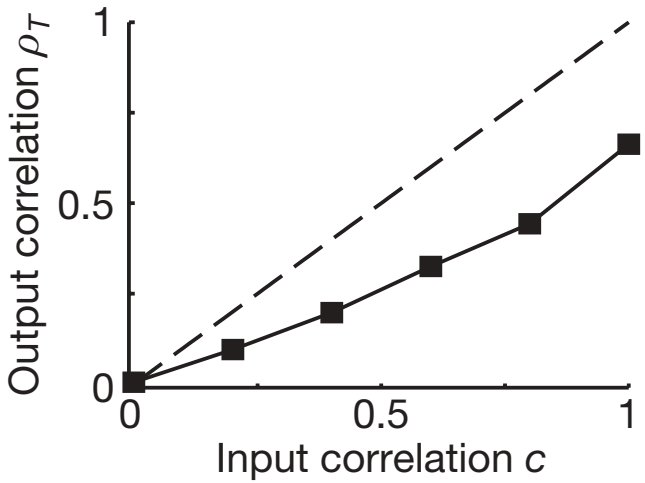

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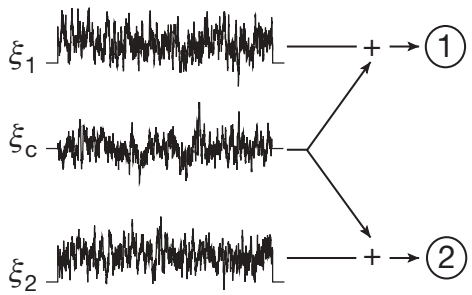

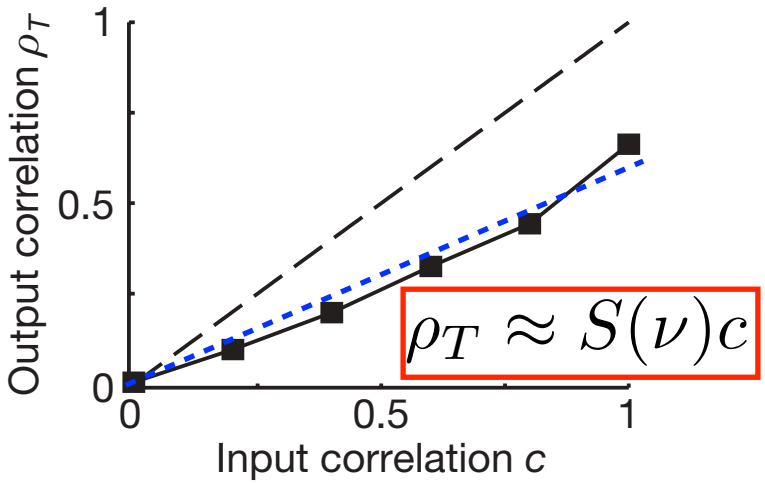

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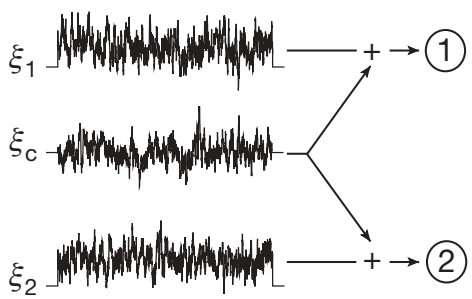

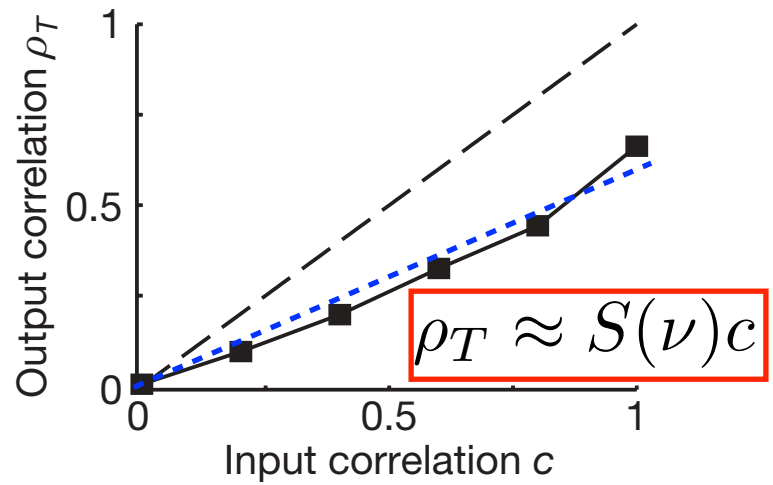

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Maybe c=0?

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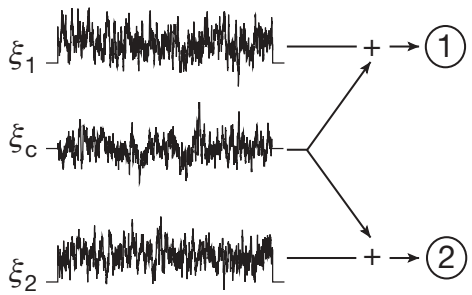

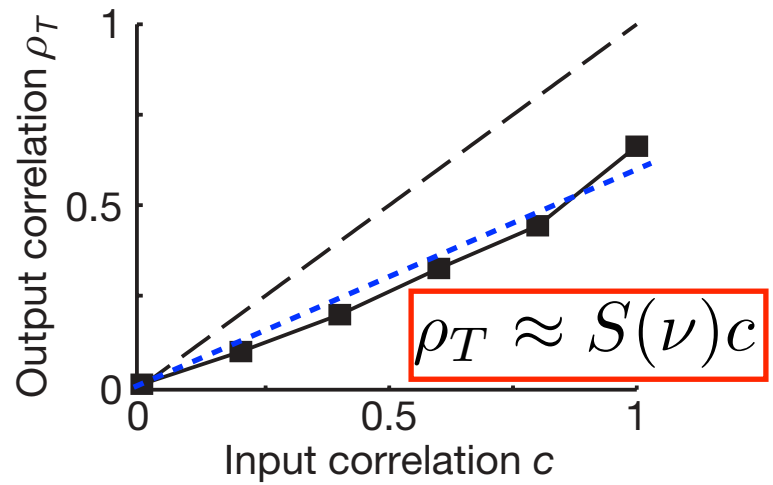

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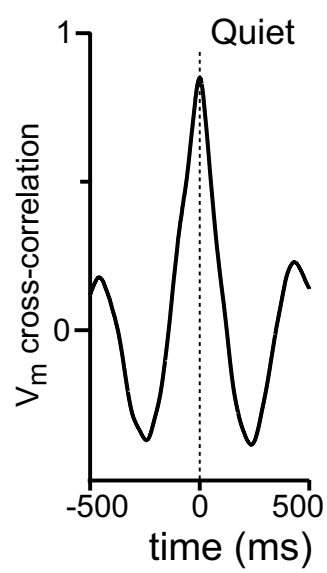
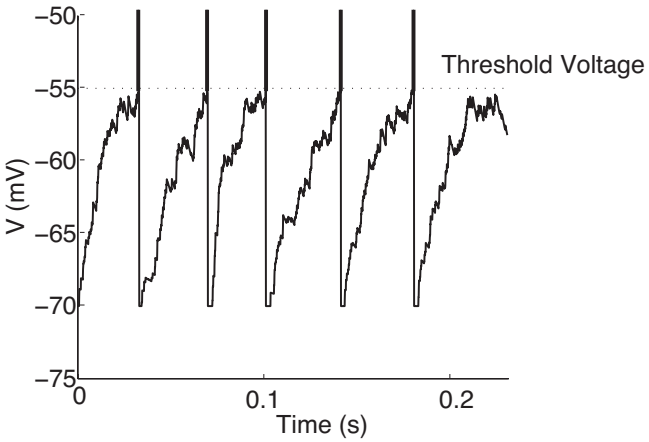


NO! c>0
Gentet et al. **Neuron**, '10

Spiking Network Model with Feedforward Inhibition

Leaky integrate-and-fire (LIF) model:



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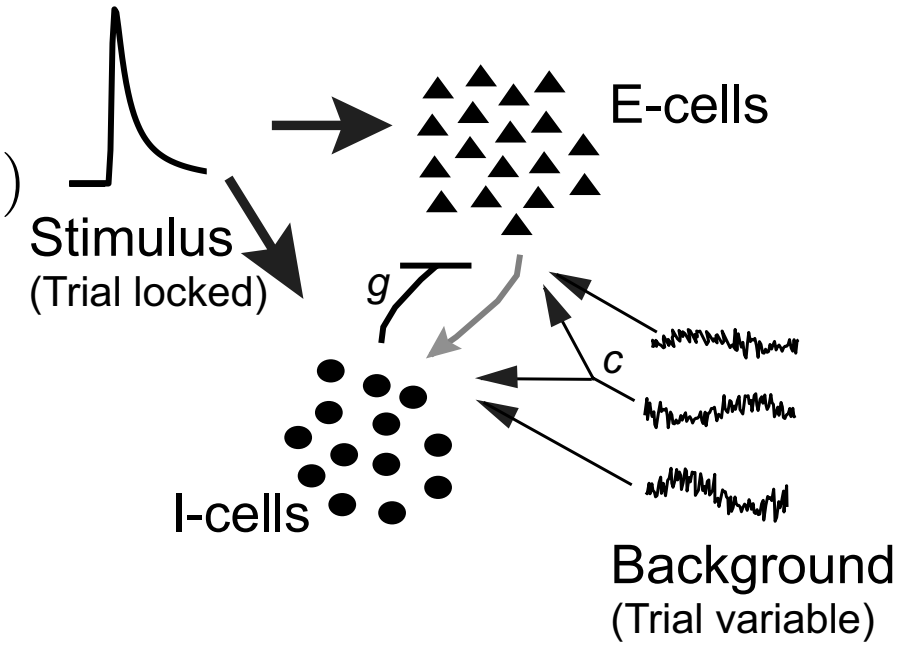
$$\tau_m \frac{dv_j}{dt} = -v_j - gS_I(t)(v_j - E_I) + Stim(t)$$
$$+\sigma\left(\sqrt{1-c}\eta_j(t) + \sqrt{c}\eta(t)\right)$$



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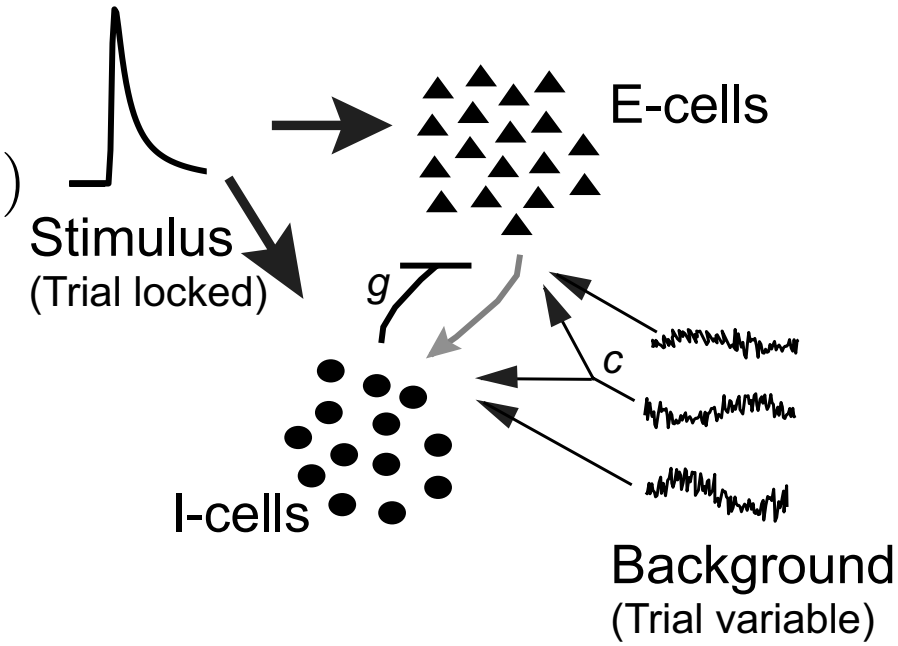
$$v_j(t) \geq v_{th},\ v_j(\tau_{ref} + t) = v_{reset}$$
$$\tau_{ref} = 5\,\mathrm{ms}$$



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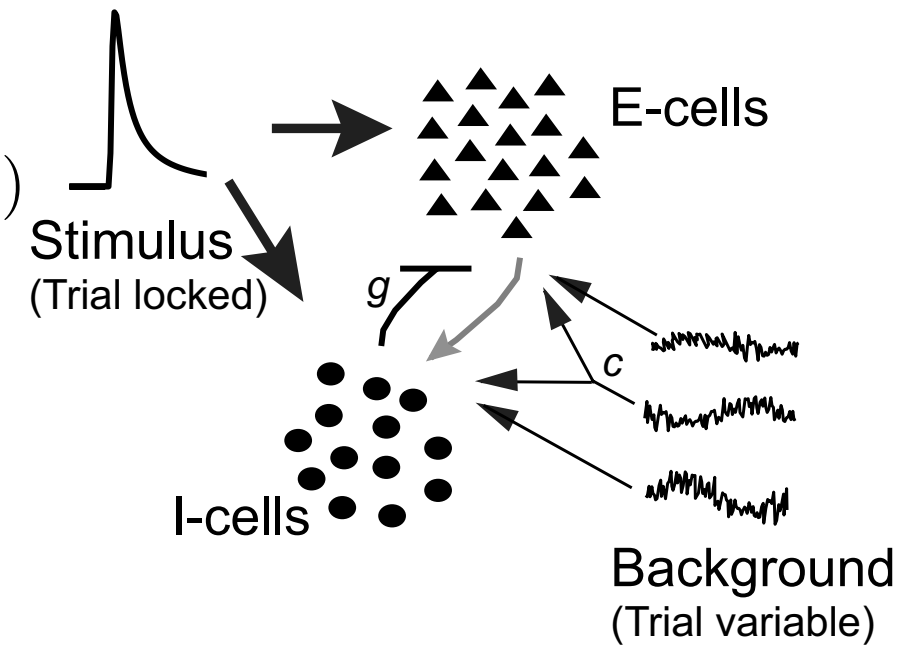

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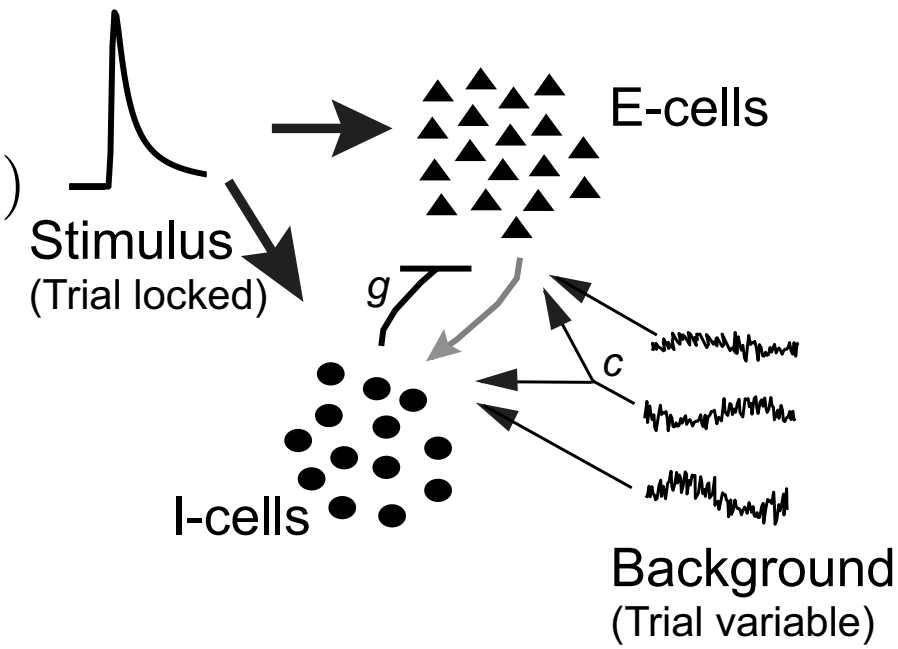
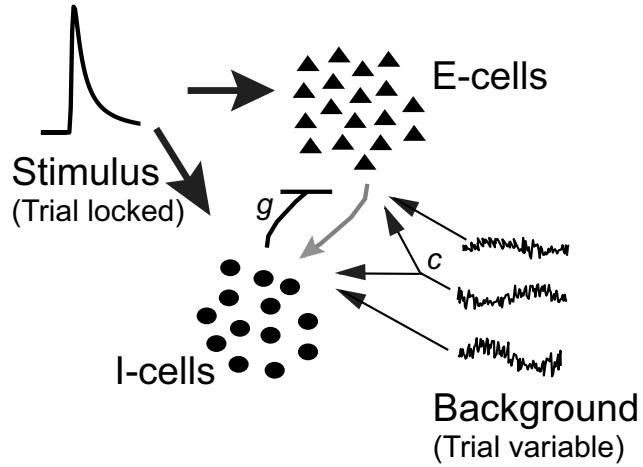


*Heterogeneity in the thresholds

Model Matches Data



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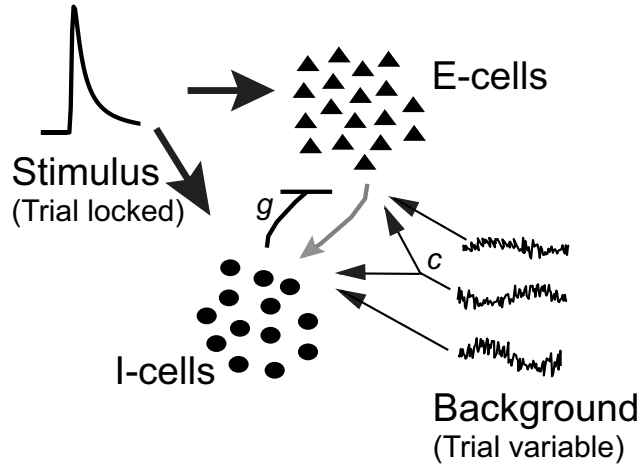

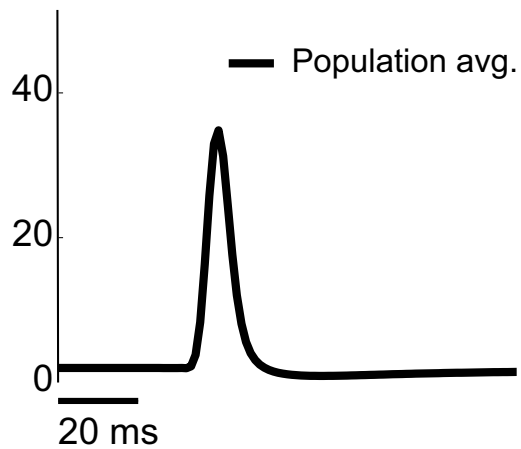

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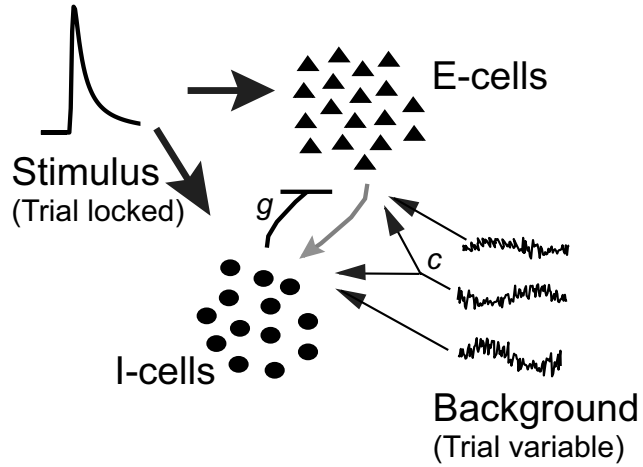

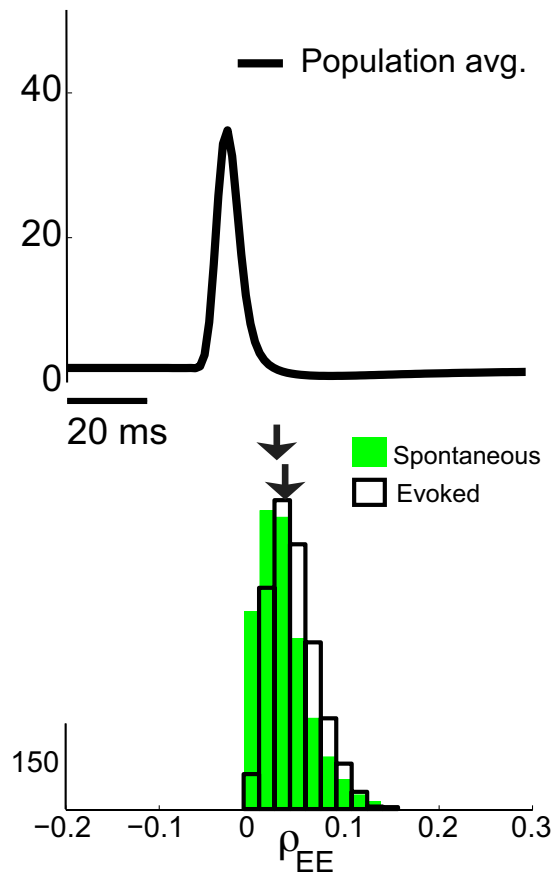

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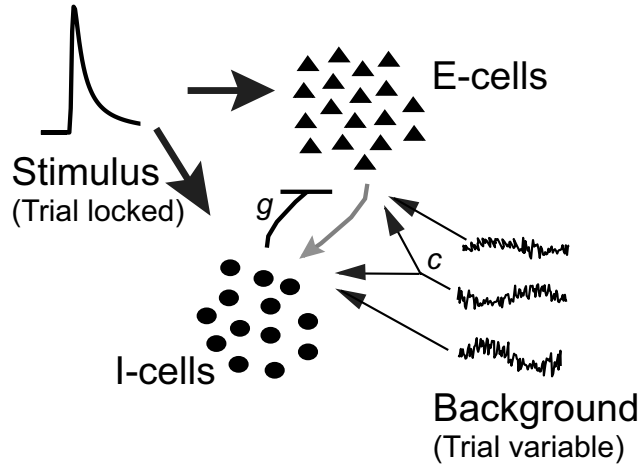
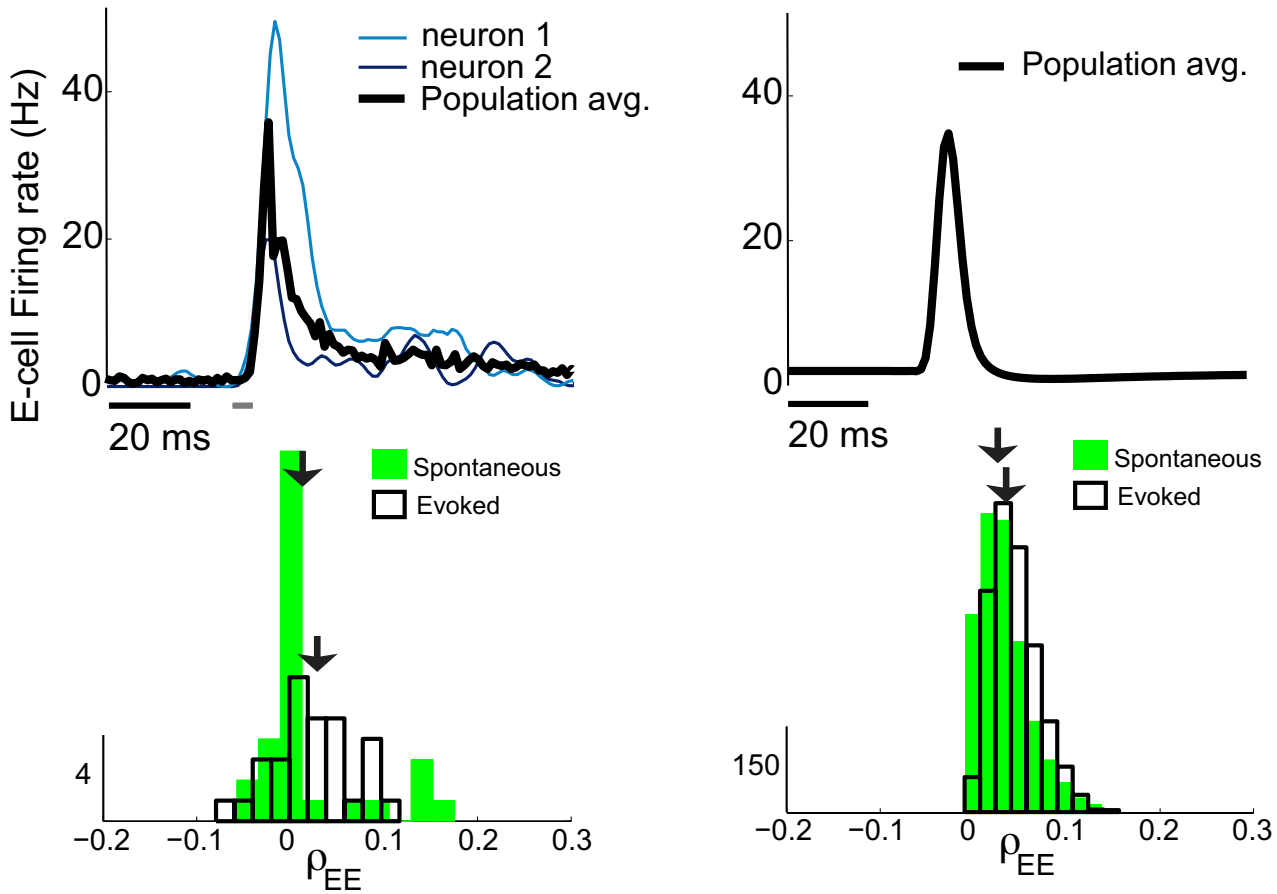


Data



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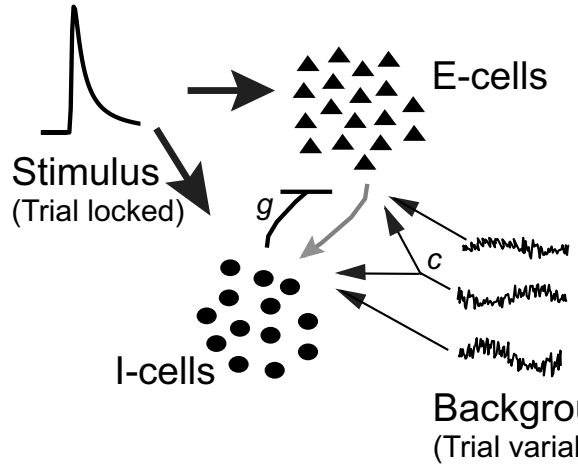
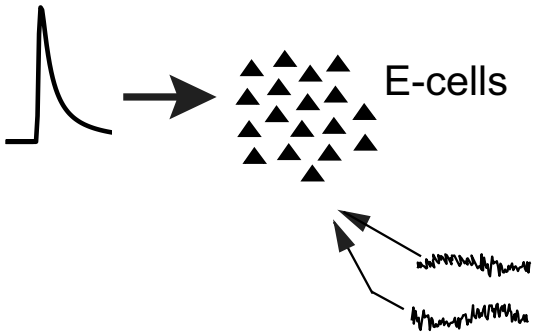
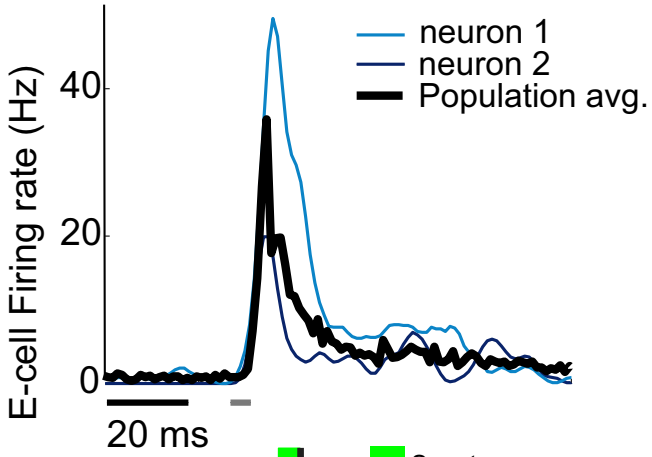
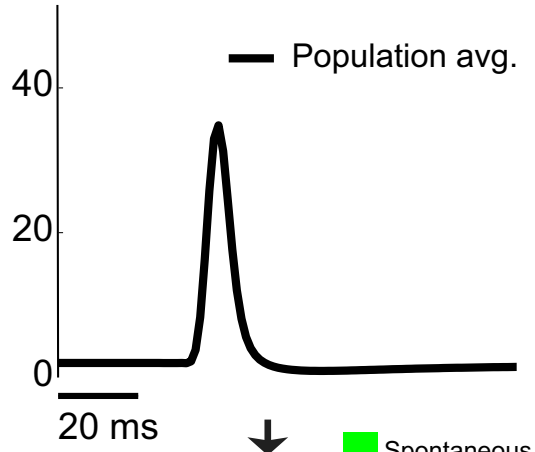


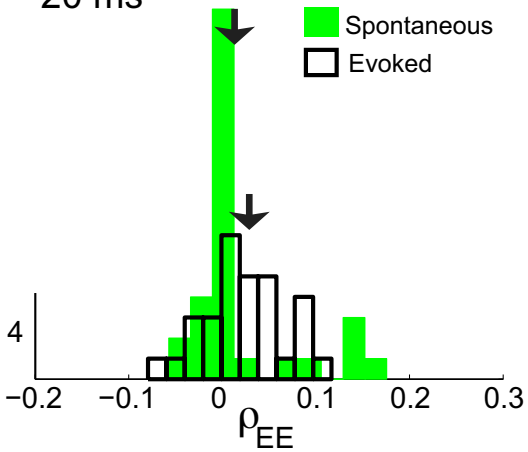


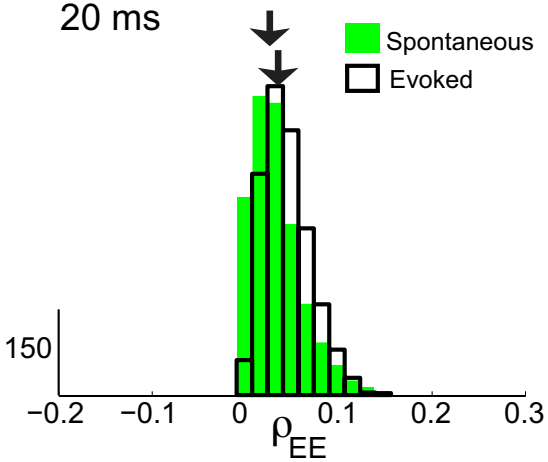
No Inhibition

Data









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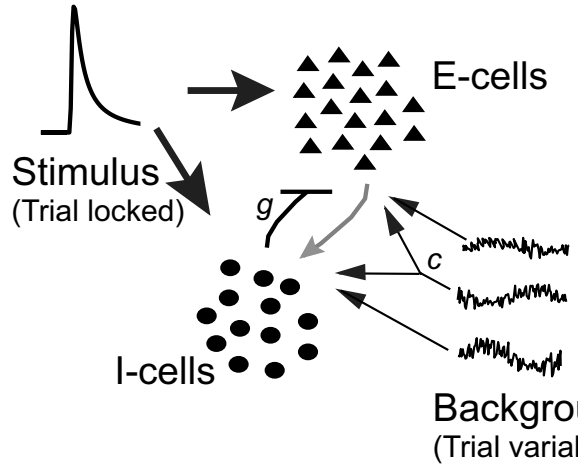

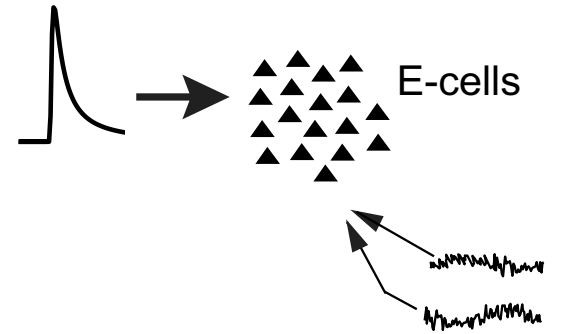

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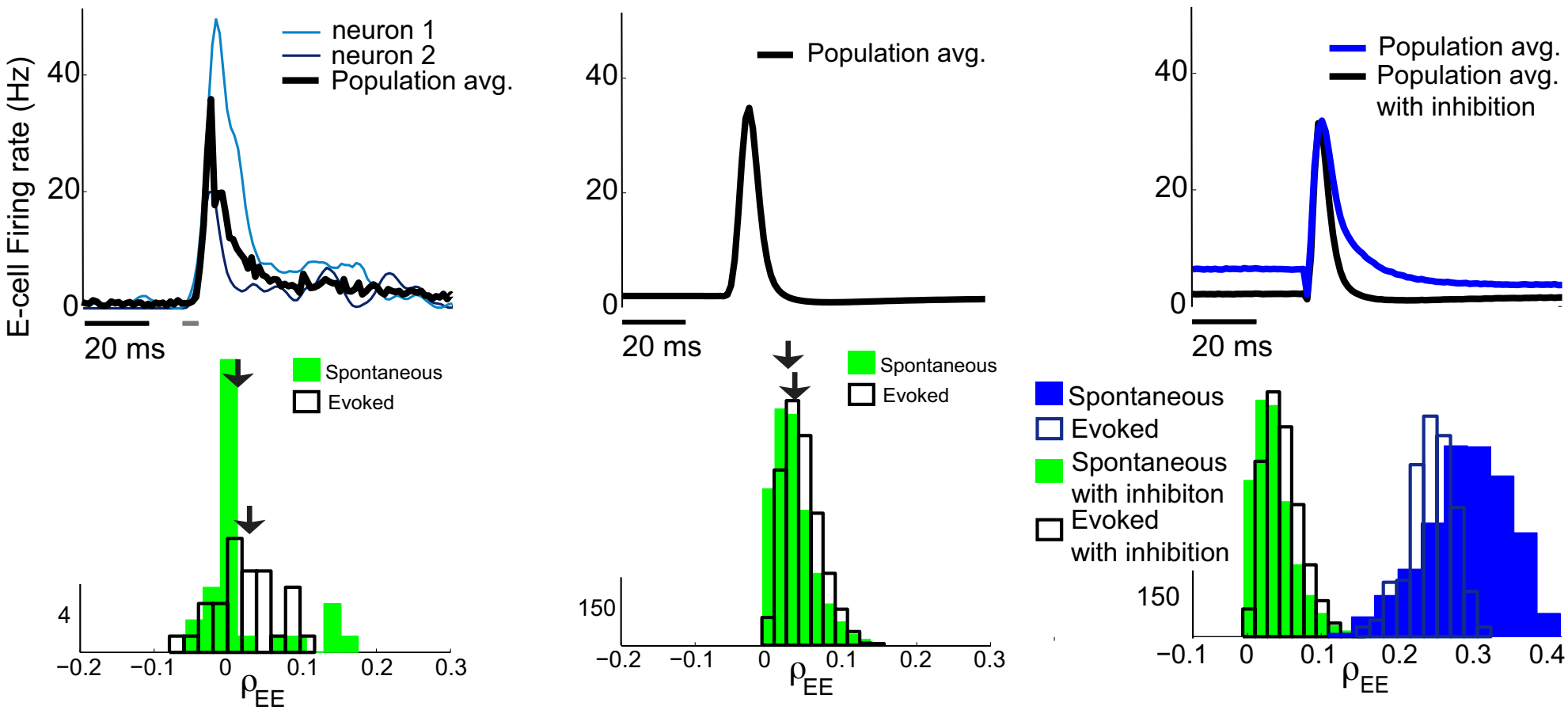
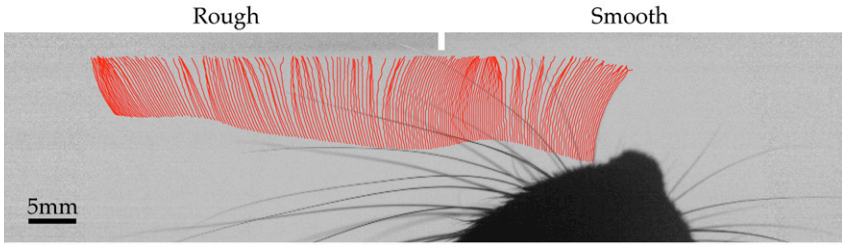
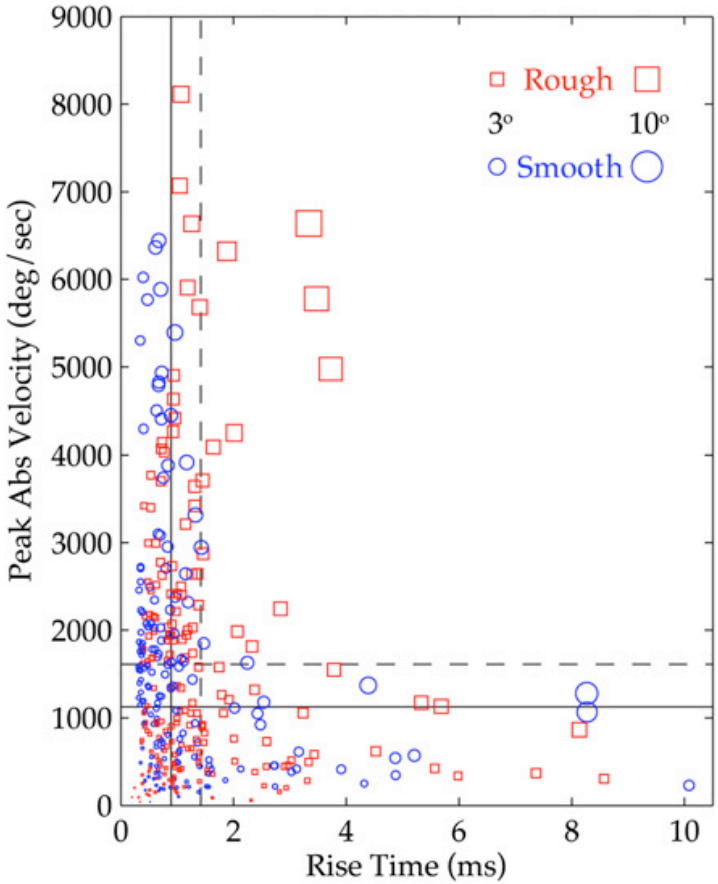


Results hold for various velocities





Ritt et al. **Neuron**, '08

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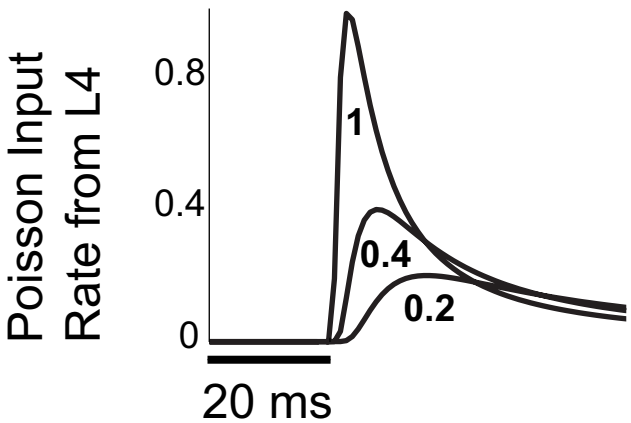

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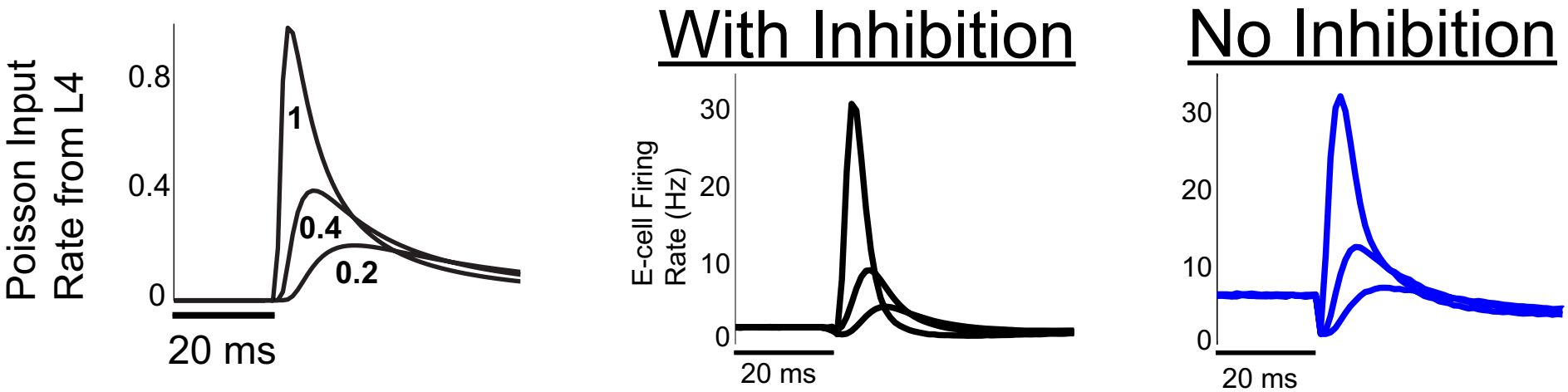

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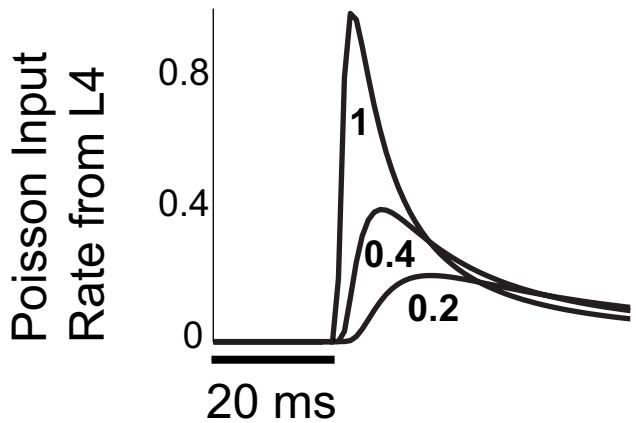

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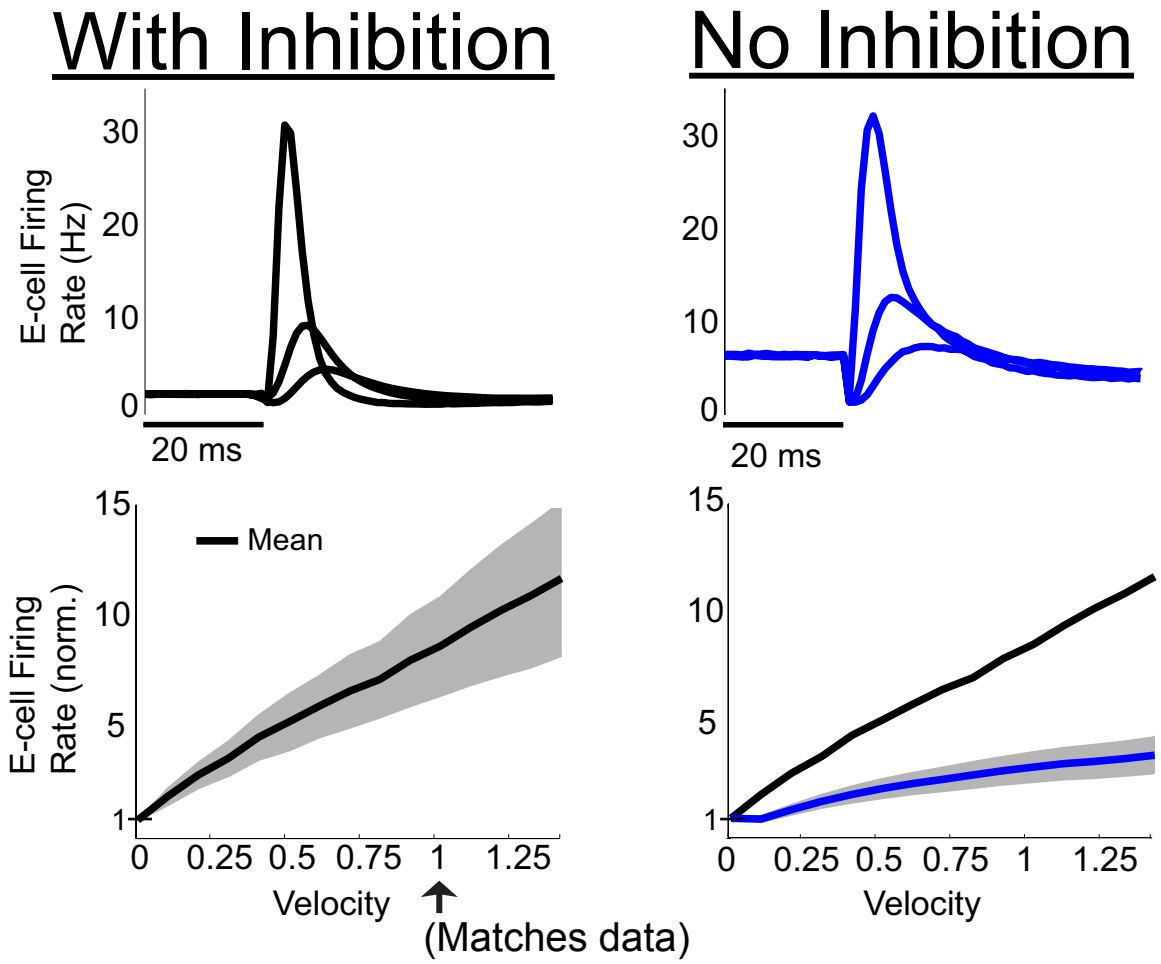

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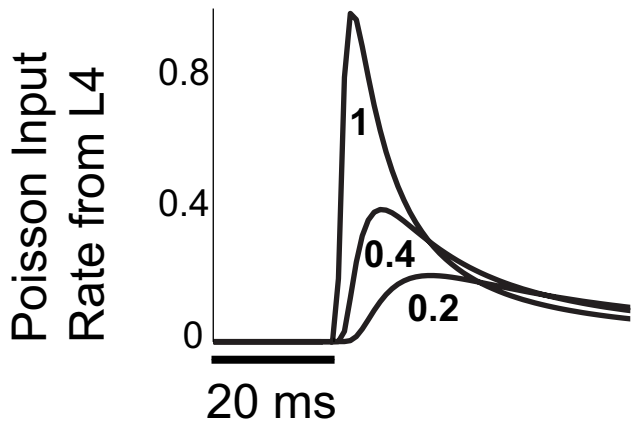

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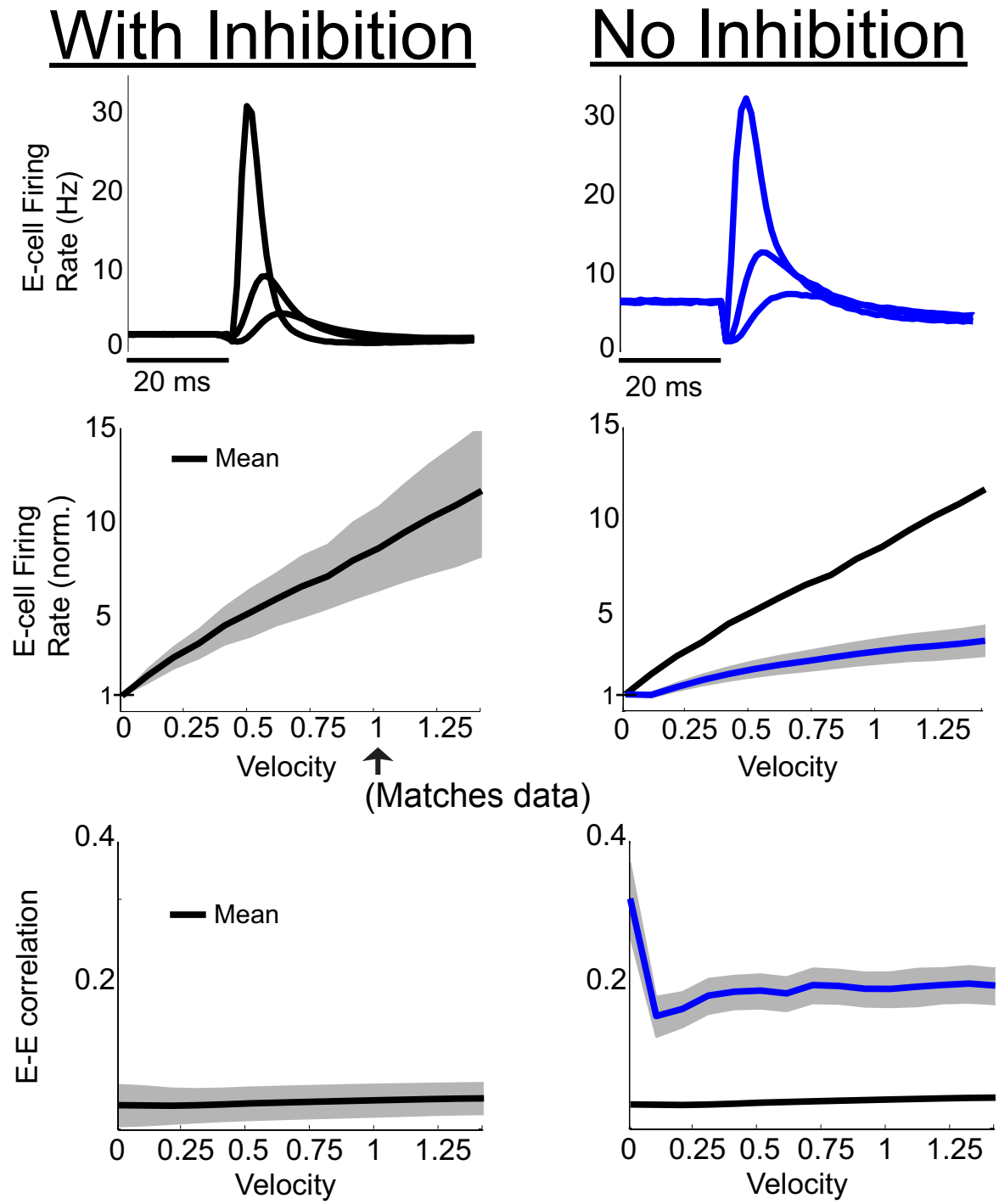

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Reduced binary network

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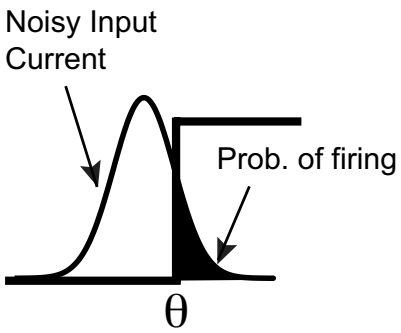

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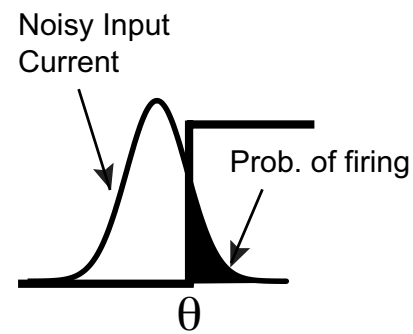

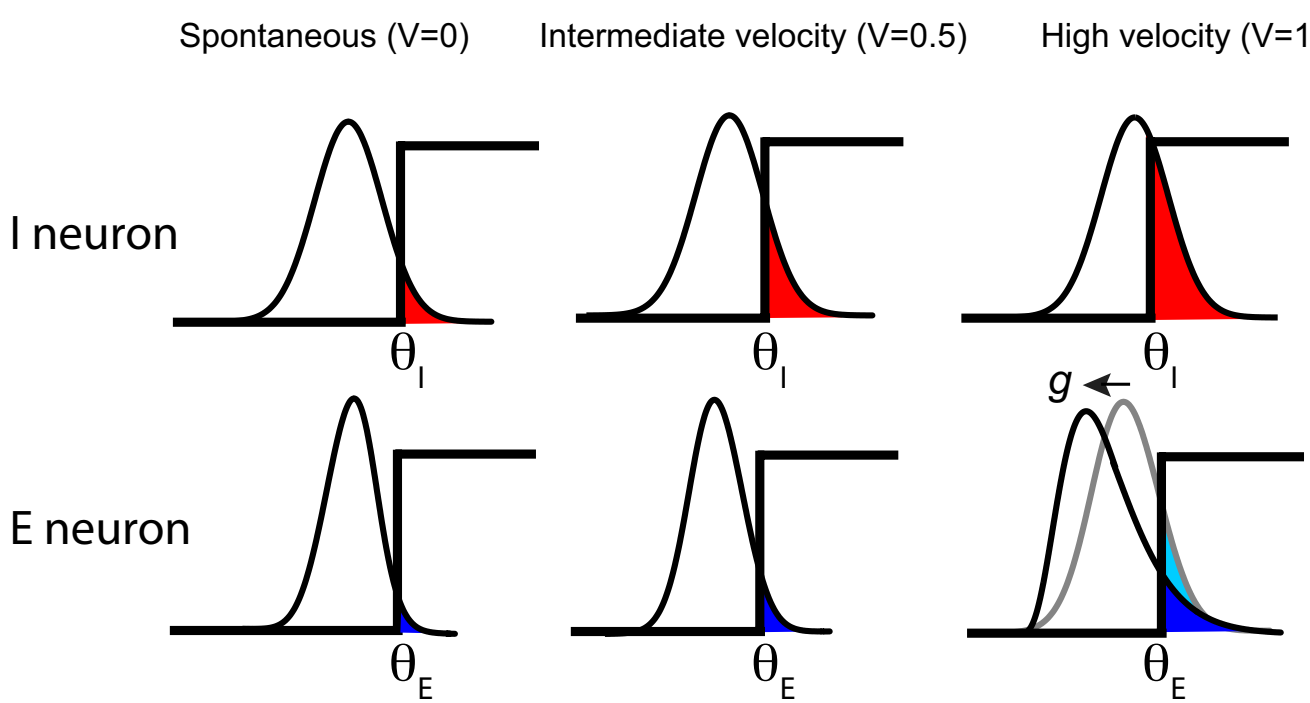

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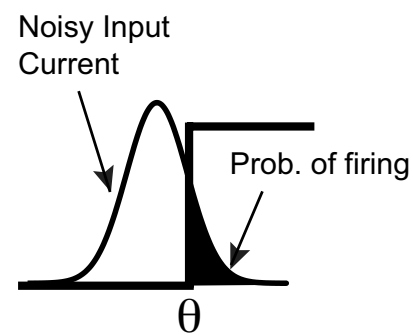
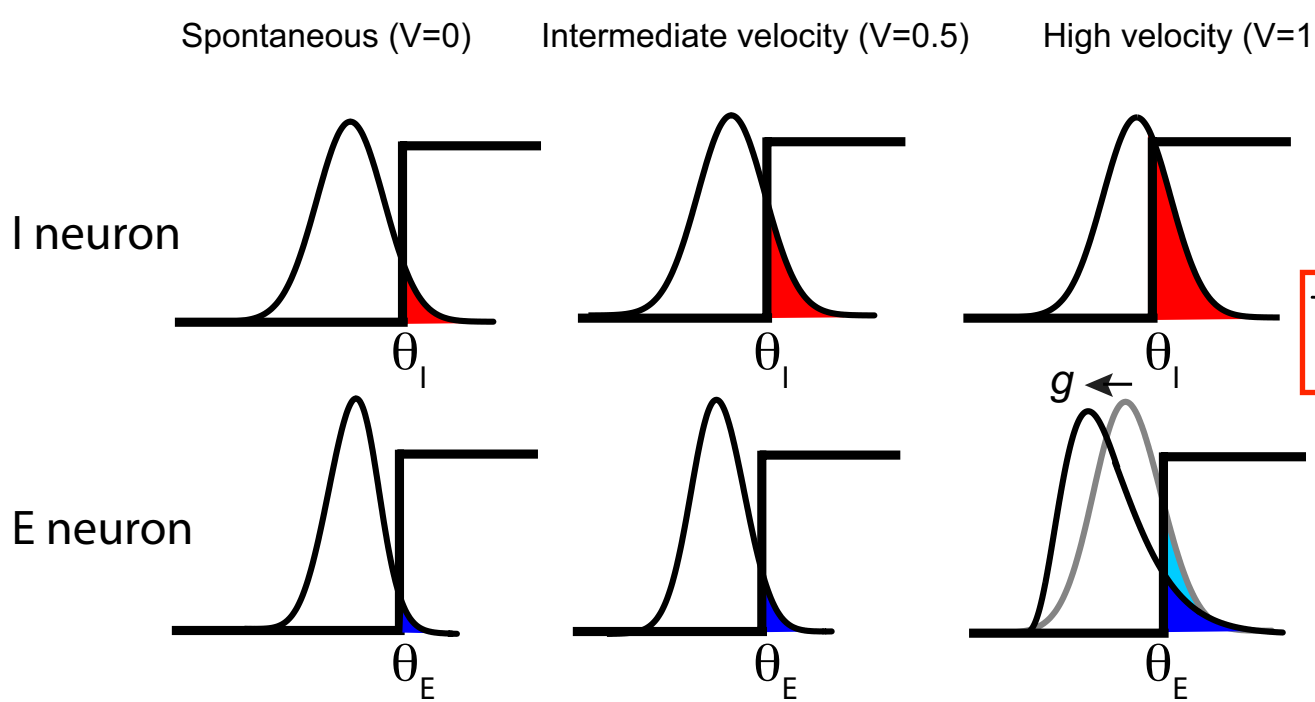
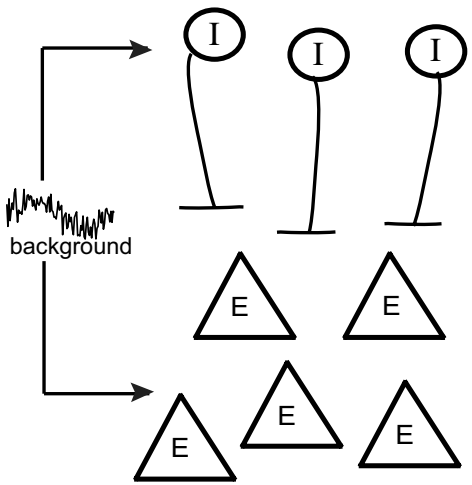




$$V \nearrow, \theta_{E/I} \searrow$$

Binary Network



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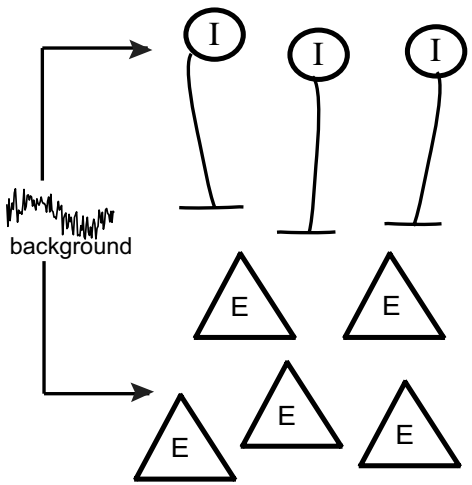

$$I_j = H(\theta_I + \eta_j)$$

$$E_k = H\left(\theta_E + \eta_k + \frac{g}{N_i}\sum_{j=1}^{N_i} I_j\right)$$

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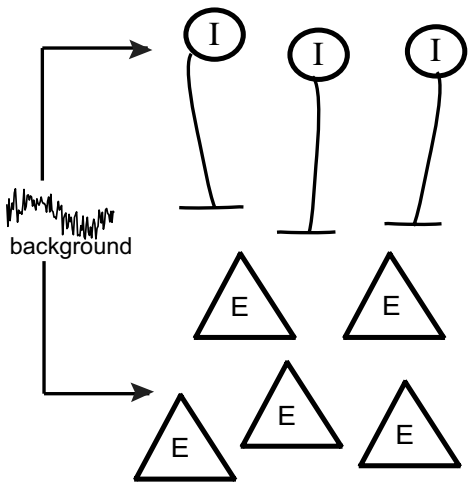
Binary Network



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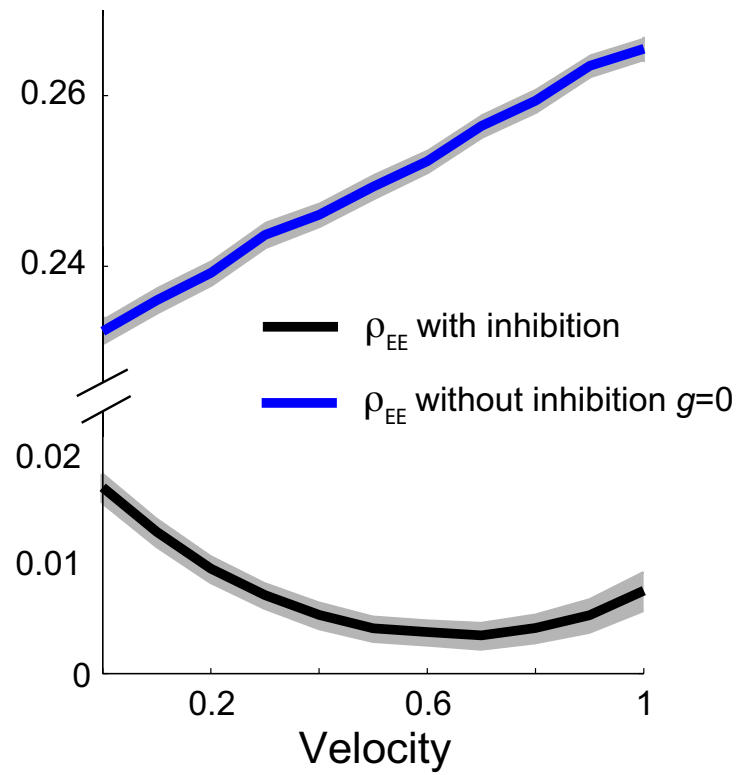
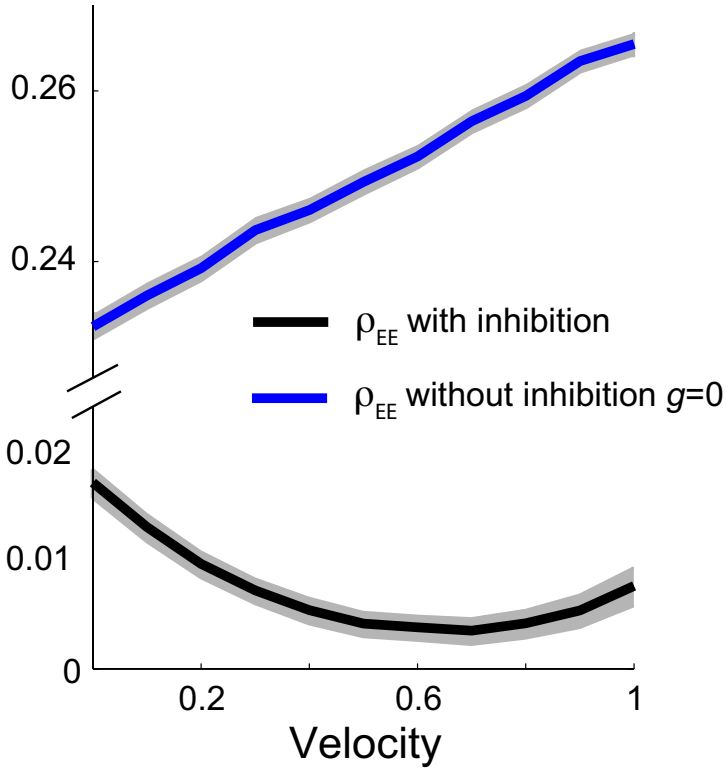


Binary Network Motivates Analysis



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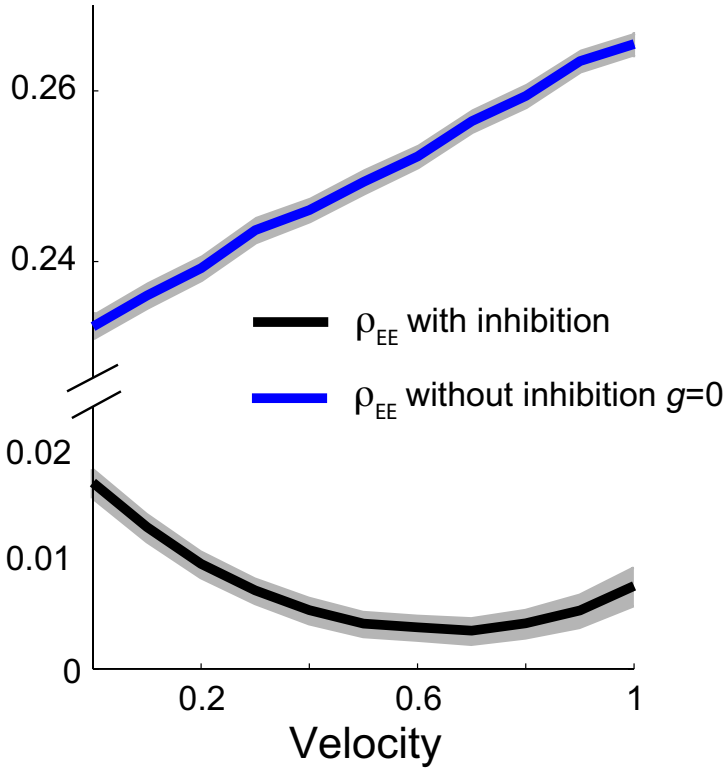
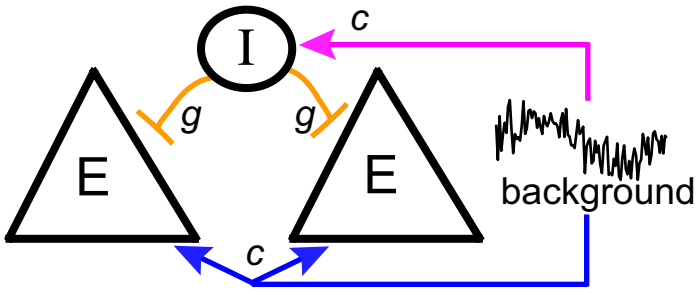


Small sub-network for tractability:



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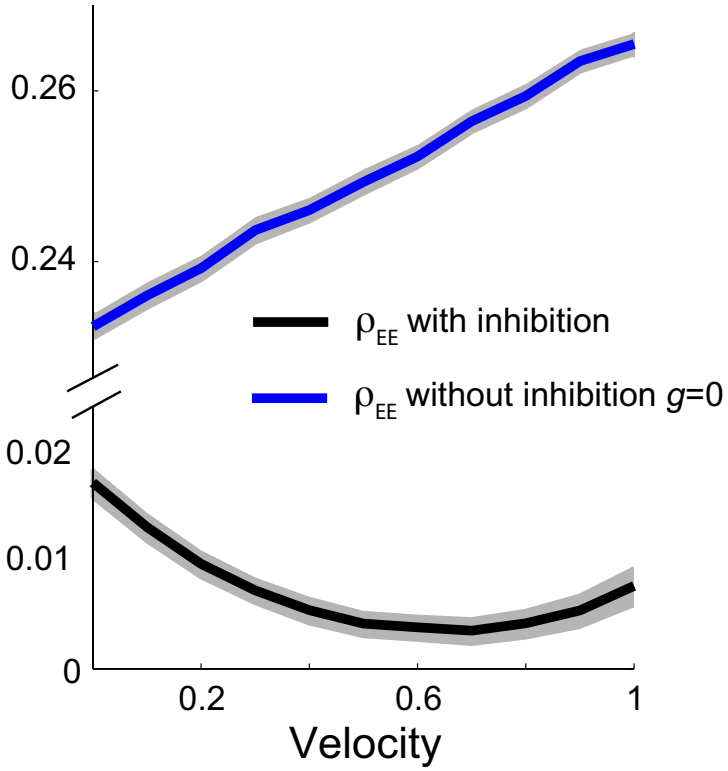

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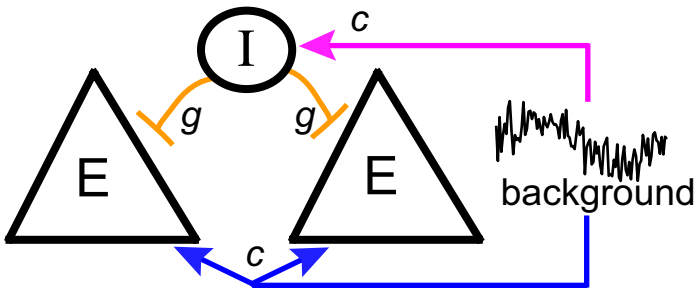
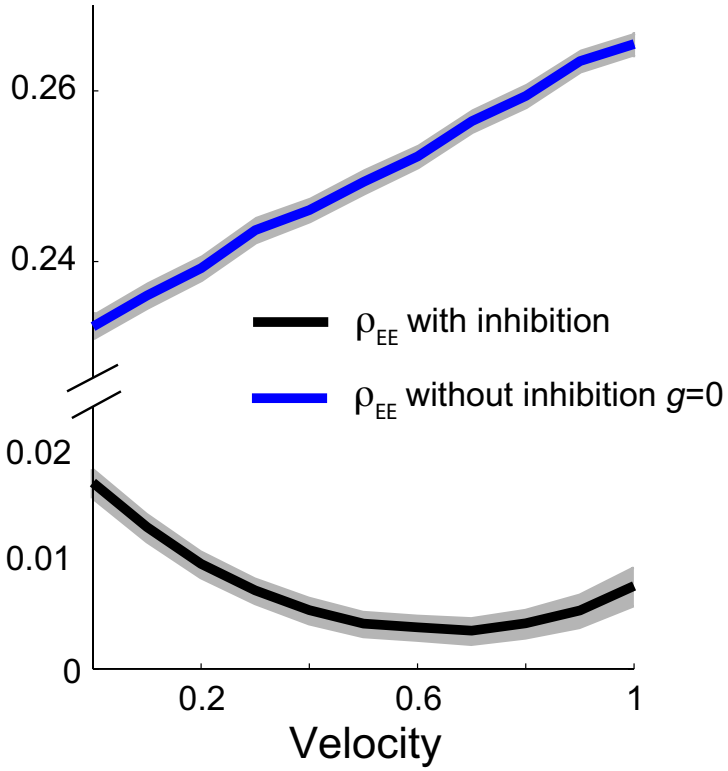


$$\nu_E = \left(\int_{\theta_E}^{\infty} \int_{-\infty}^{\theta_I} + \int_{\theta_E+g}^{\infty} \int_{\theta_I}^{\infty} \right) G_2 \, dx \, dy,$$

Binary Network Motivates Analysis



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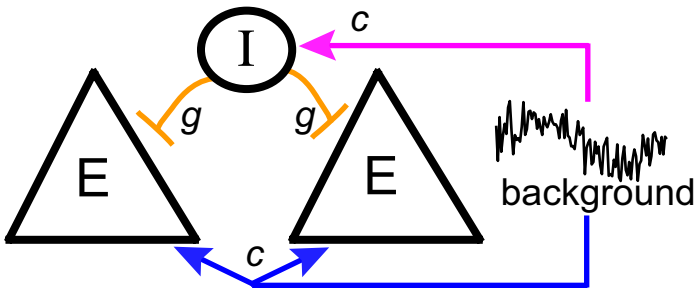

$$\nu_E = \left(\int_{\theta_E}^{\infty} \int_{-\infty}^{\theta_I} + \int_{\theta_E+g}^{\infty} \int_{\theta_I}^{\infty} \right) G_2 \, dx \, dy,$$

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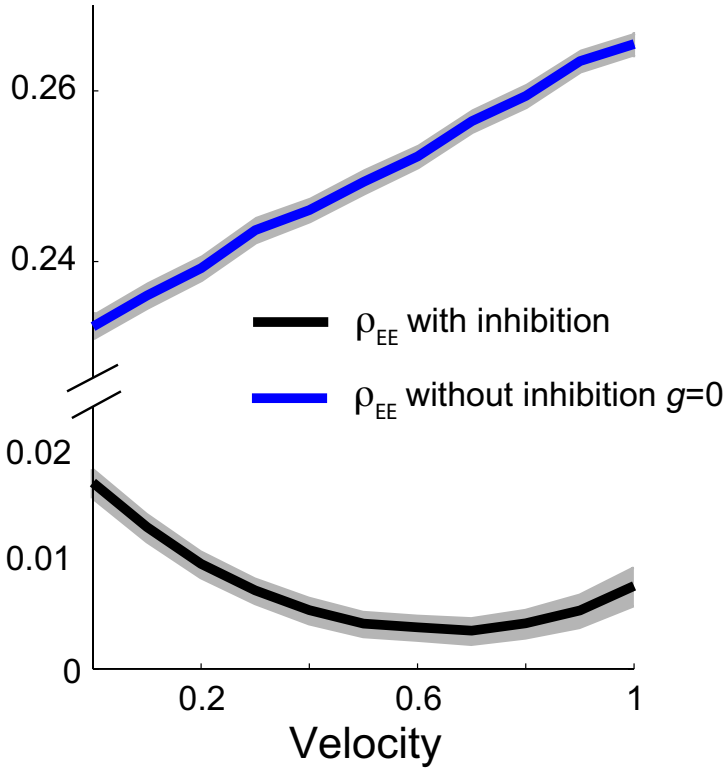
Binary Network Motivates Analysis



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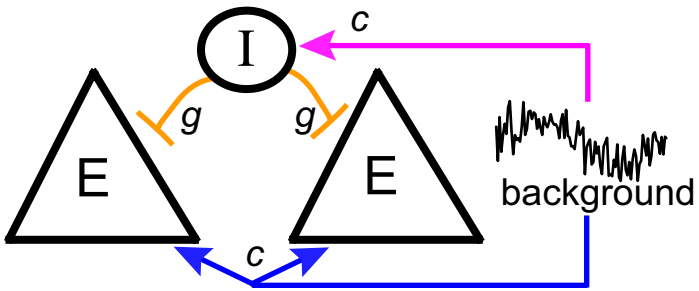

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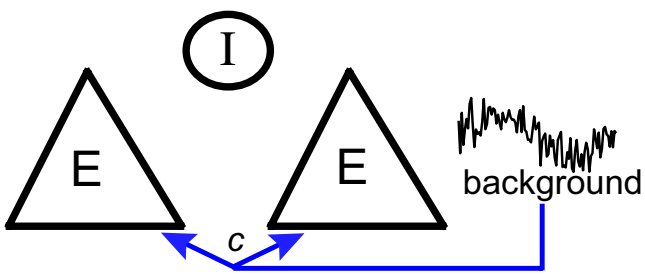

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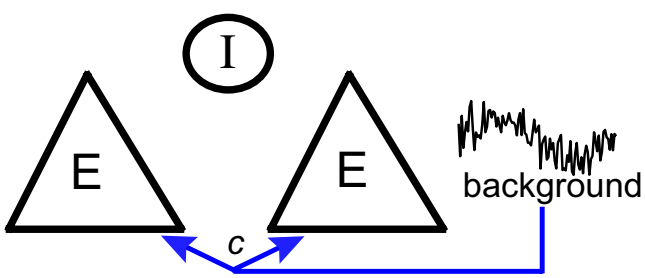

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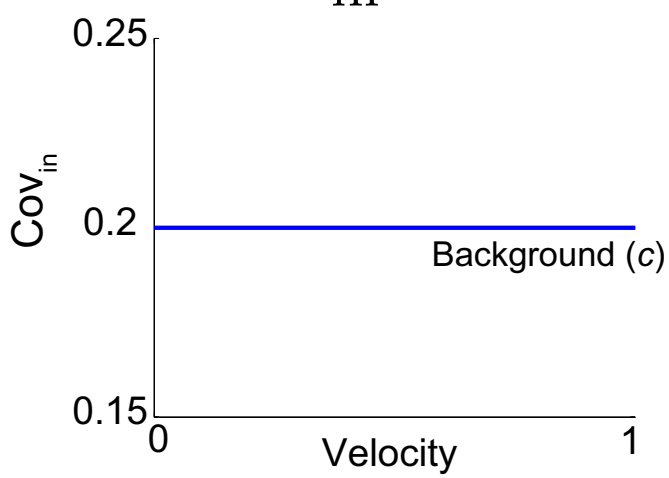

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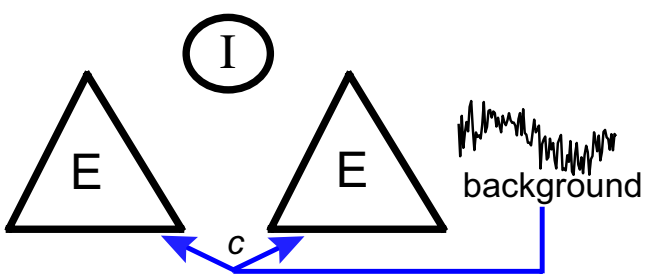

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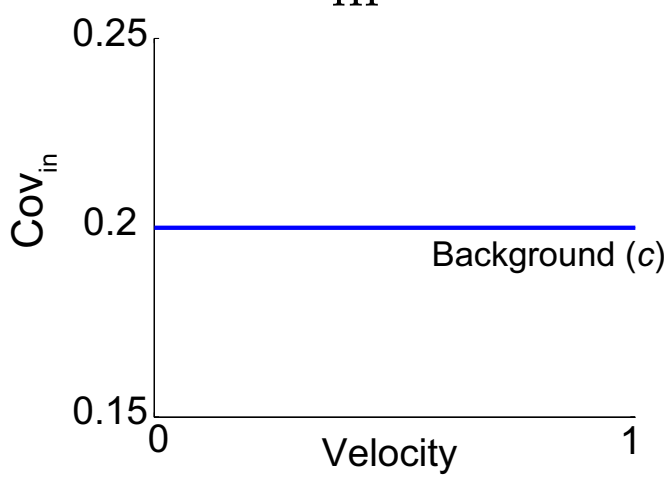

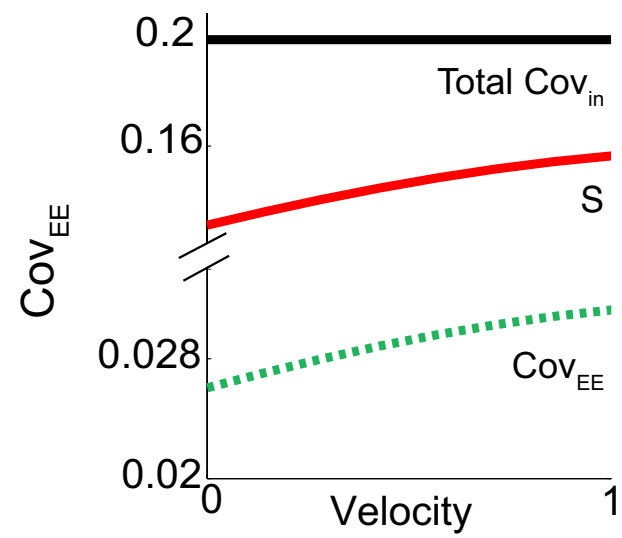

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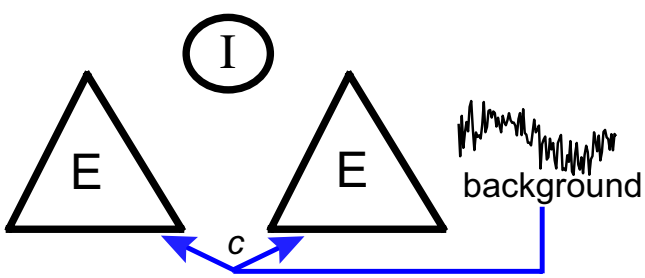

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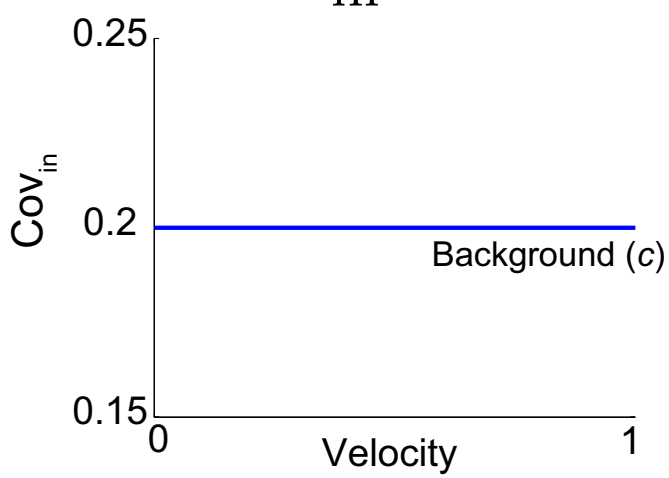

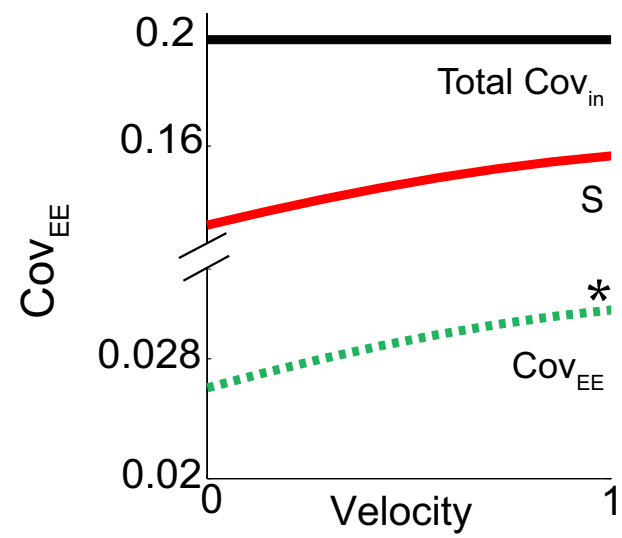

*Correlation increases with firing rate (velocity).

de la Rocha, Doiron, et al., **Nature** 2007.

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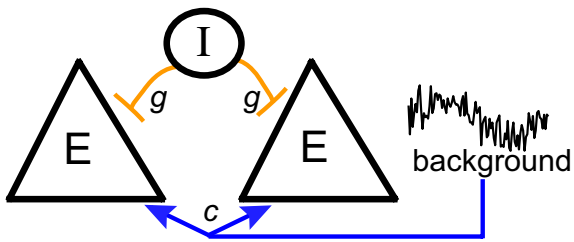

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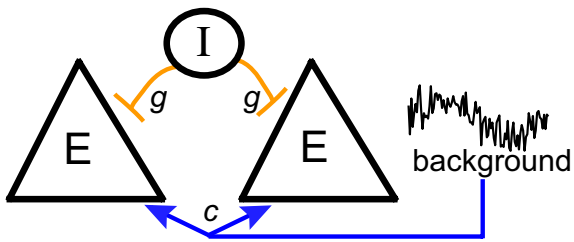

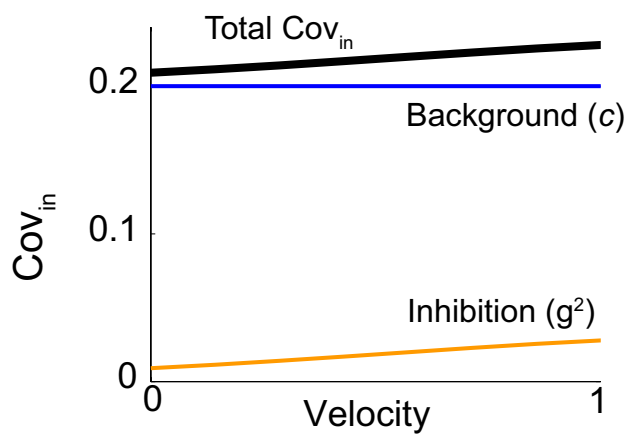

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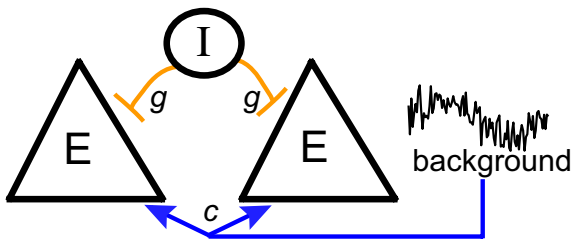

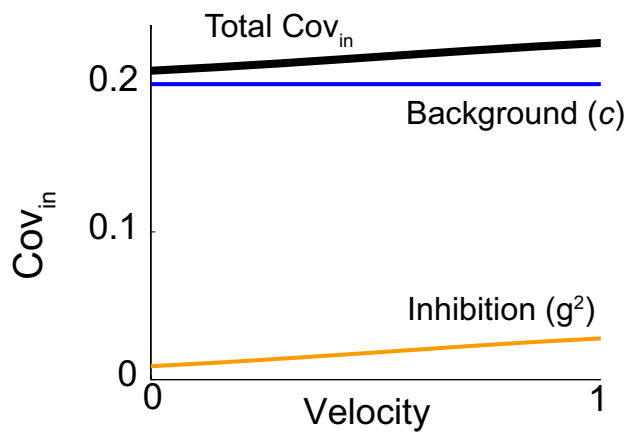

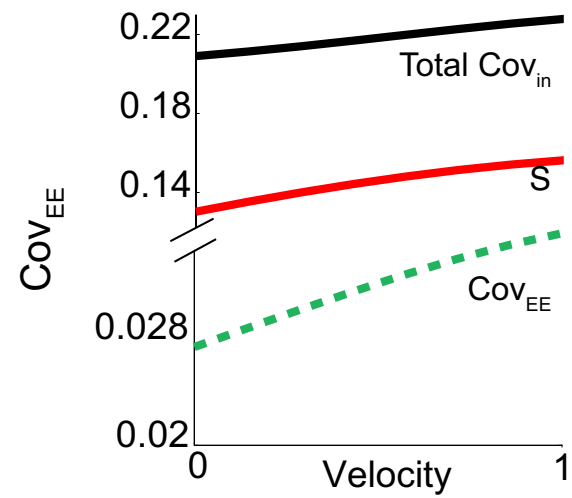

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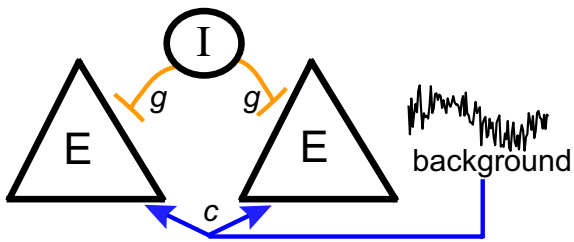

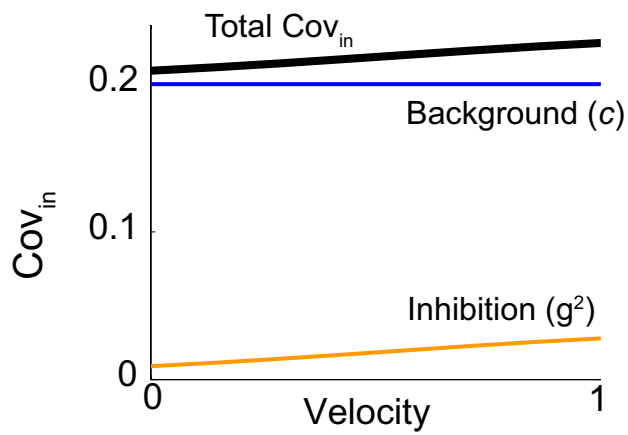

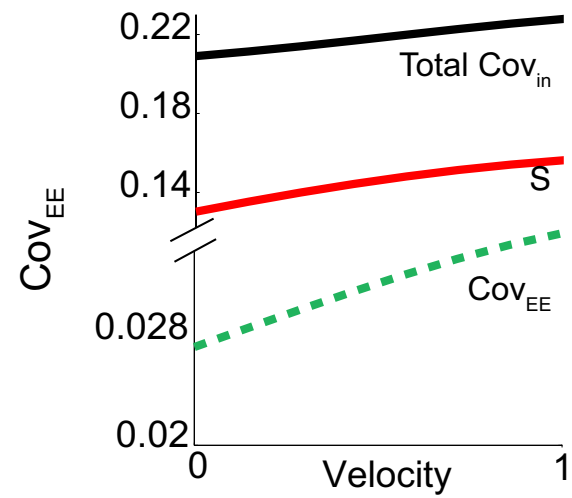

Inhibition can synchronize and shape rhythms.

van Vreeswijk, Abbott, Ermentrout, **JCNS** '94; *Cardin et al.,* **Nature** '09

Whittington, Traub, Kopell, et al., **IJ Psychophys.** '00; *Börgers & Kopell,* '03.

Wang & Buzsaki, **J Neurosci.** '96

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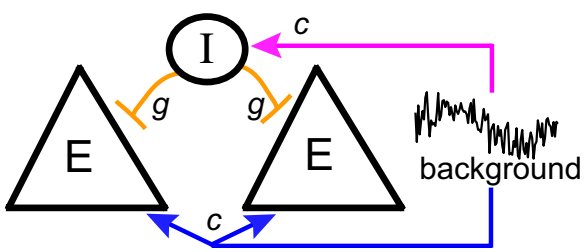

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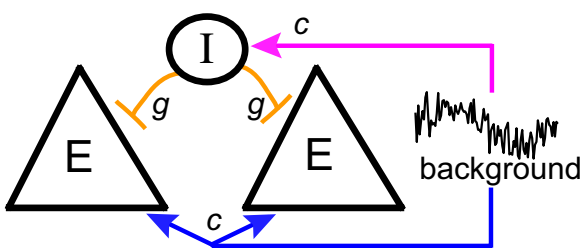

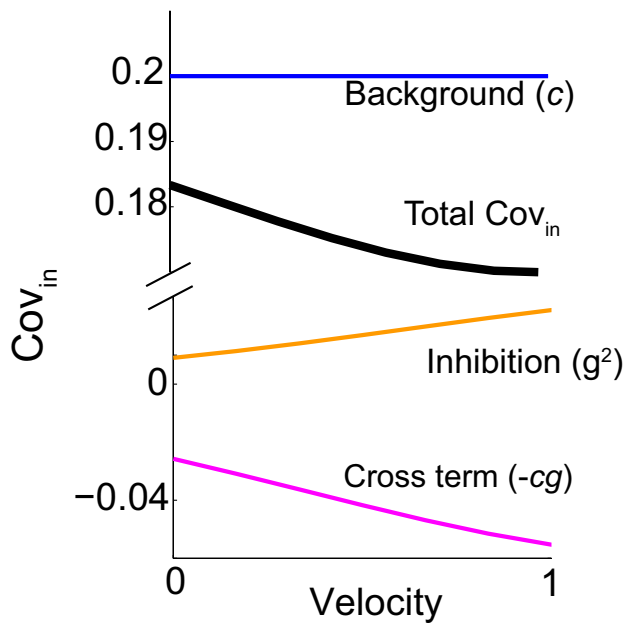

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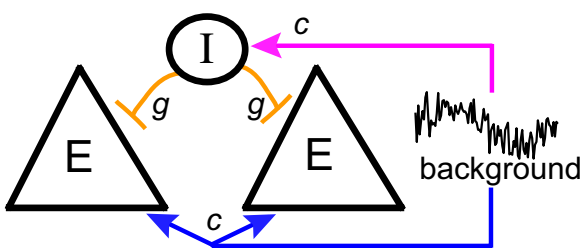

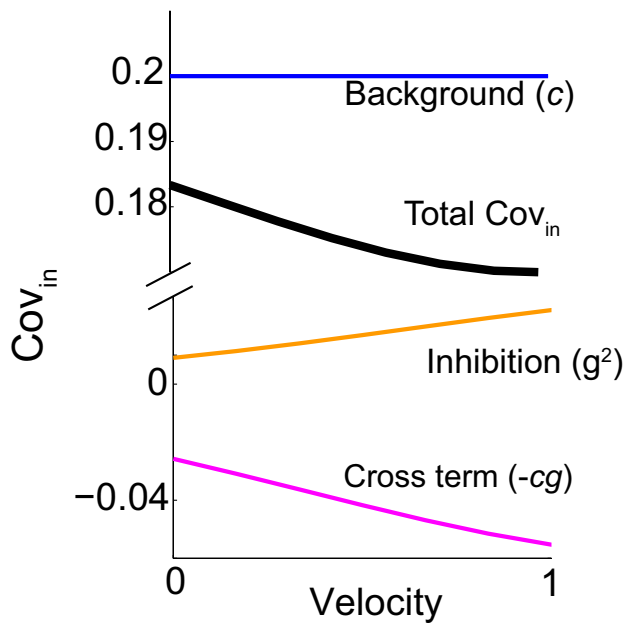

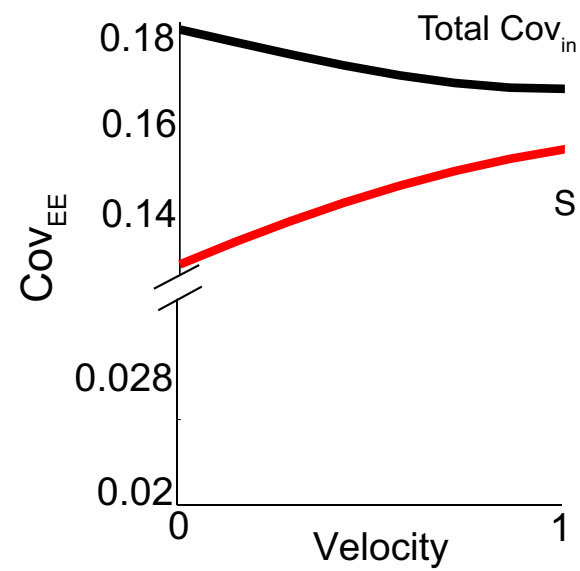

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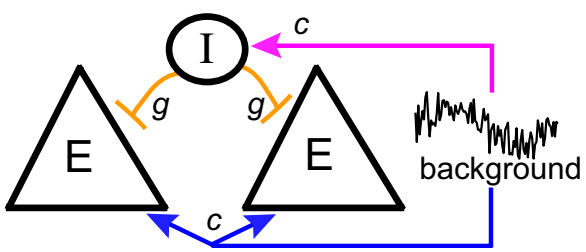

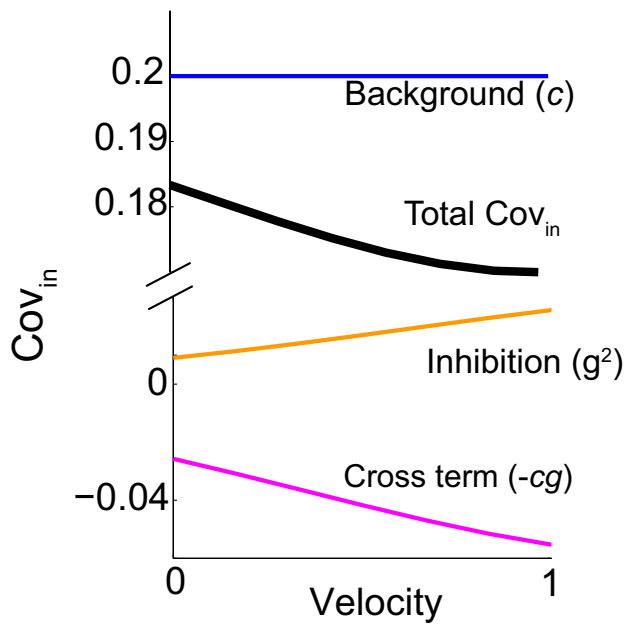

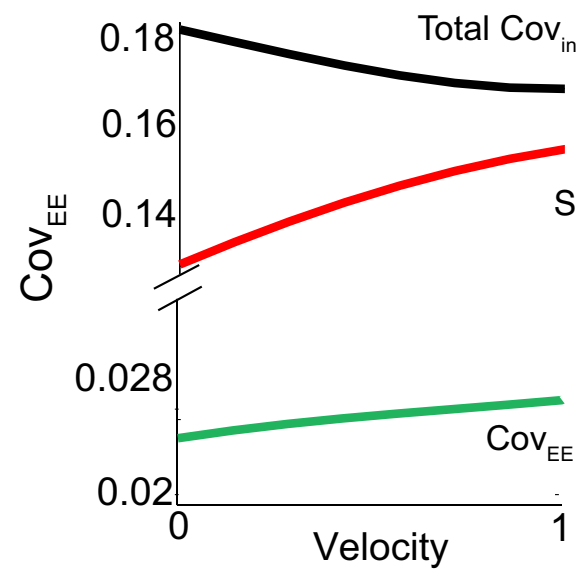

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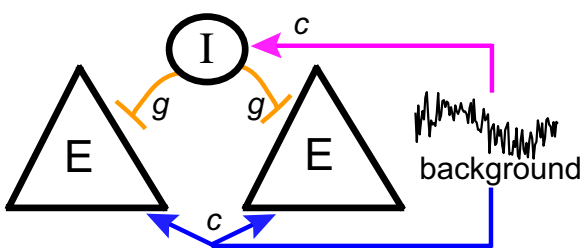
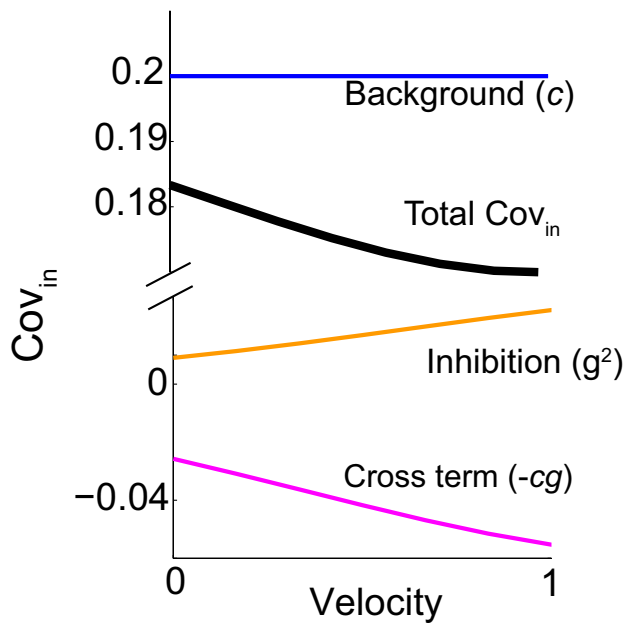
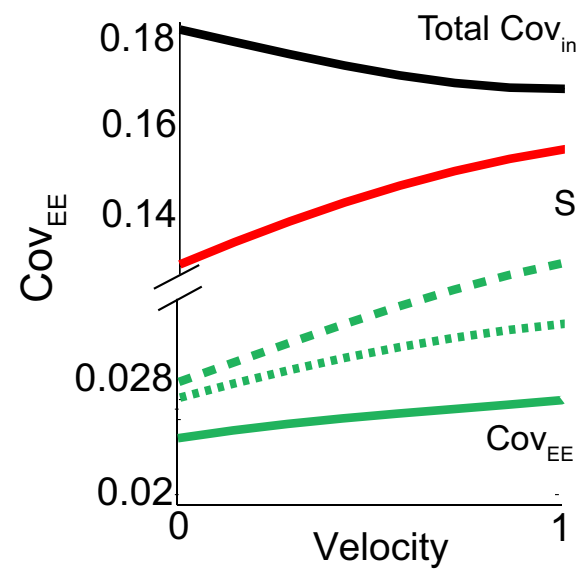
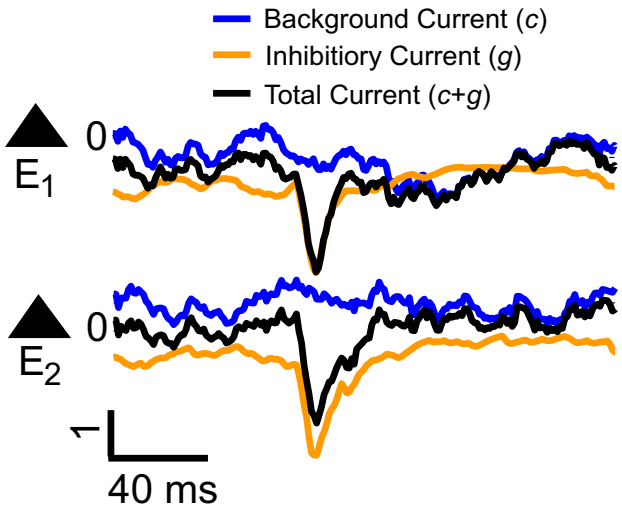






Validate theory with full spiking model:



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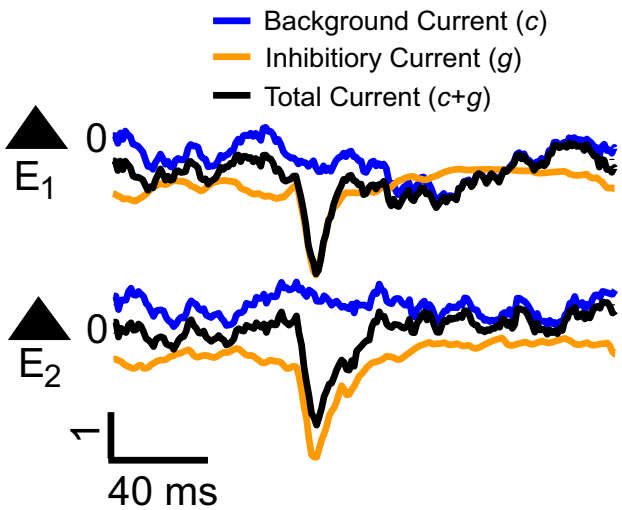

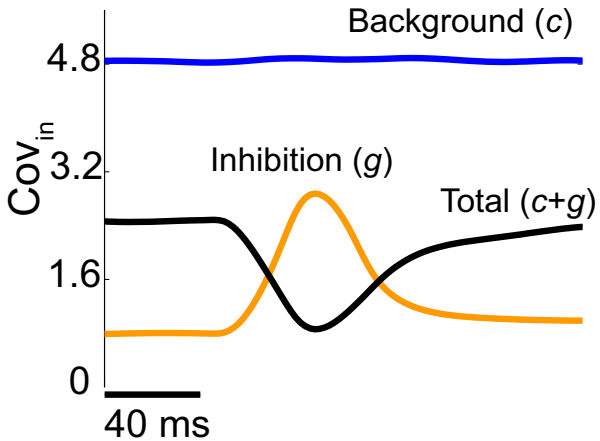

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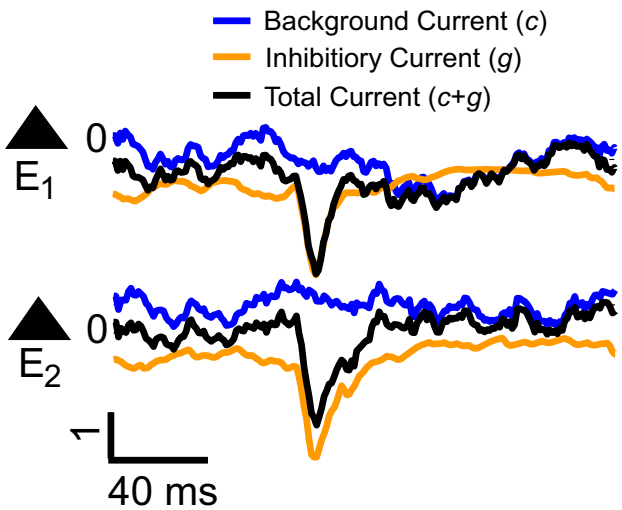

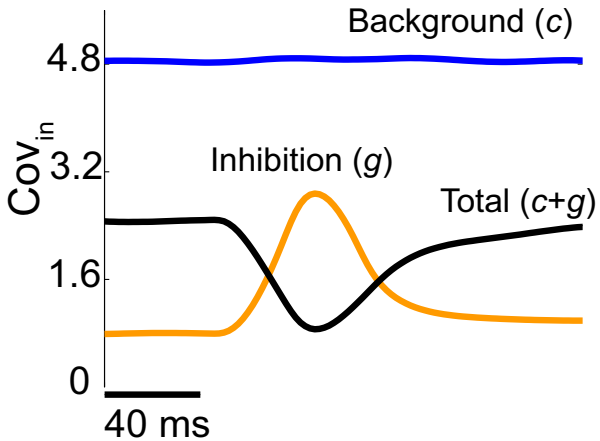

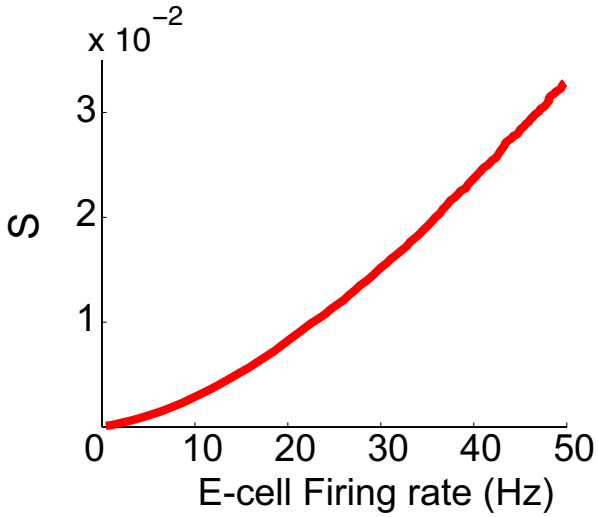

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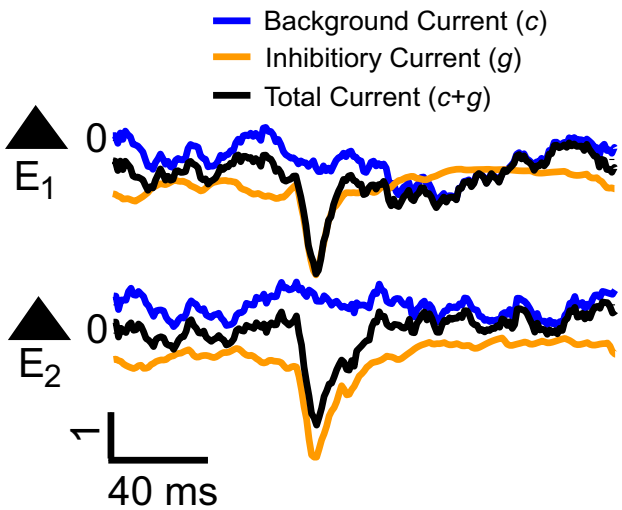

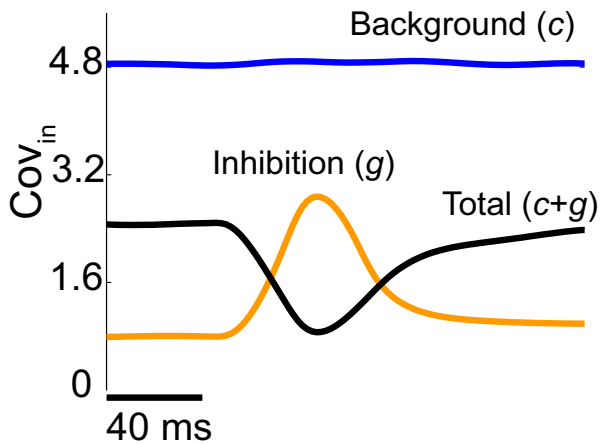

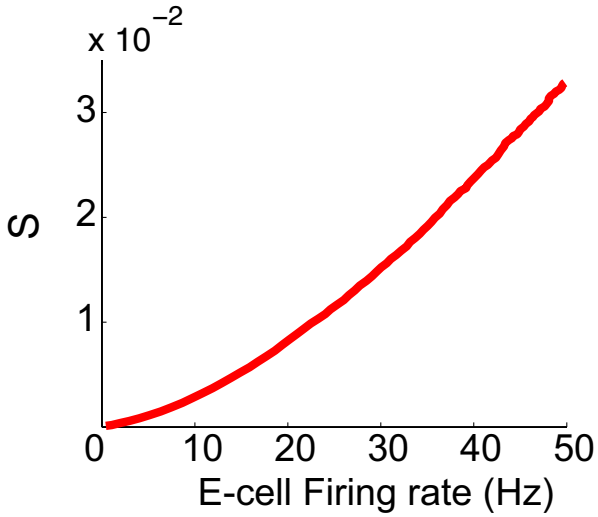

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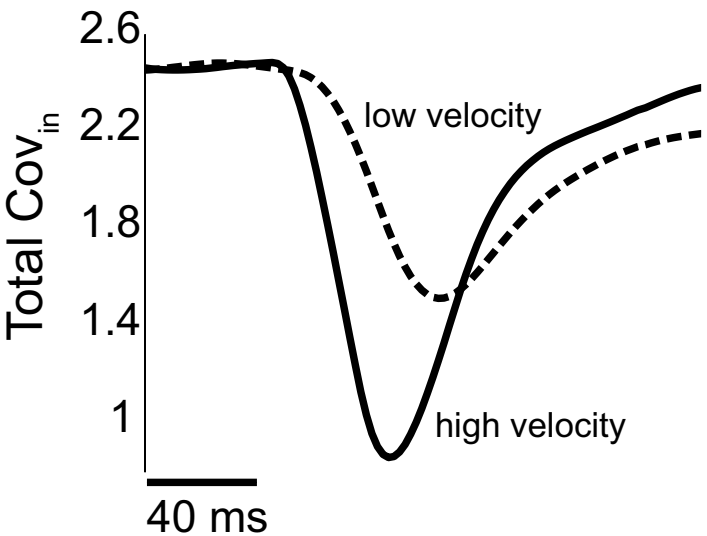

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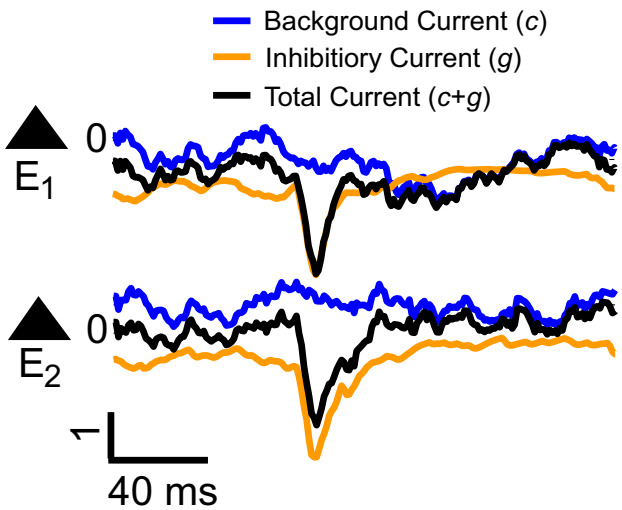

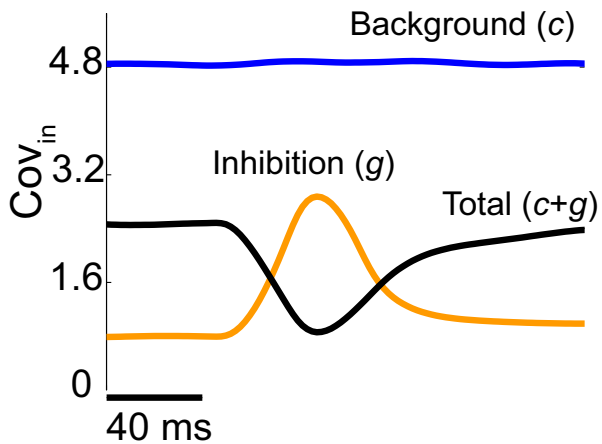

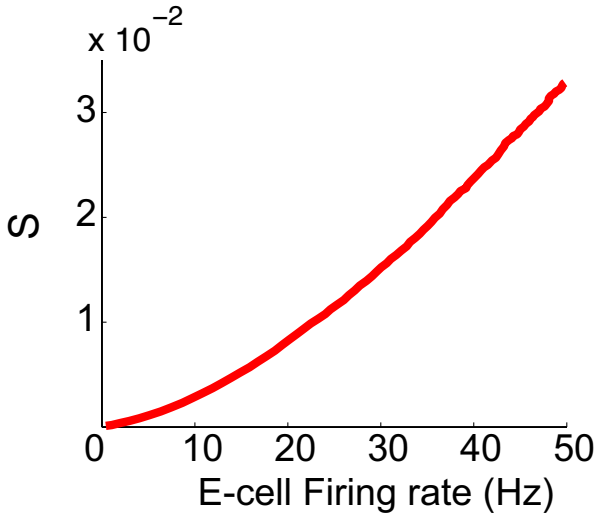

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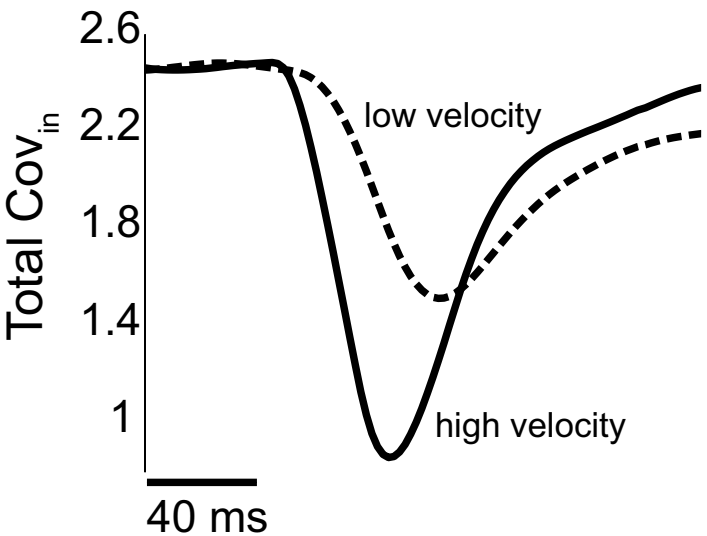

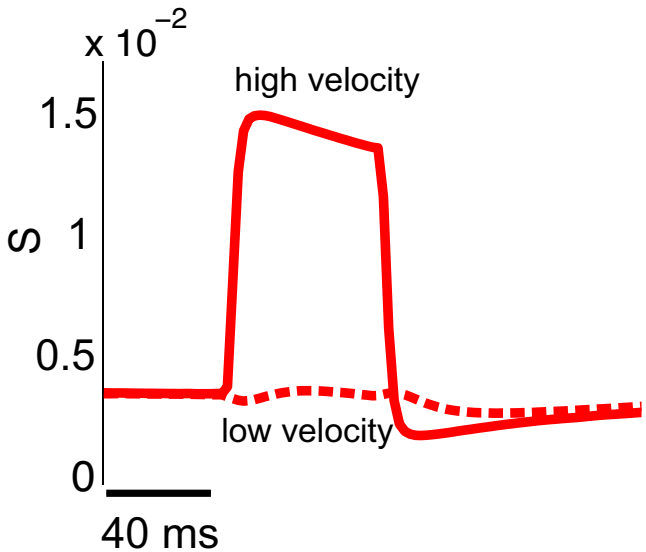

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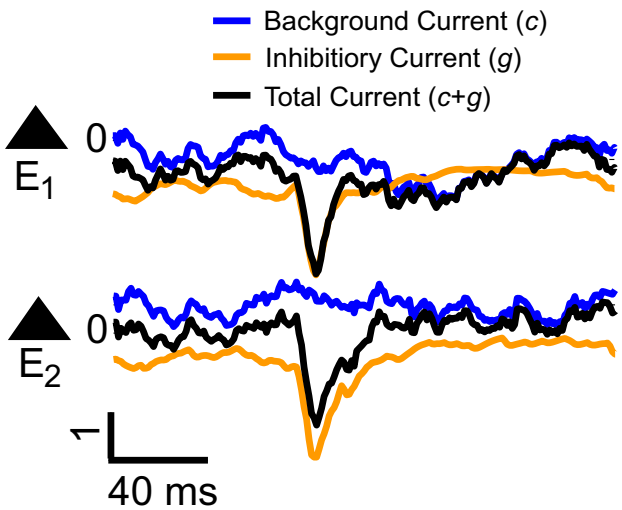

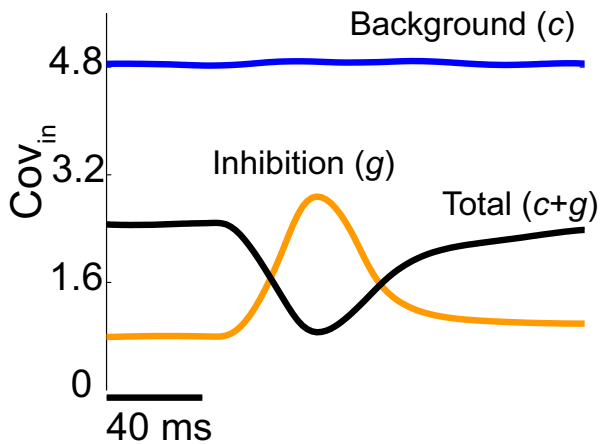

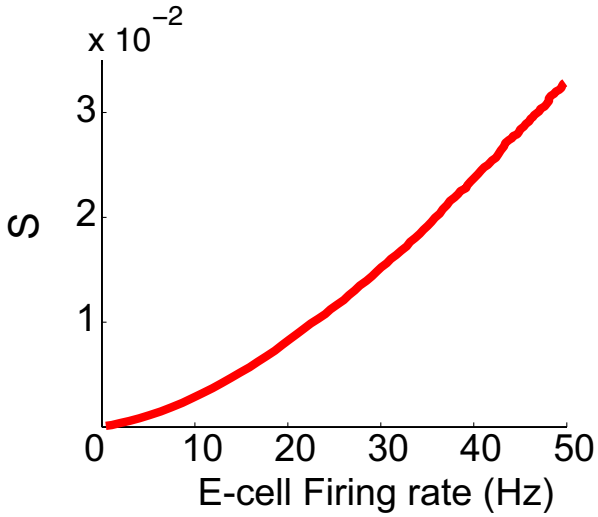

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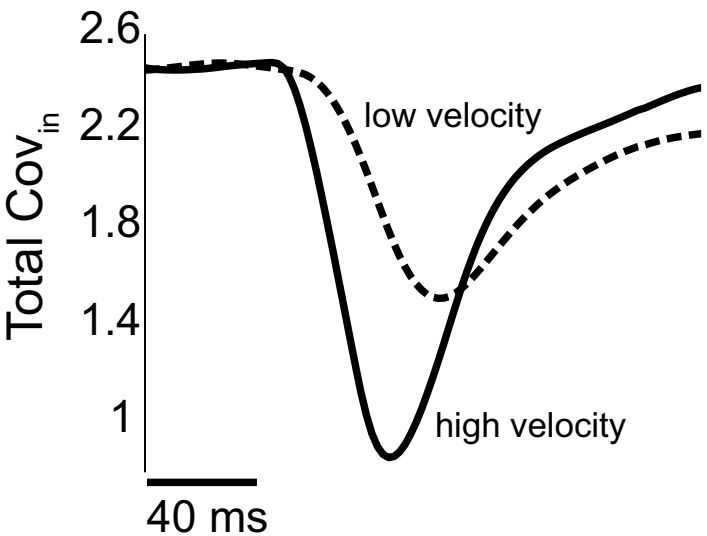

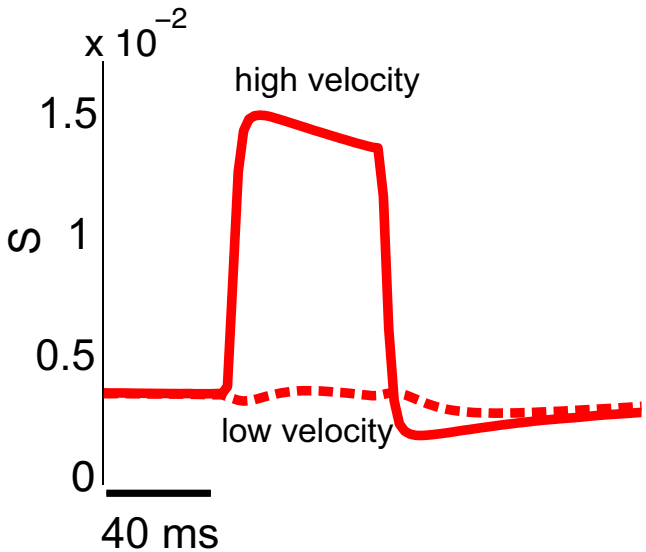

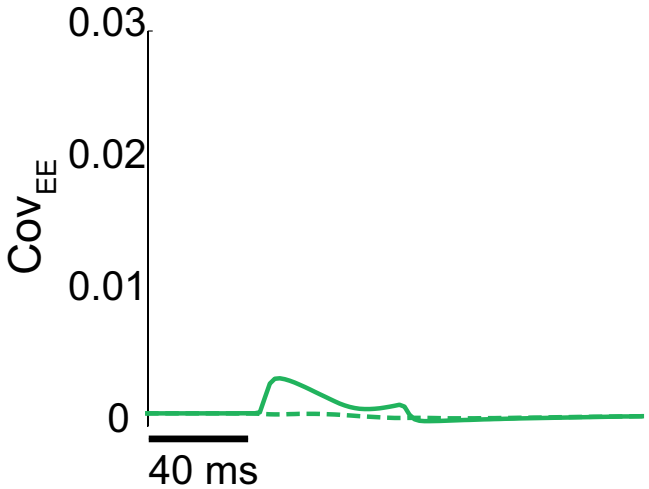

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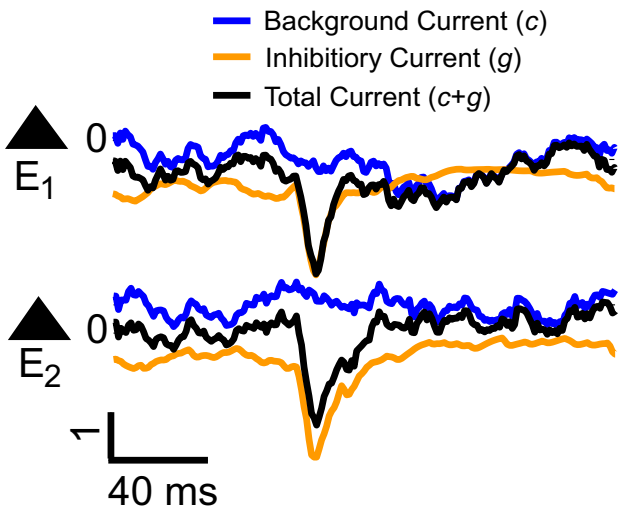

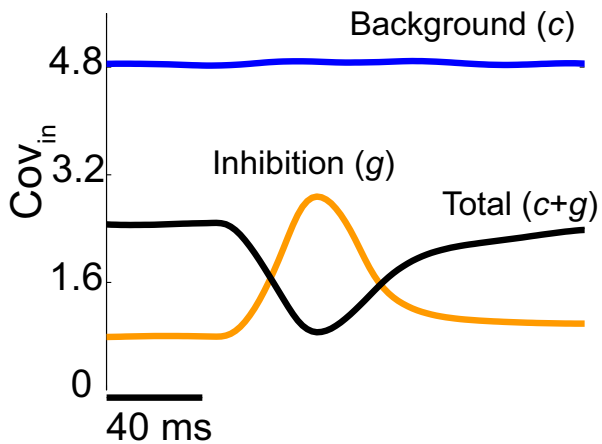

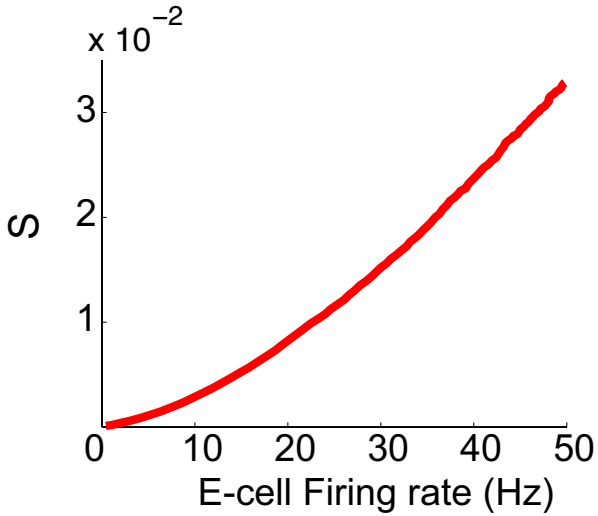

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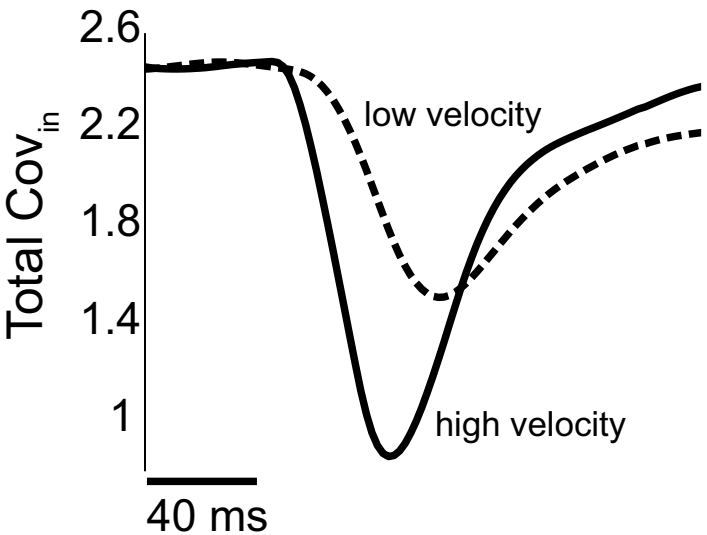
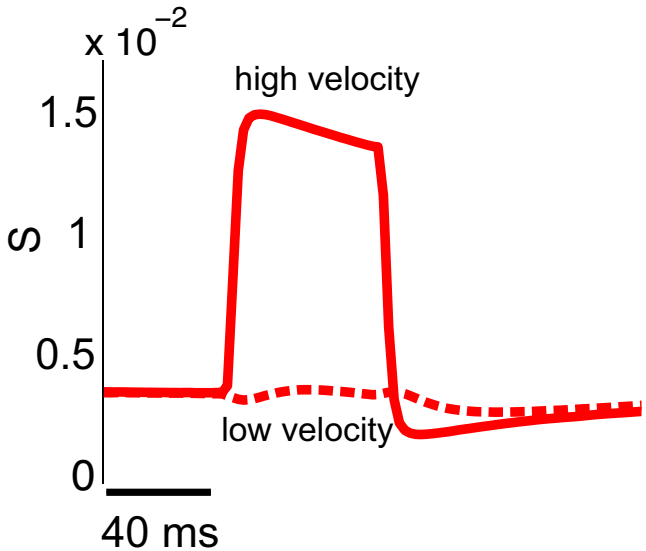
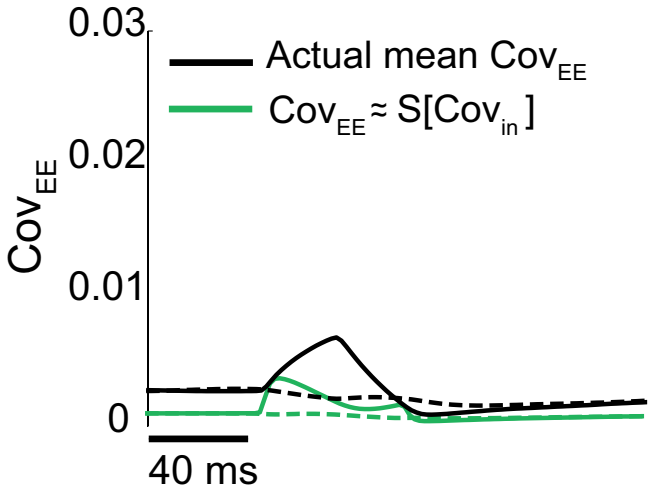
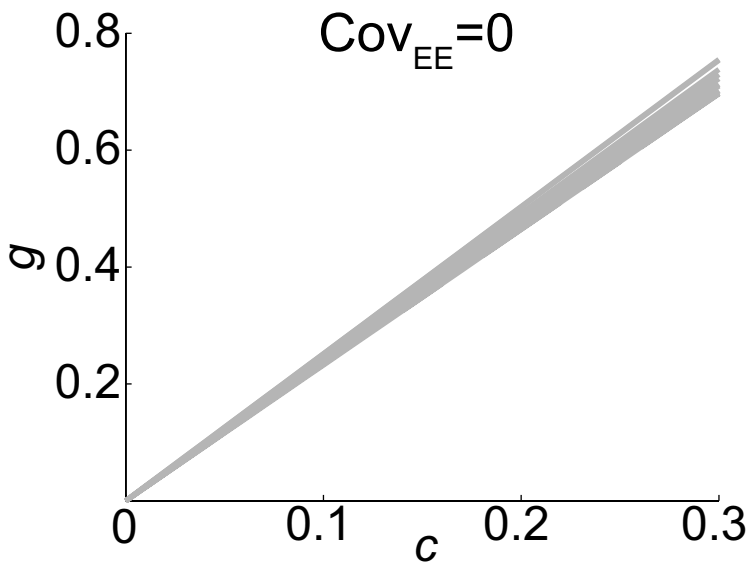






Are 'c' and 'g' necessarily large?

Are '*c*' and '*g*' necessarily large?



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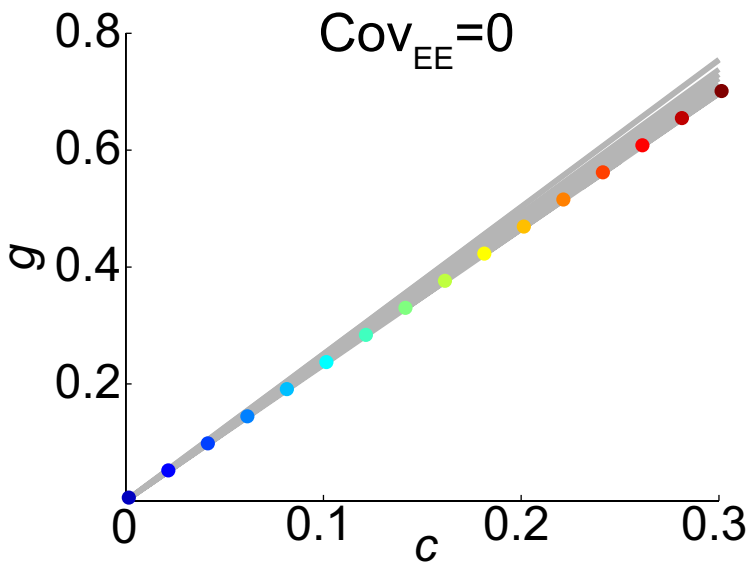

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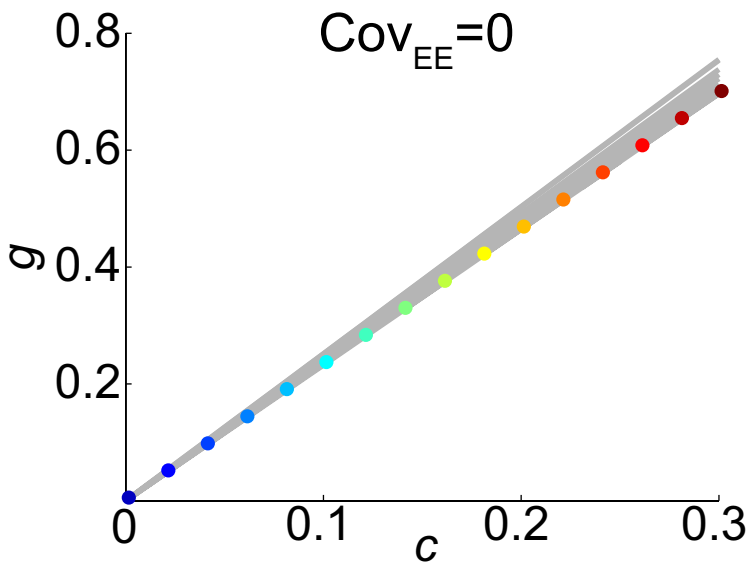

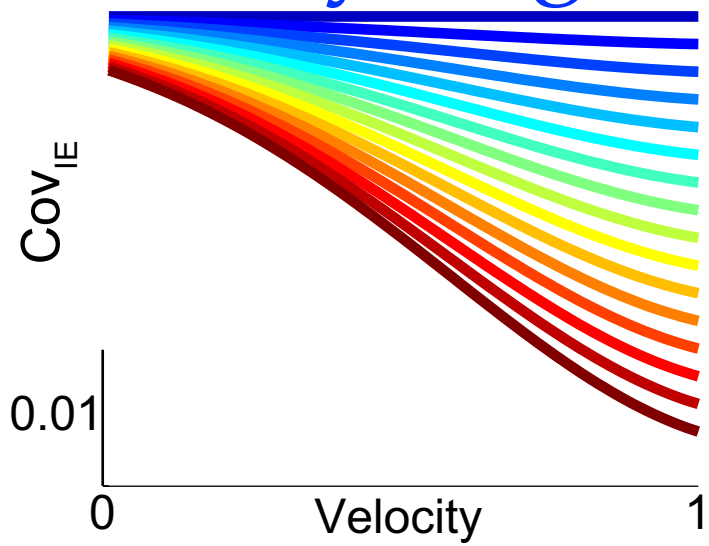

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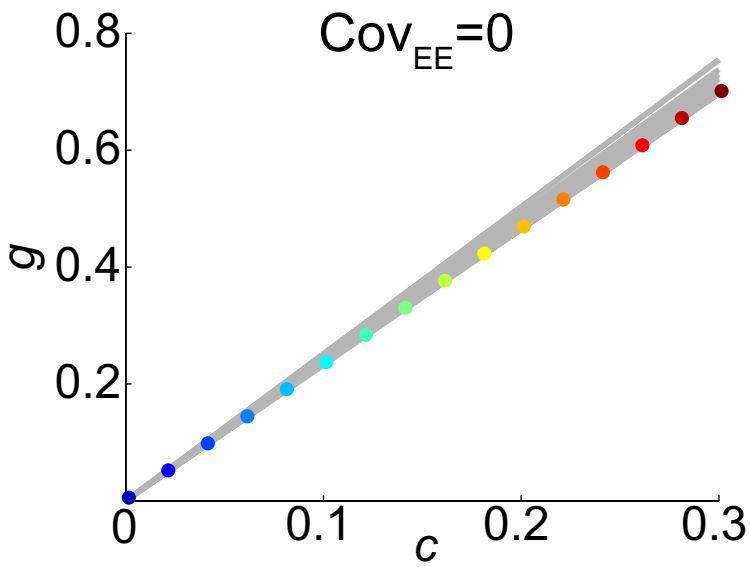

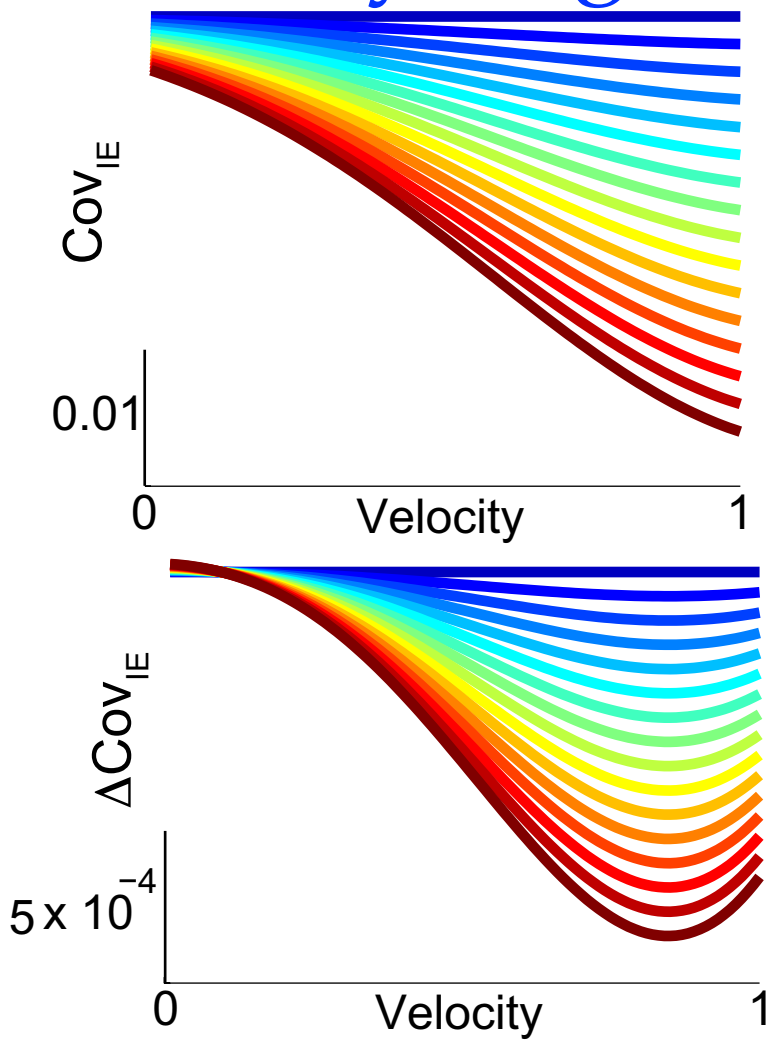

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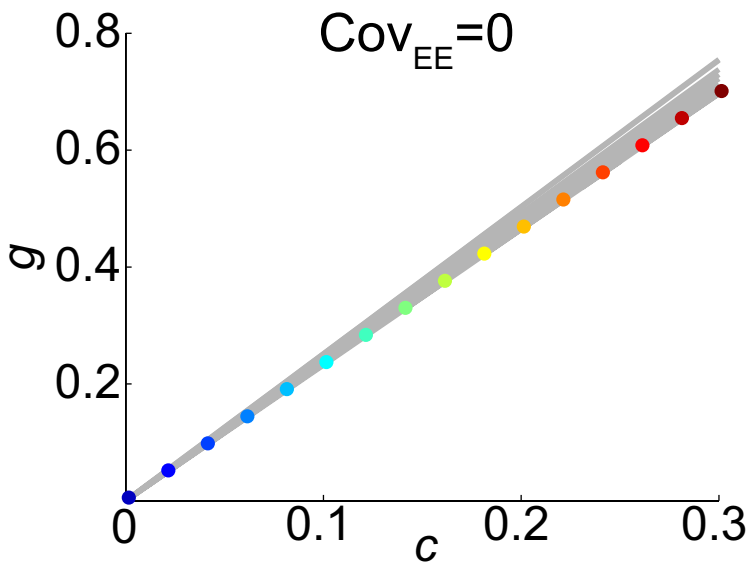
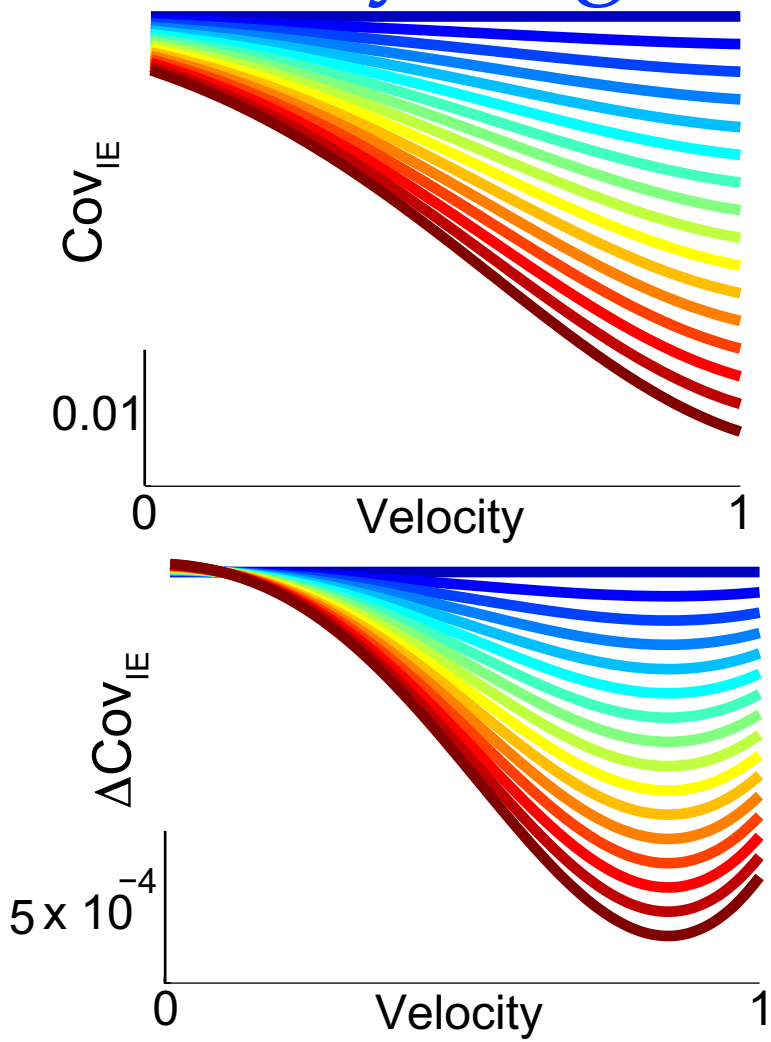
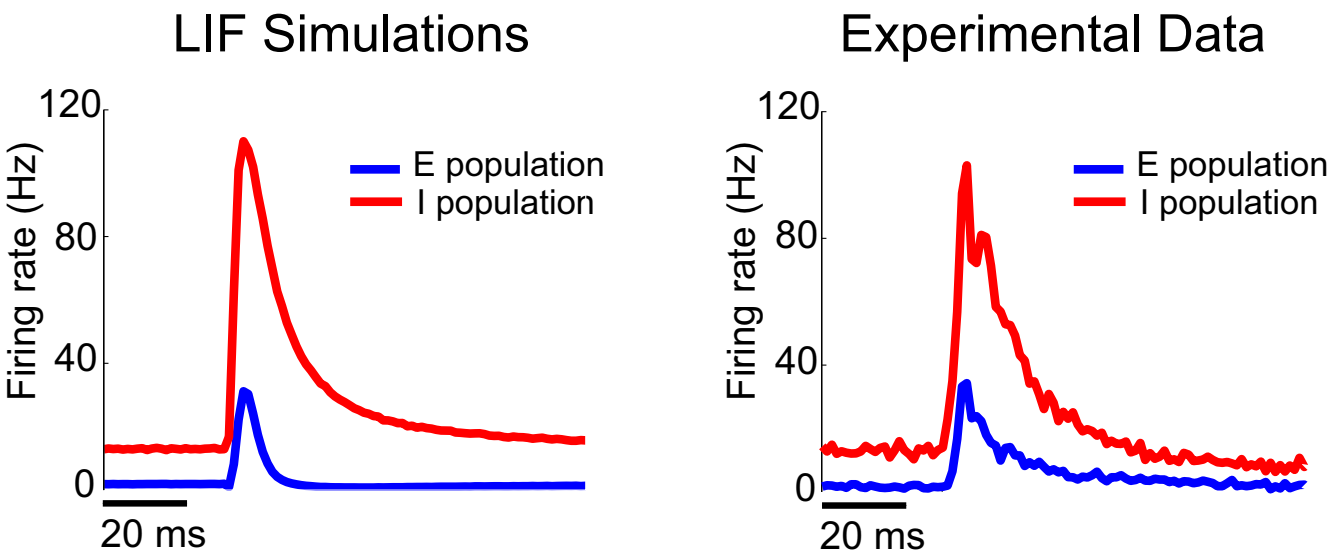




Model prediction:

- The I-E correlation decreases in the evoked state.
- The width of the I-E correlation histogram decreases in the evoked state.

Model Prediction Confirmed:



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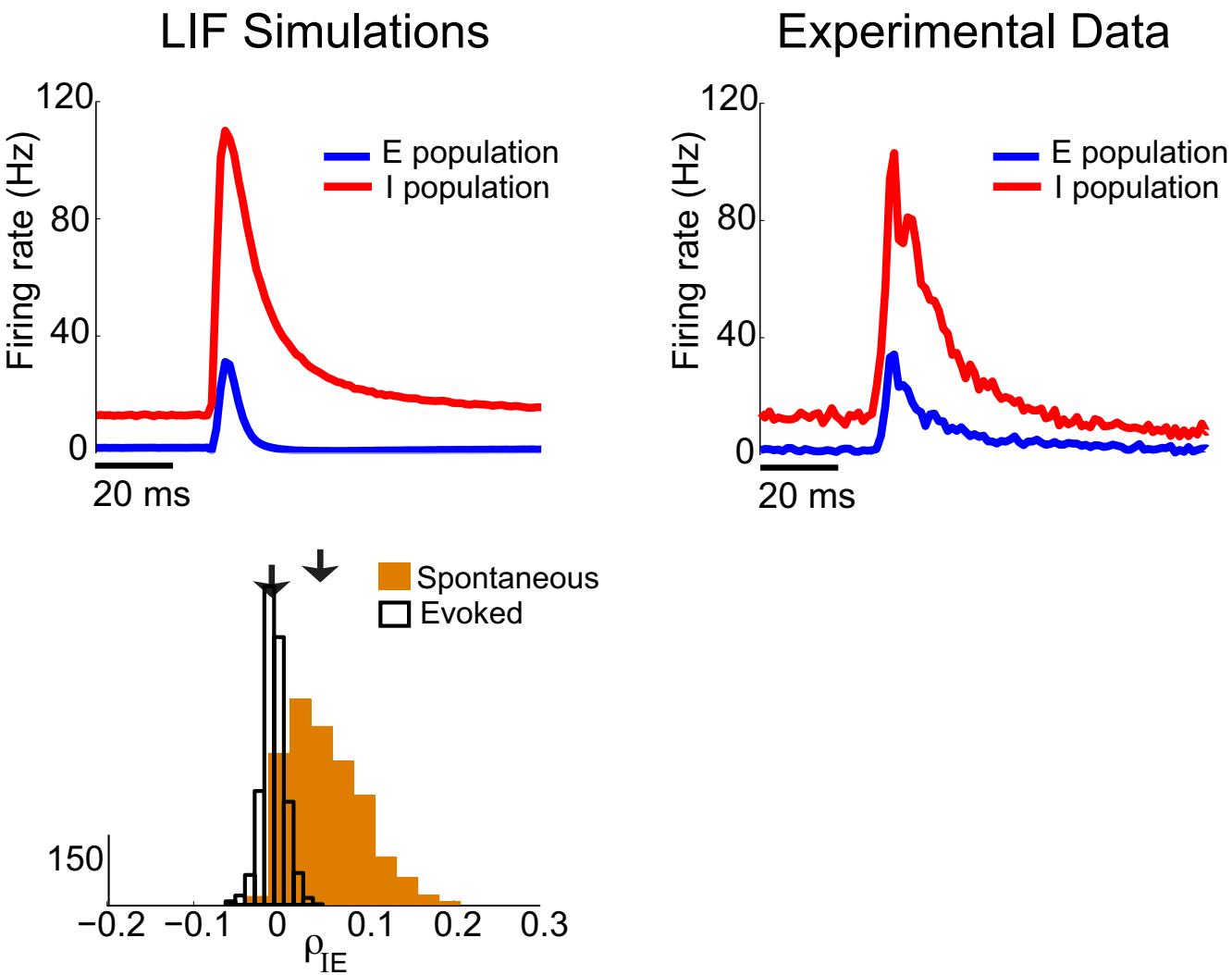

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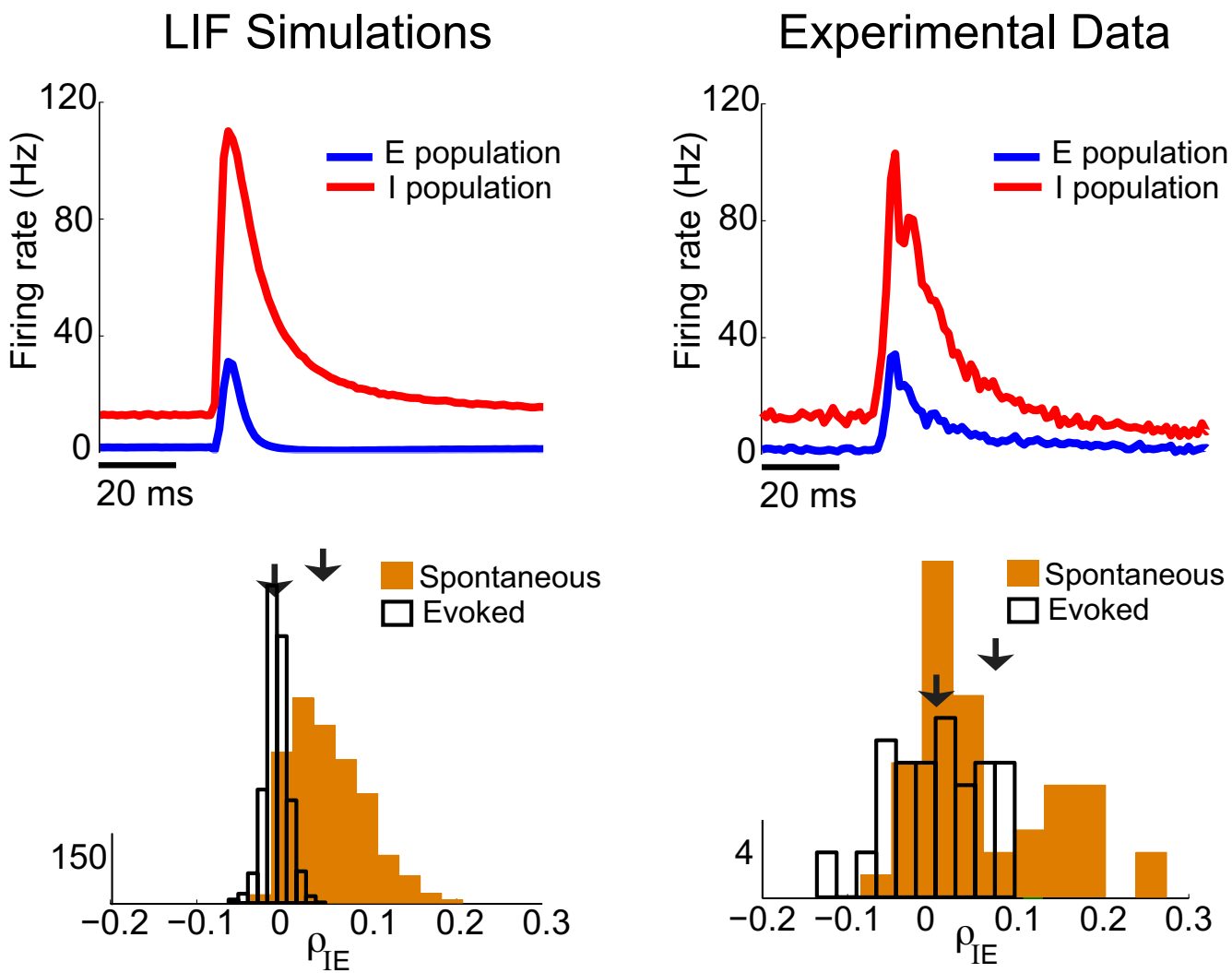

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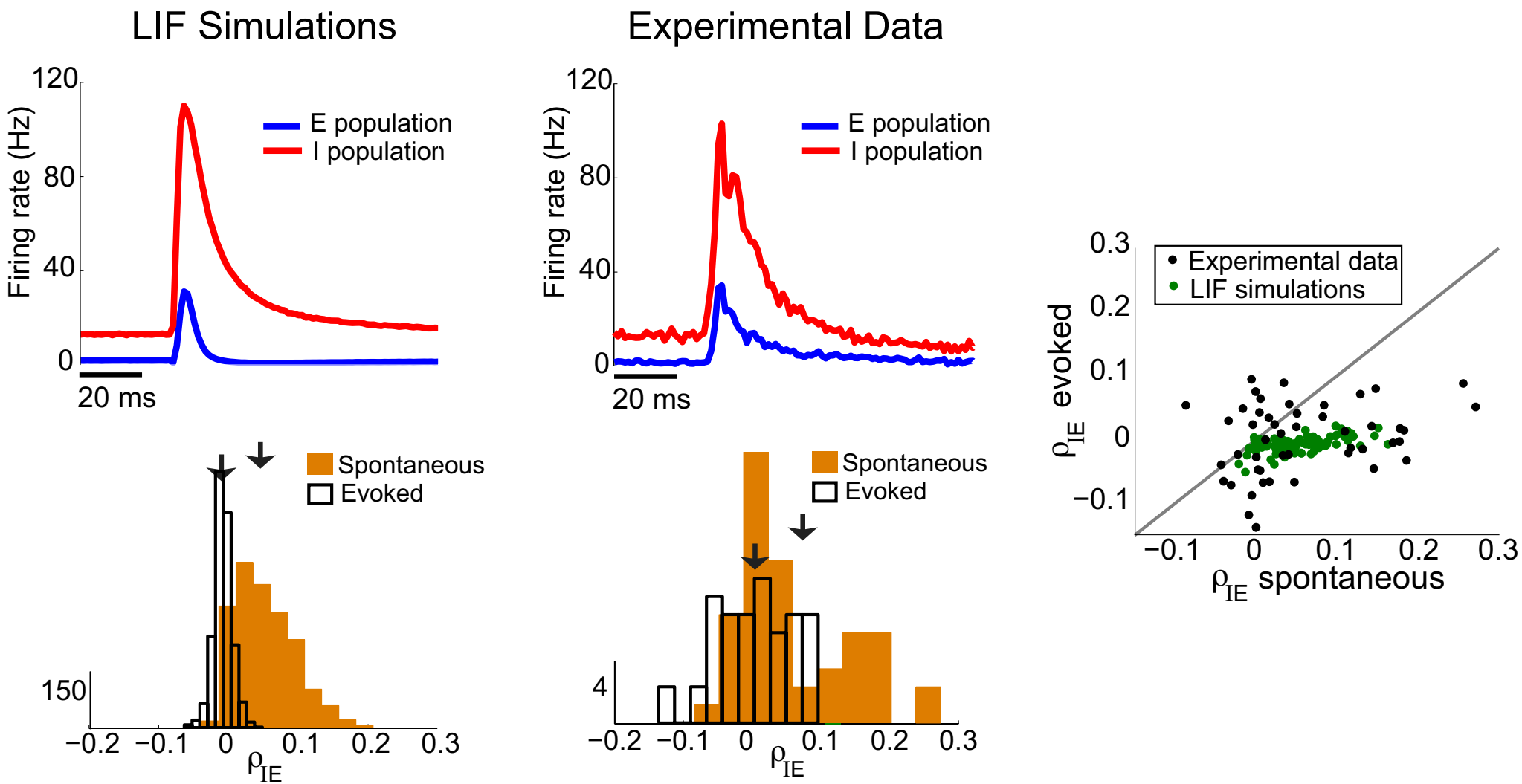
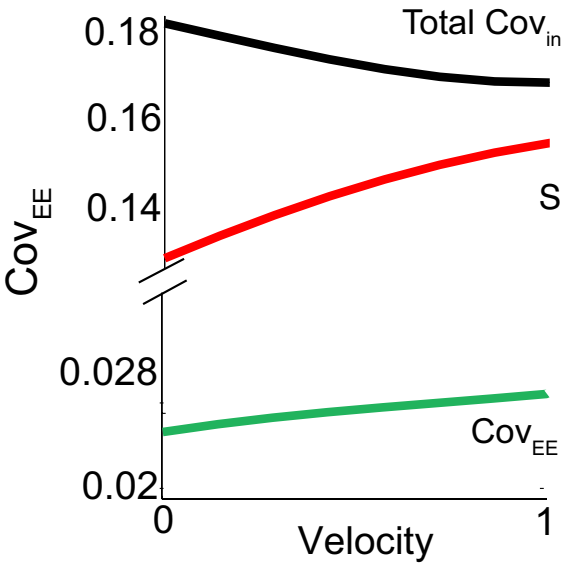


How does this scheme fit in with other work?



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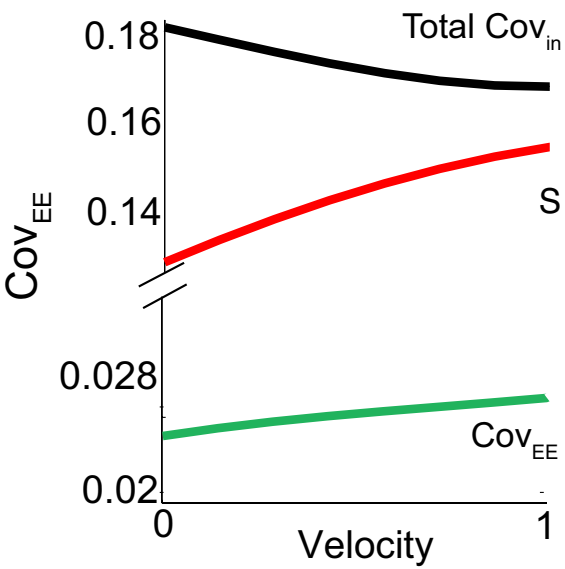

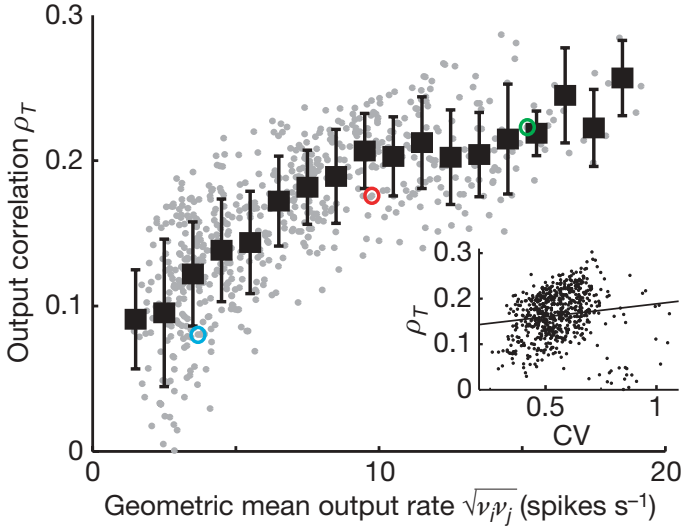

[No coupling]

Correlation between neural spike trains increases with firing rate.

de la Rocha, Doiron, et al., **Nature** 2007.

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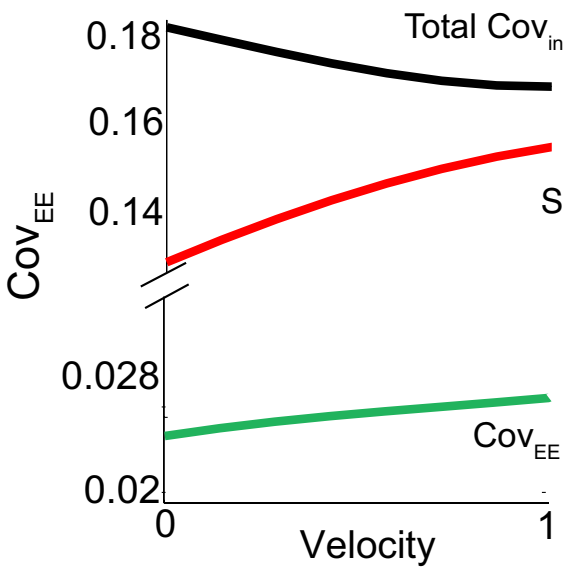

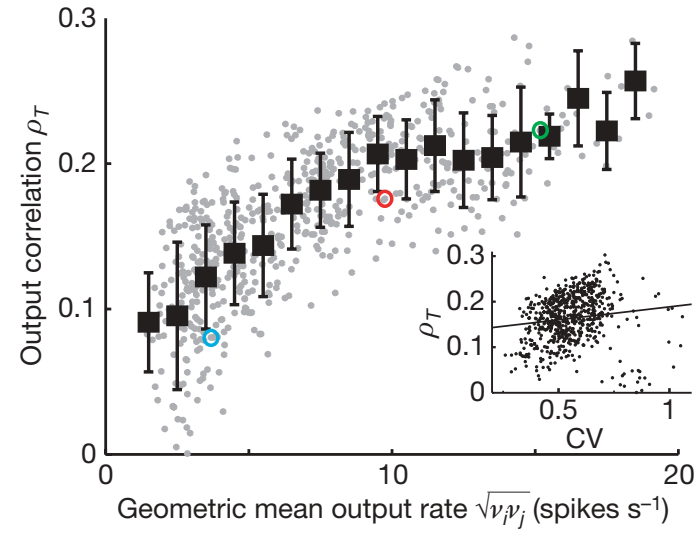

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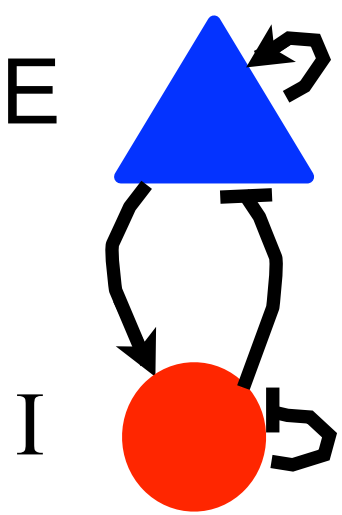

The Asynchronous State in Cortical Circuits.

Renart, et al., **Science** 2010.

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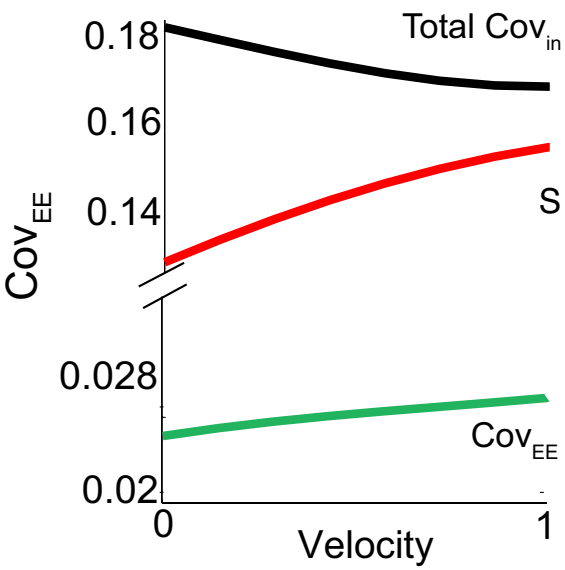

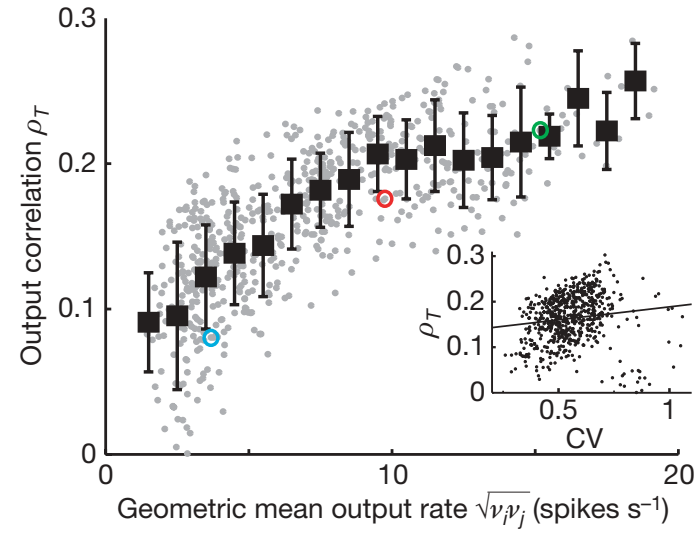

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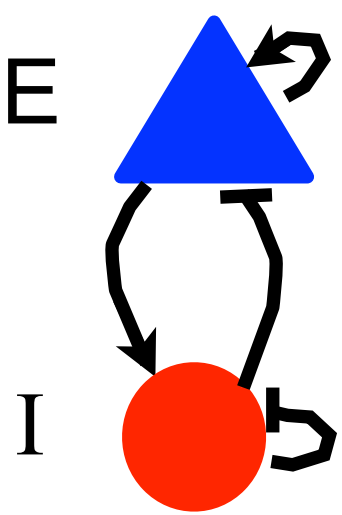

Cancellation of input correlation:

$$c = \underbrace{c_{EE}}_{>0} + \underbrace{c_{II}}_{>0} + \underbrace{2c_{EI}}_{<0}$$

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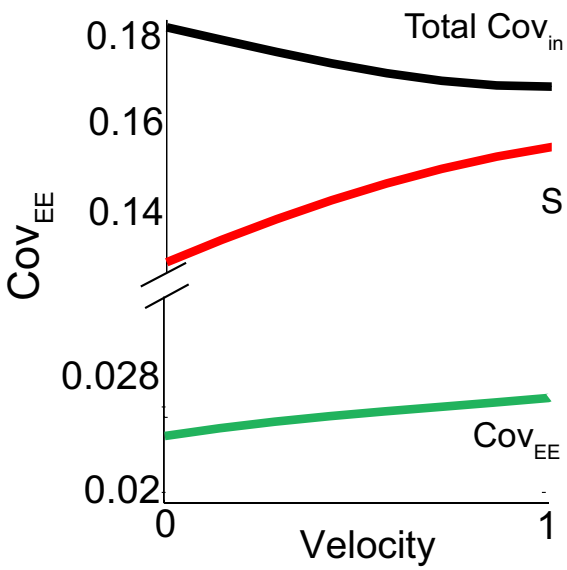

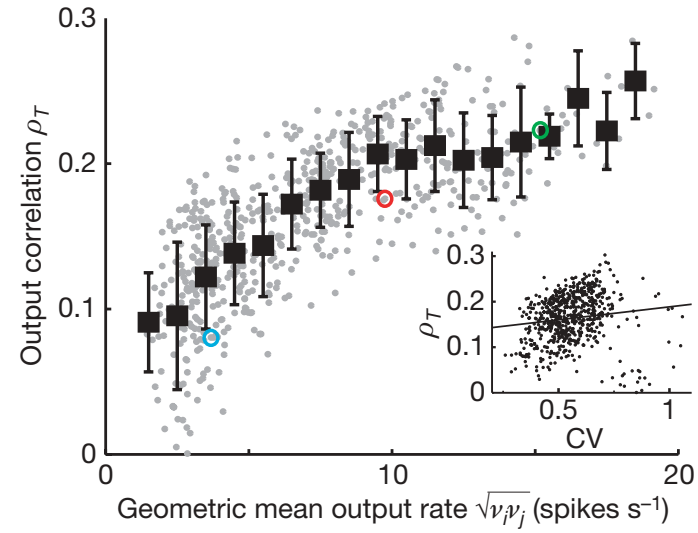

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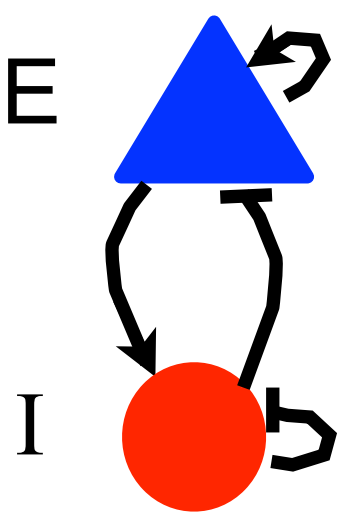

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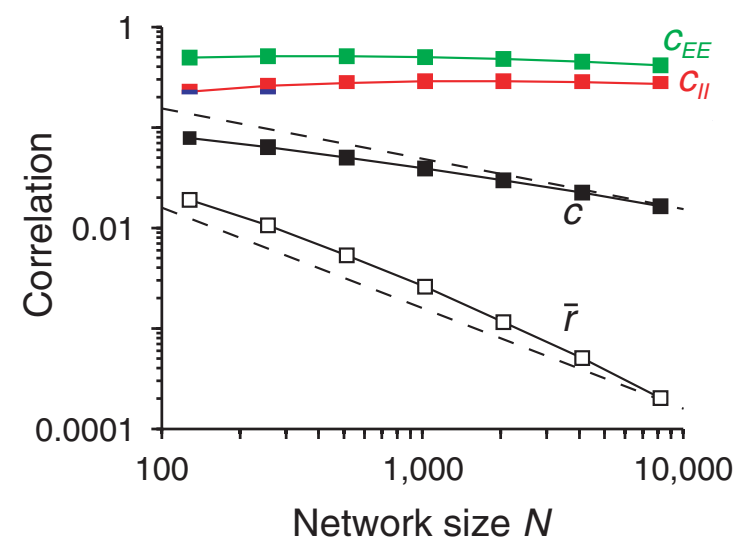

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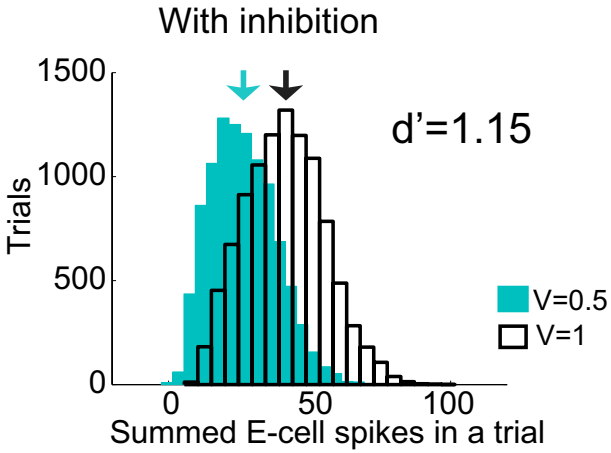
Low correlation enhances coding



$$\text{Code} = \sum_{i=1}^{N} w_i R_i(t)$$

$$d' = \frac{|\mu_1 - \mu_{0.5}|}{(\sigma_1 + \sigma_{0.5})/2}$$

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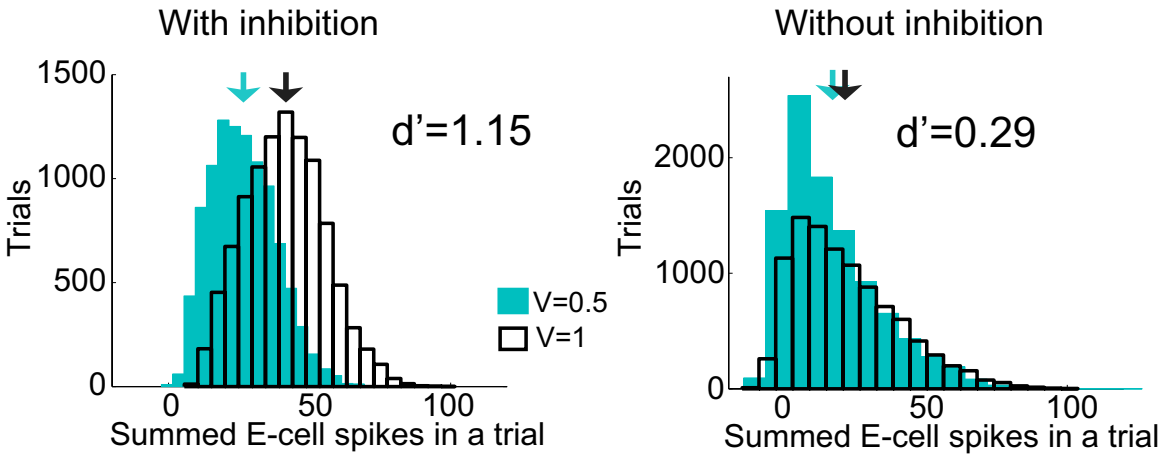

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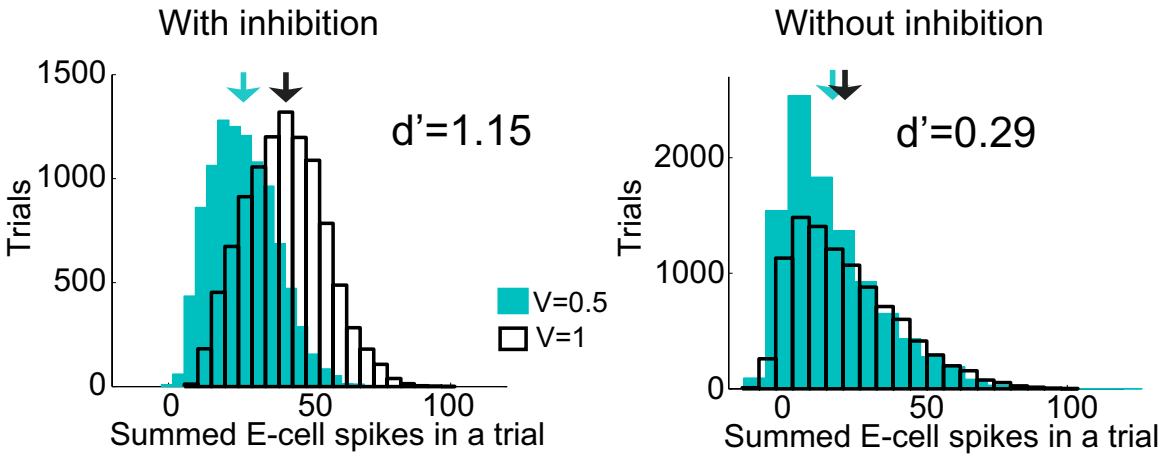

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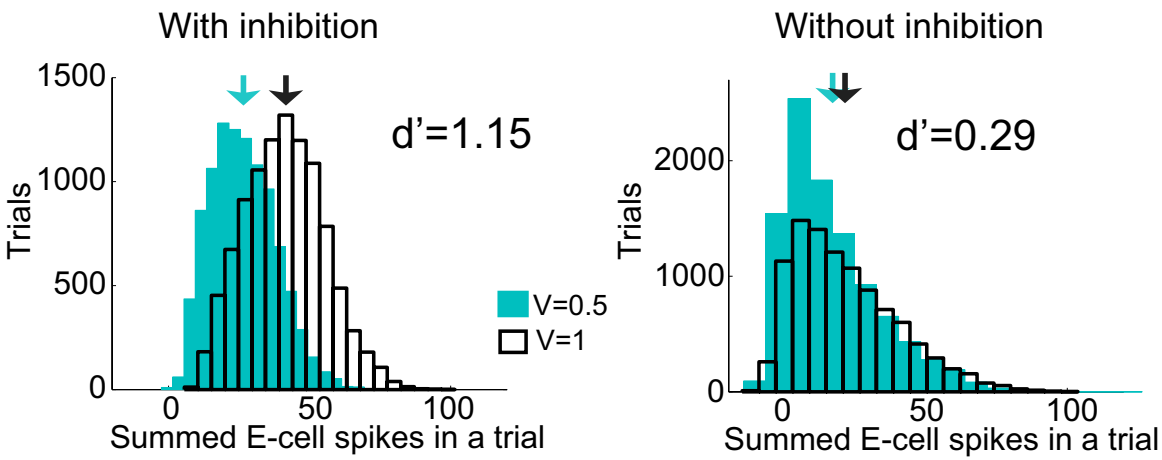
Fisher Information:

$$J = \mathbf{r}'^T_E Q^{-1} \mathbf{r}'_E$$

Low correlation enhances coding



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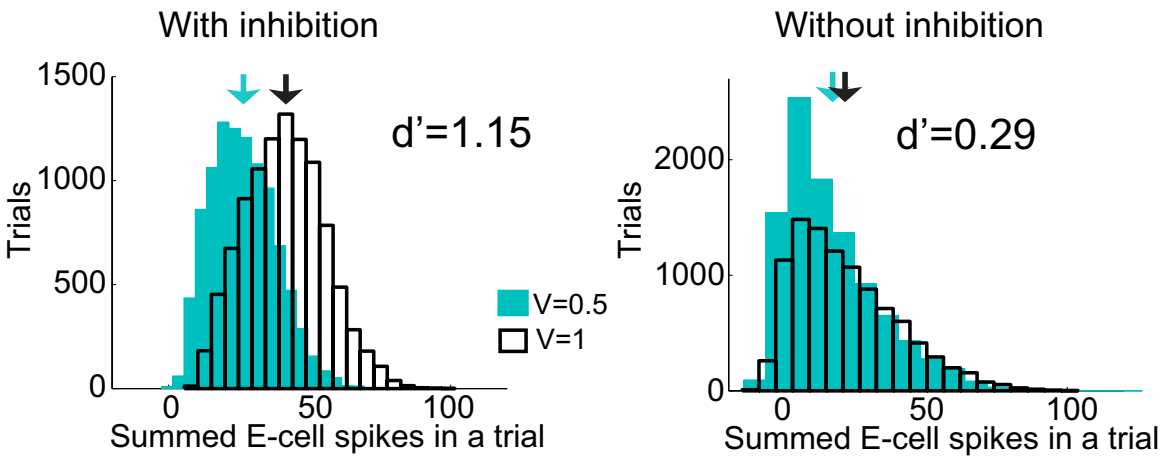

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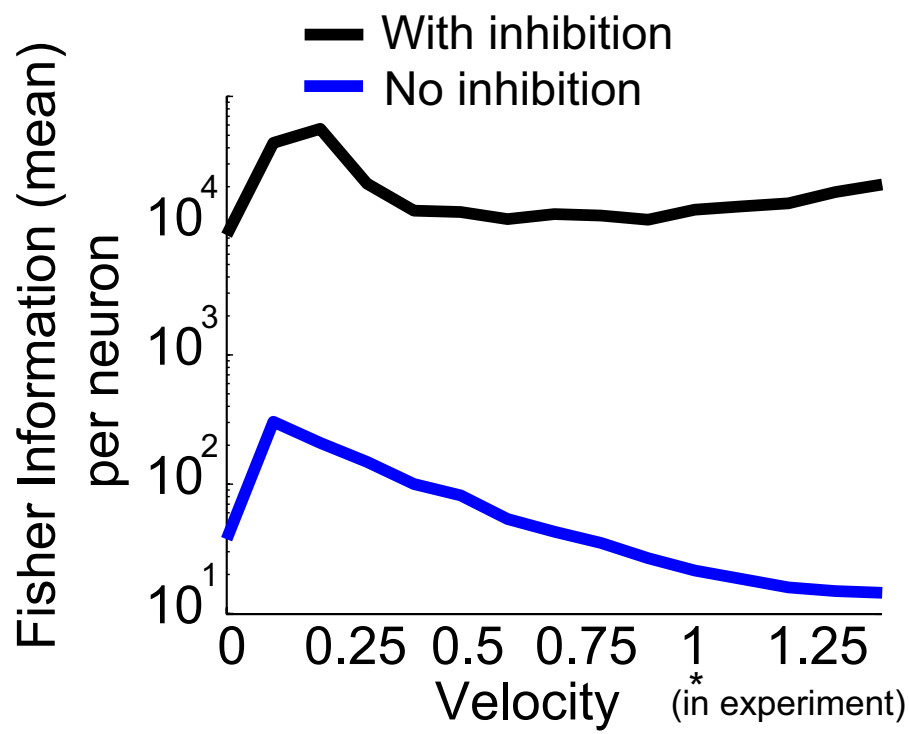

Conclusions

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- Have a better understanding of how neural networks encode information efficiently to higher layers.

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- Sloan Fellowship (Brent Doiron).
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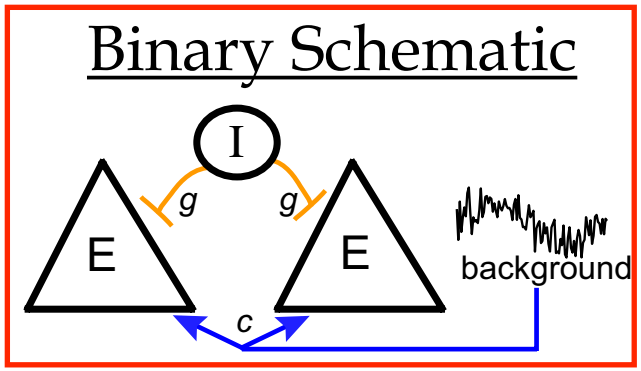
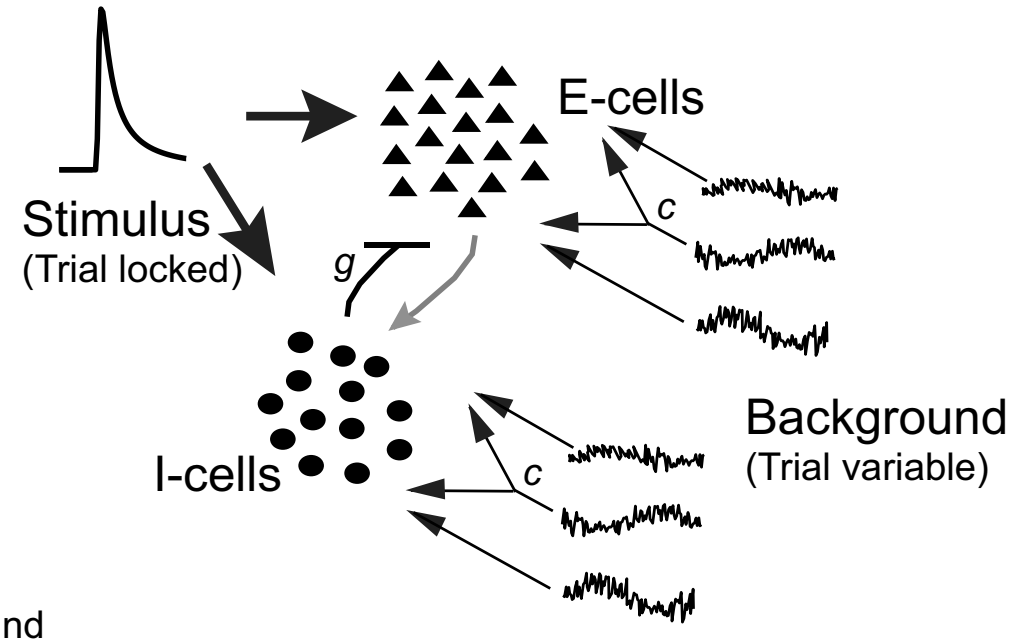
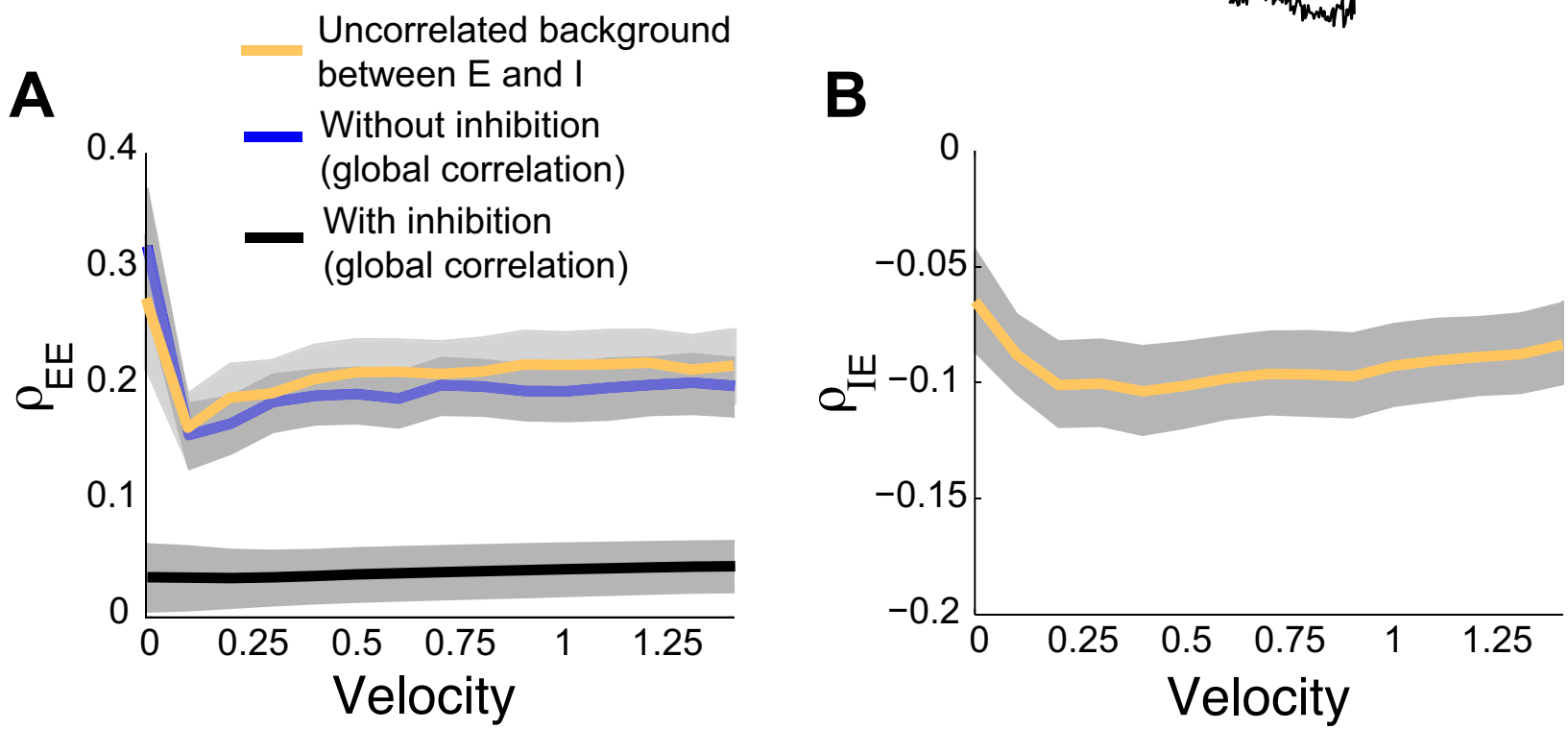
- CIHR Postdoctoral Fellowship (Jason Middleton).



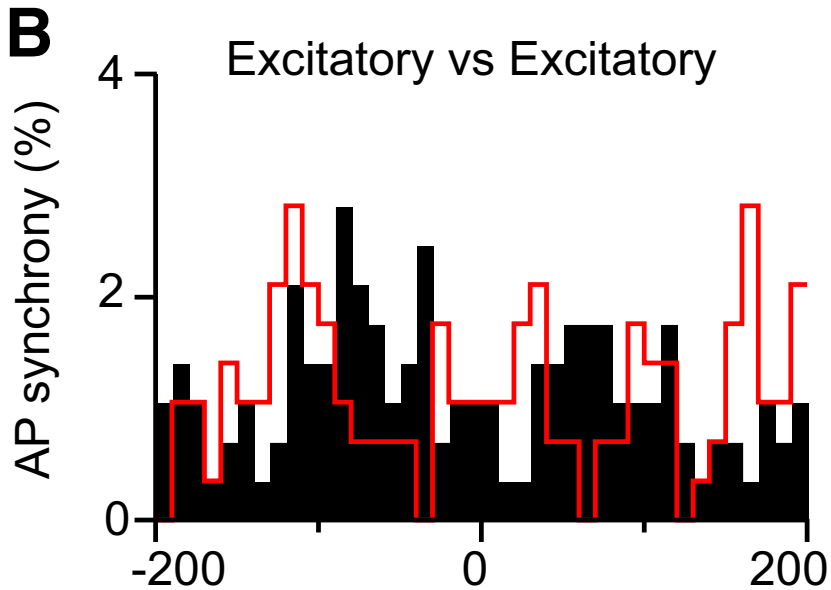
Uncorrelated background between E and I:

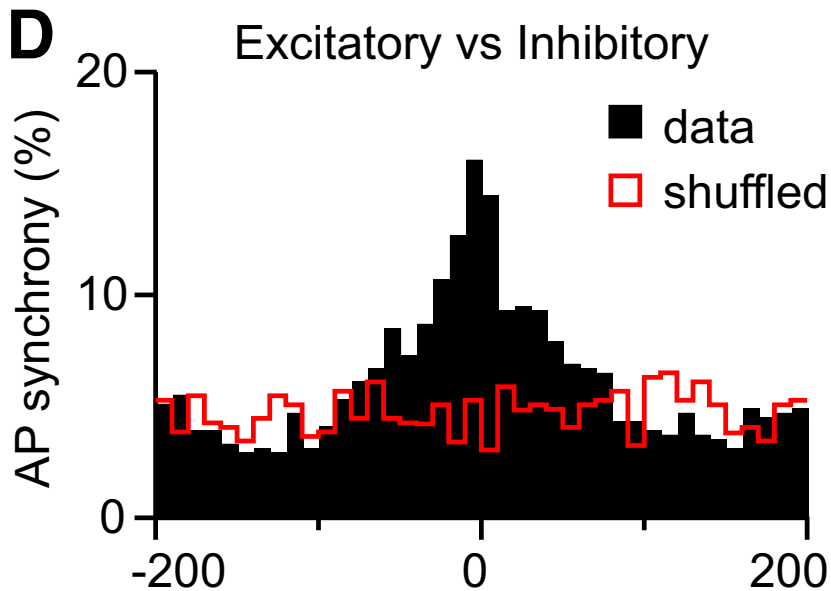




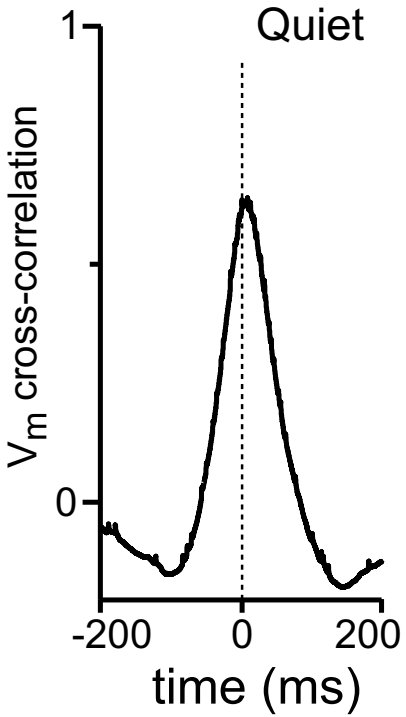
Petersen's Data

Spike count cross-correl.





Excit. & Inihib. (FS) input correl.



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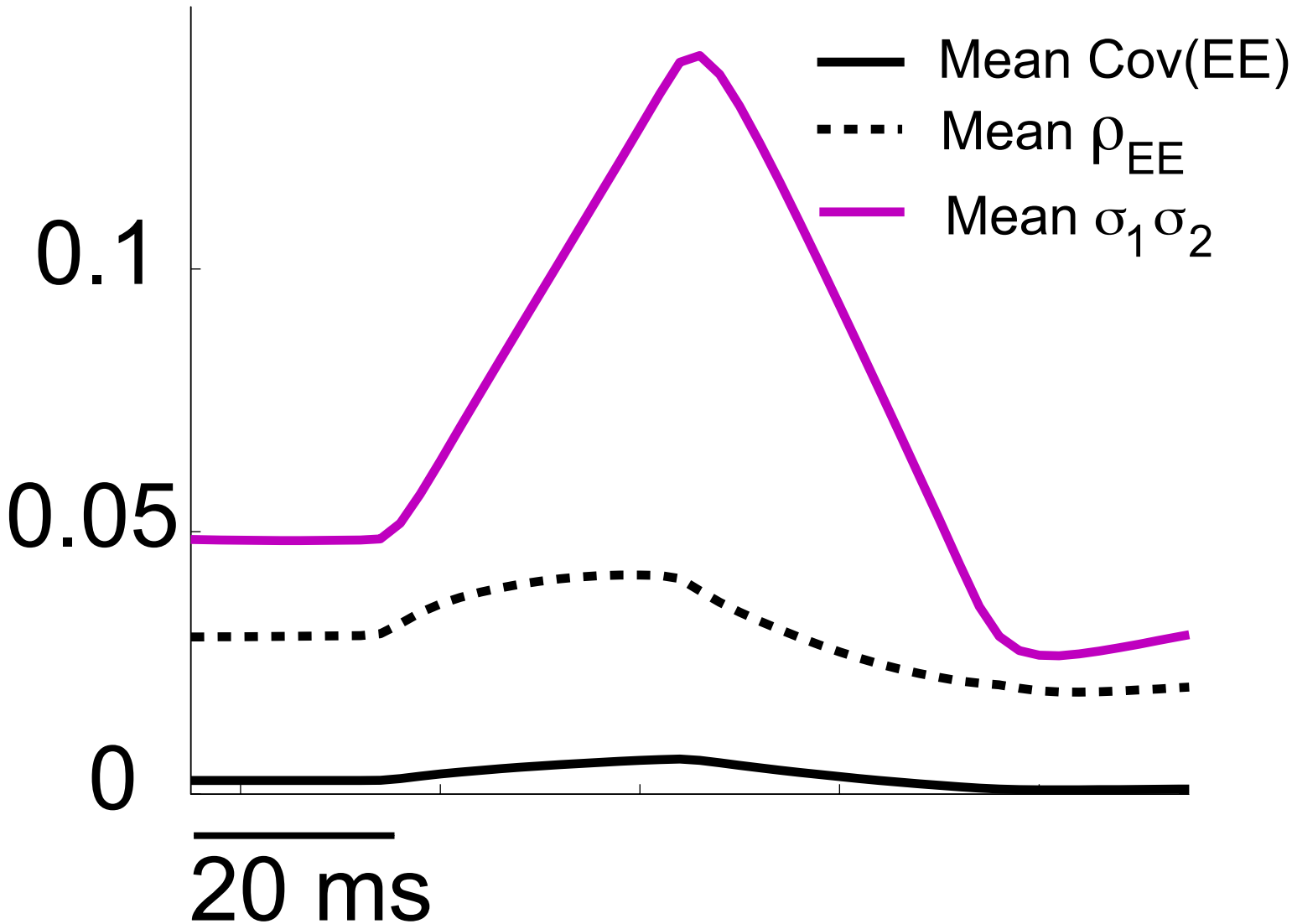
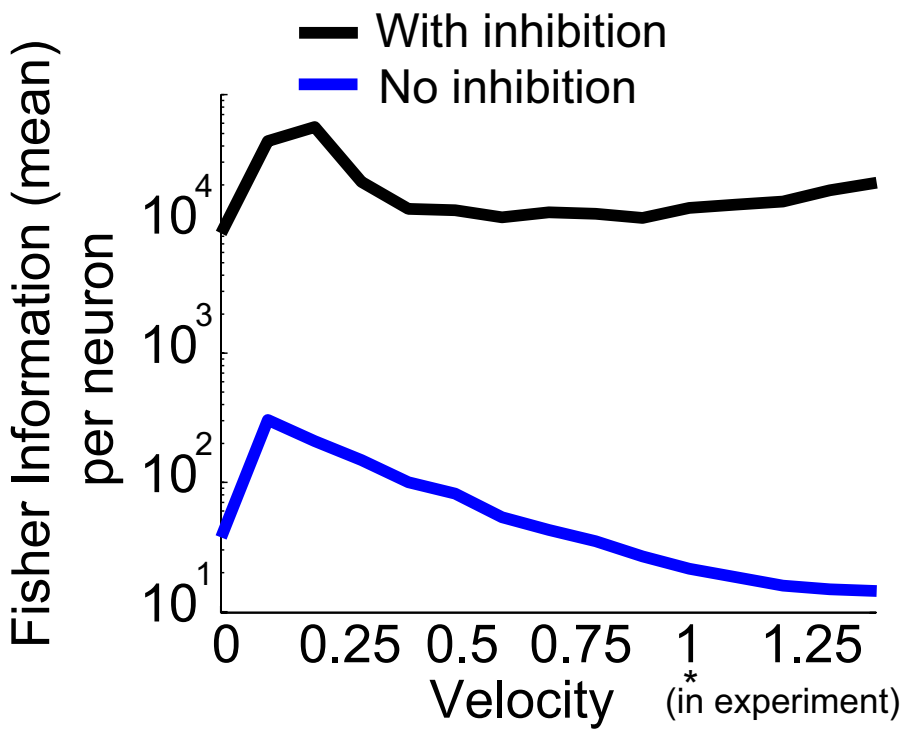
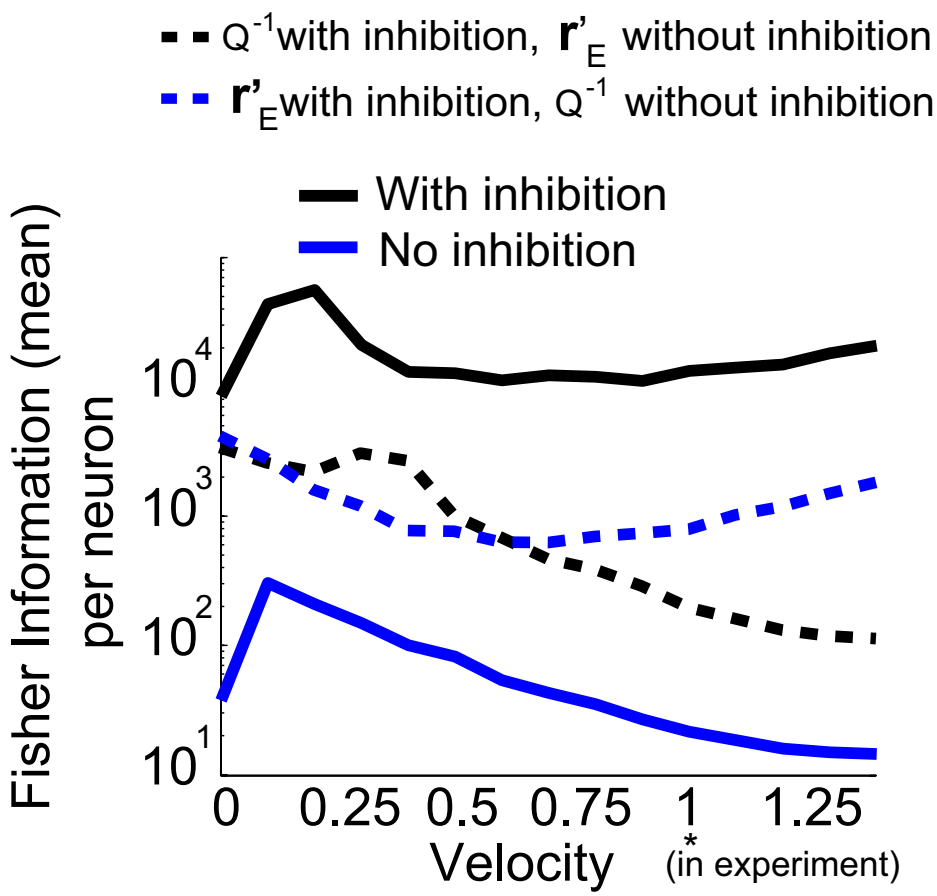

Mean Cov(EE)
Mean ρ_{EE}
Mean $\sigma_1\sigma_2$
0.1
0.05
0
20 ms


With inhibition
No inhibition
Fisher Information (mean)
per neuron
10^4
10^3
10^2
10^1
0
0.25
0.5
0.75
1
1.25
Velocity
*
(in experiment)


Q-1 with inhibition, r'E without inhibition
r'E with inhibition, Q-1 without inhibition
With inhibition
No inhibition
Fisher Information (mean)
per neuron
10^4
10^3
10^2
10^1
0
0.25
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Velocity
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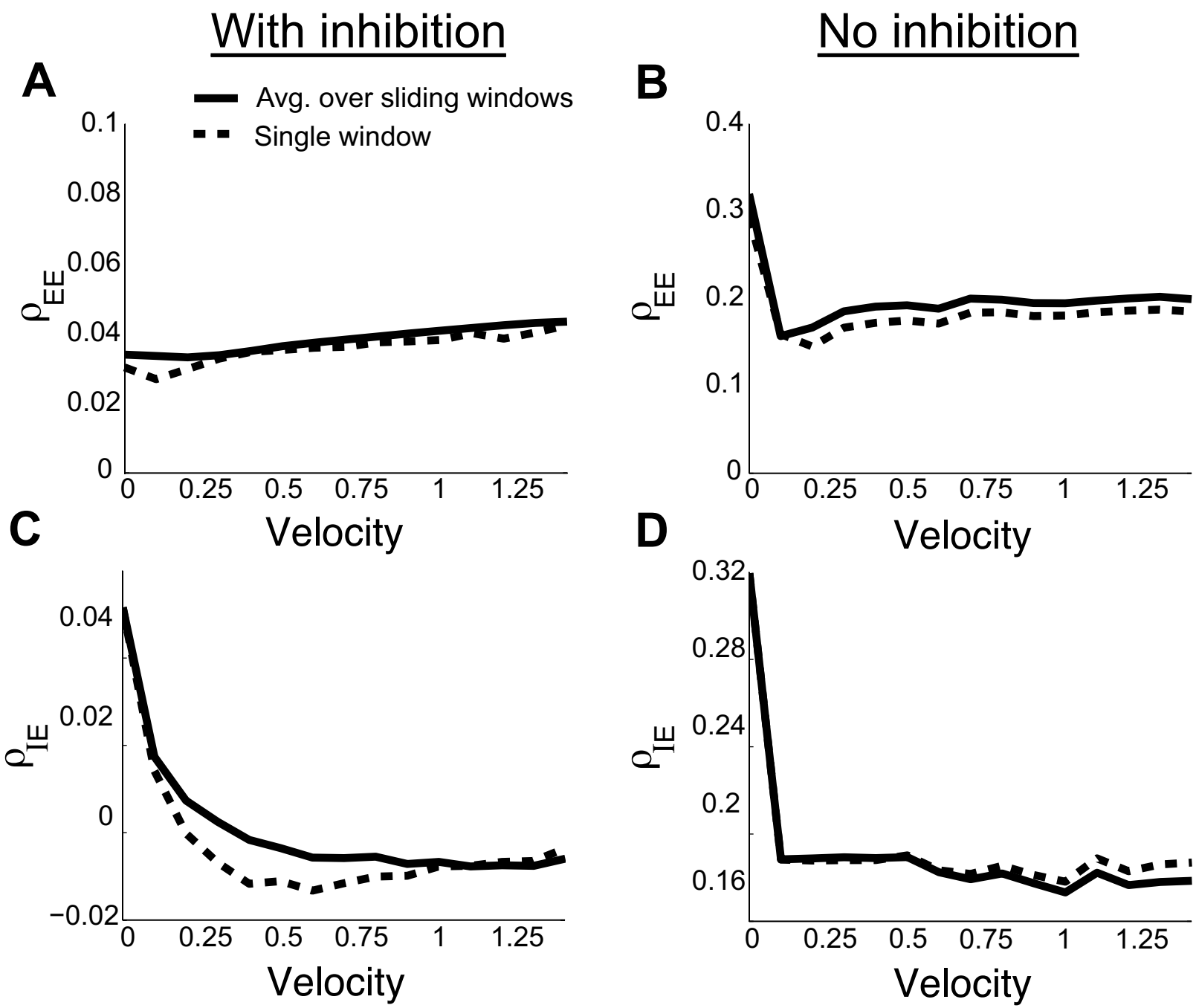
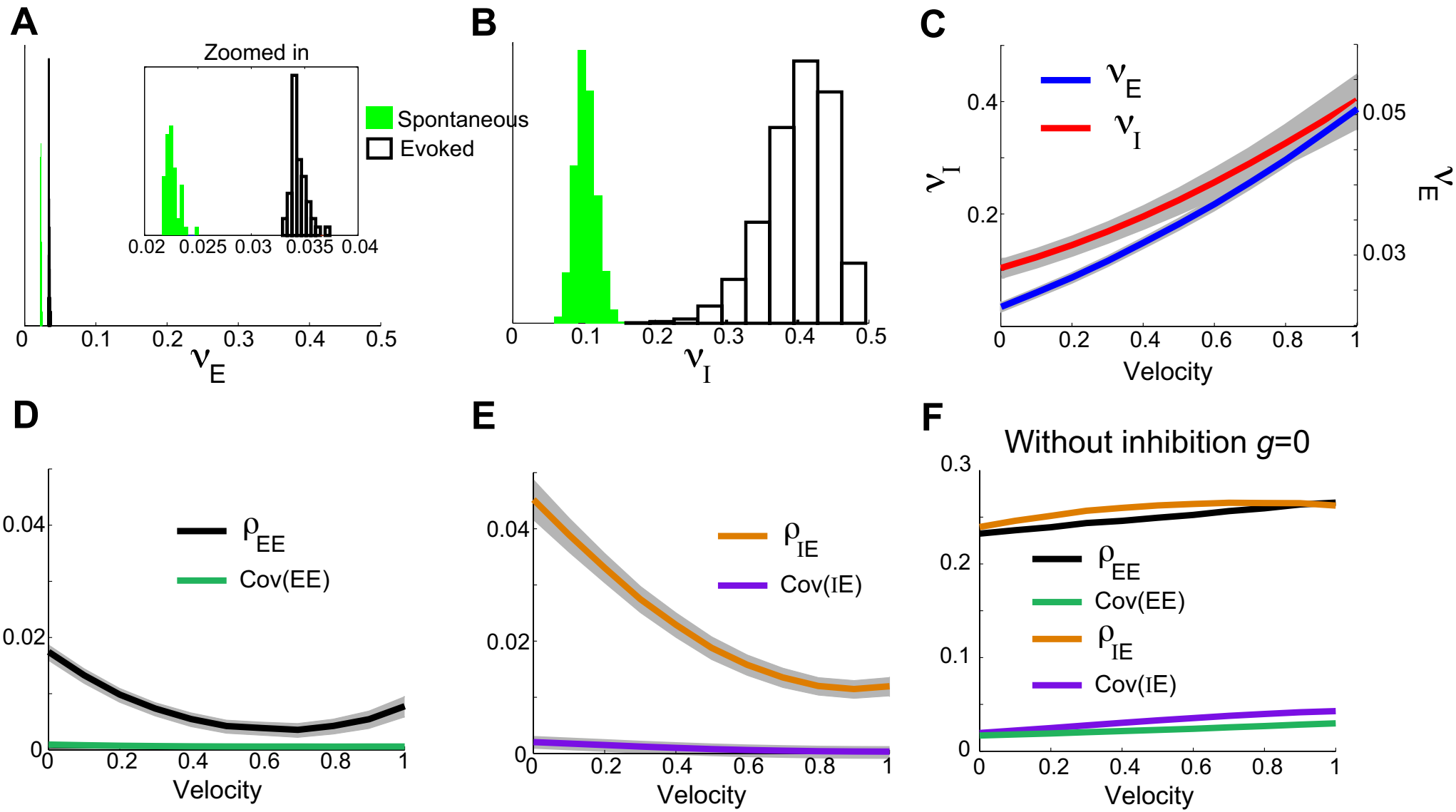

With inhibition
No inhibition
A
B
C
D
Avg. over sliding windows
Single window
ρ_{EE}
ρ_{IE}
Velocity
0.1
0.08
0.06
0.04
0.02
0
0.4
0.3
0.2
0.1
0.32
0.28
0.24
0.16
−0.02
0.25
0.5
0.75
1
1.25

Large Binary Network