BioE332 Lecture 3: Balanced networks

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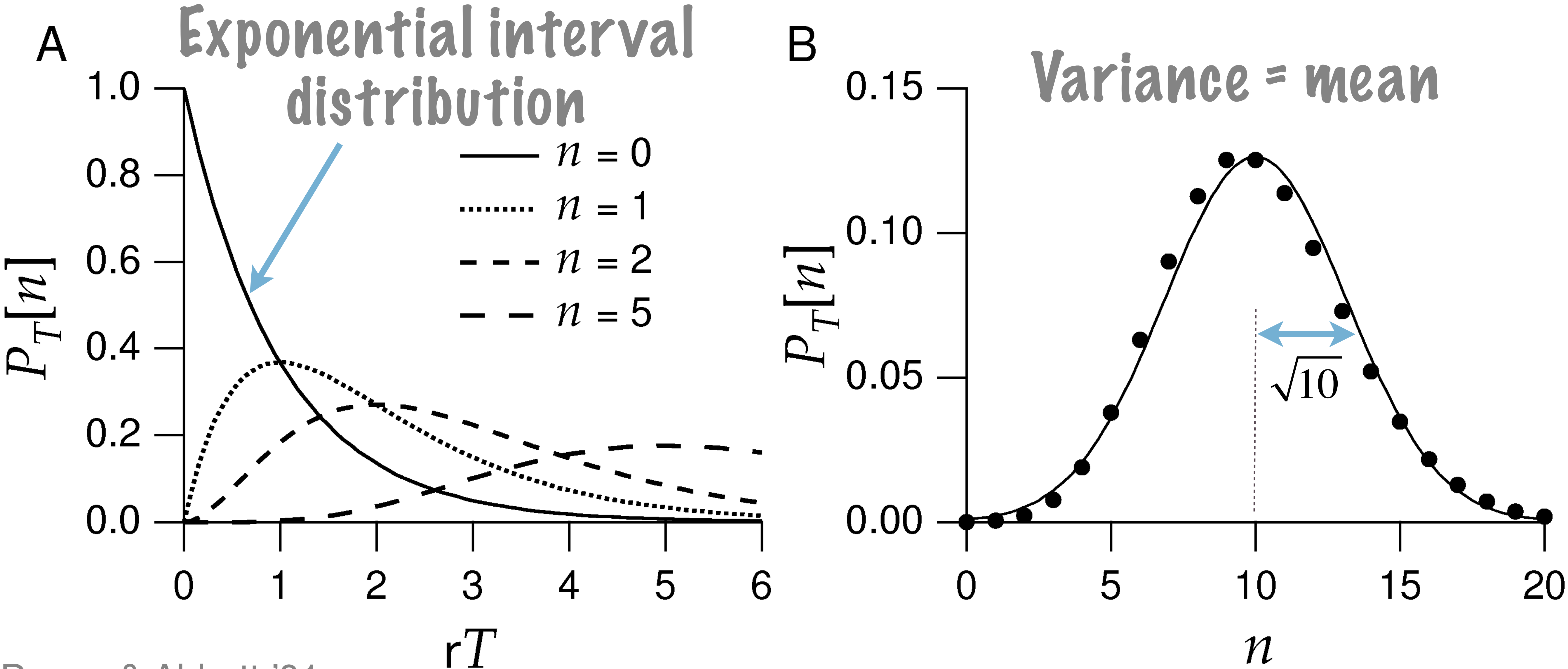
Poisson process



Dayan & Abbott '01

A: Probability that 0, 1, 2, and 5 spikes occur in a period T when the mean rate is r.

B: Probability n spikes occur in a period T=10/r — approximately Gaussian for rT>>1.

Defining properties

* Event counts' variability is measured by:

$$\text{Fano factor} \equiv \frac{\sigma_n^2}{\langle n \rangle}$$

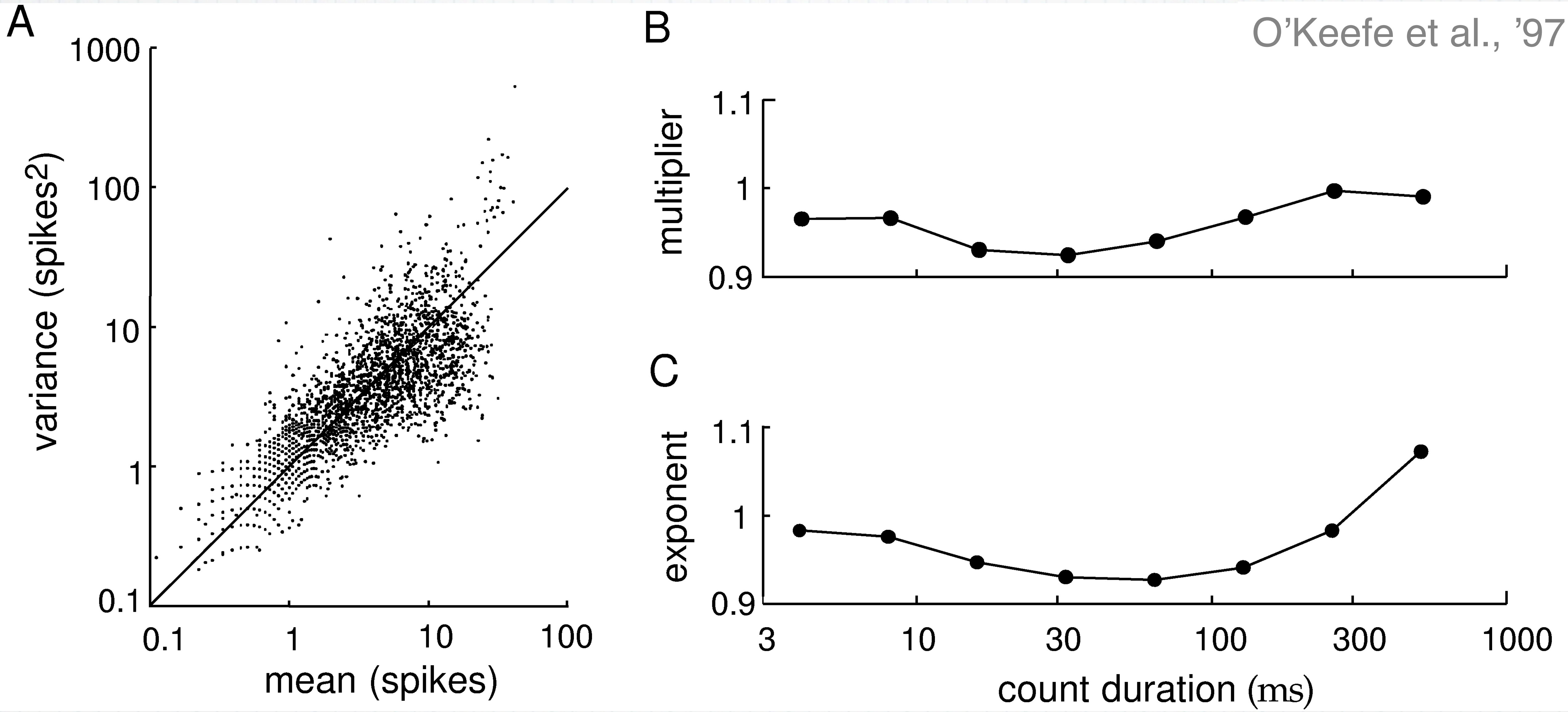
* Event intervals' variability is measured by:

$$\text{CV} \equiv \frac{\sigma_\tau}{\langle \tau \rangle}$$

* For a Poisson process:

$$\sigma_n^2 = \langle n \rangle = rT \qquad \langle \tau \rangle = \frac{1}{r} \text{ and } \sigma_\tau^2 = \frac{1}{r^2}$$

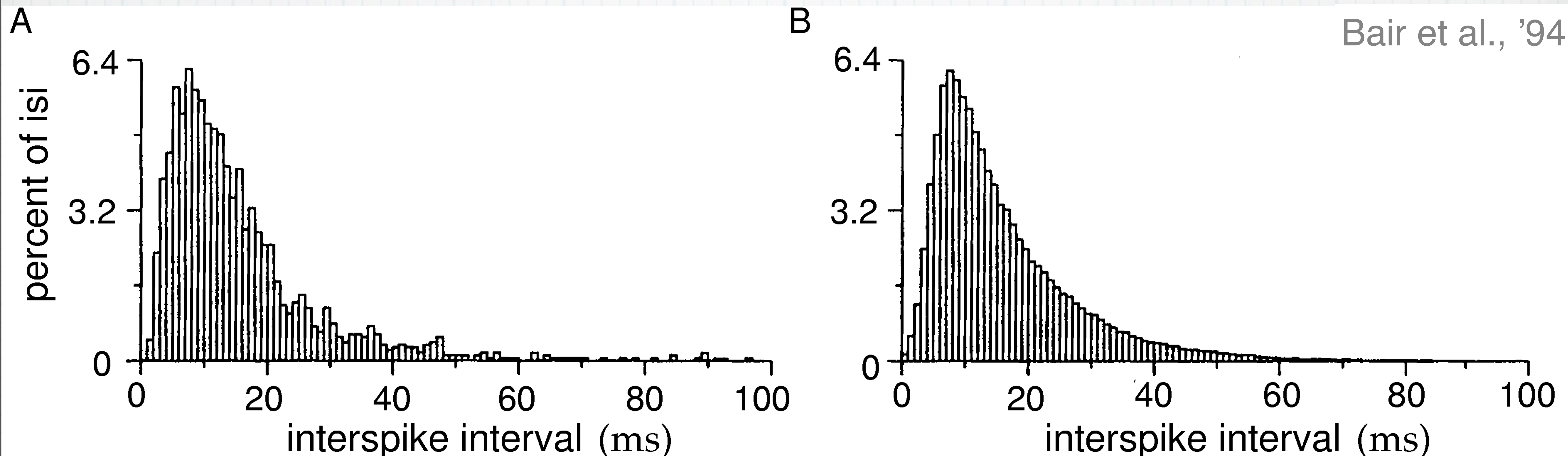
MT neurons spike-counts



A: Variance versus mean for spike counts in 256ms bins.
B,C: Multiplier and exponent for bins of different sizes.

* Spikes counts of responses to moving images are Poissonian (alert macaque).

MT neuron spike-intervals



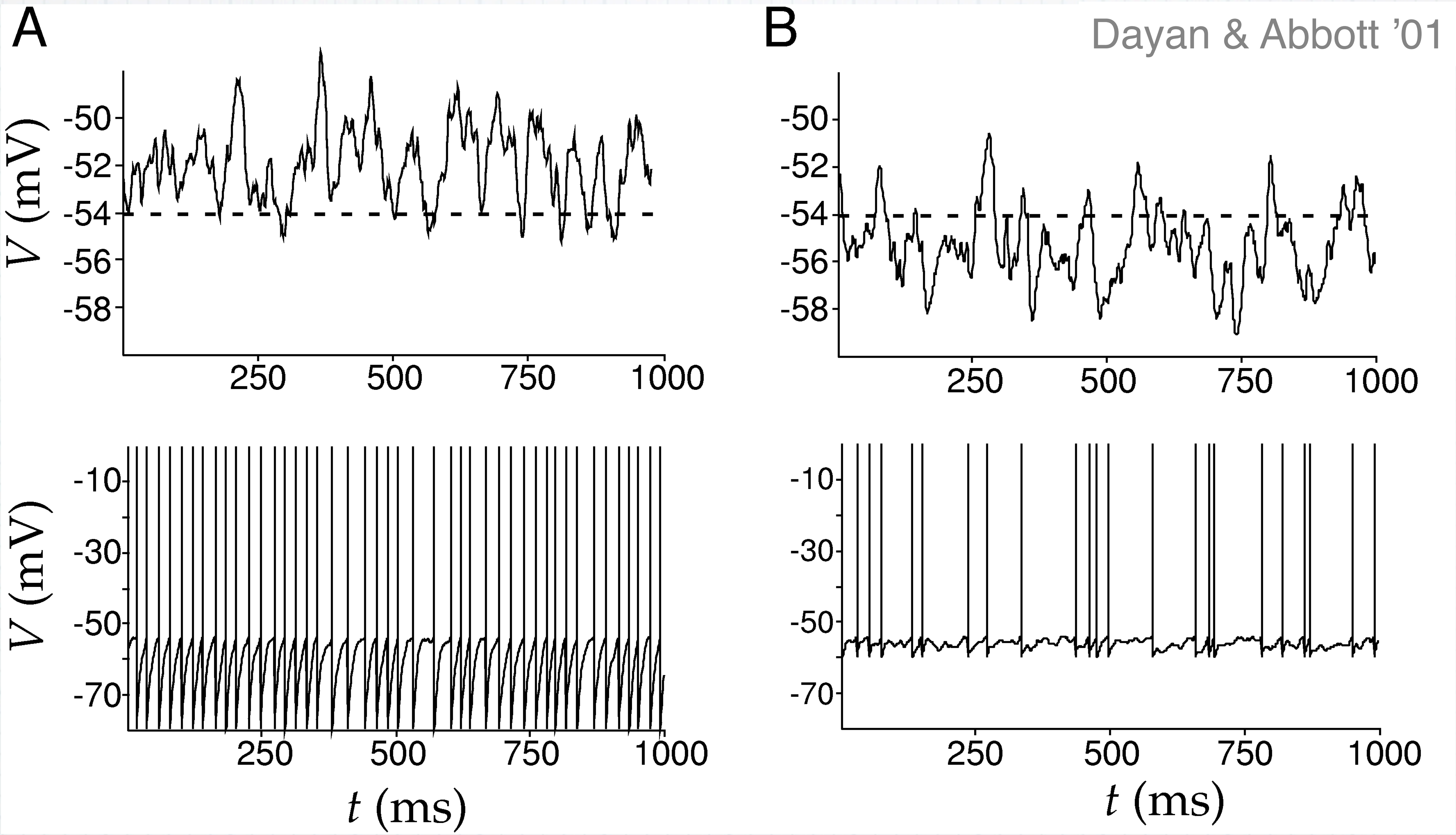
A: Measured interspike interval distribution (non-bursty cell).
B: Poisson model with a stochastic refractory period (Gaussian with 5ms mean and 2ms SD).

* Interspike intervals are Poissonian, except for very short intervals — fit by including refractory period (or with Gamma distribution).

Balanced regime

* Excitatory and inhibitory inputs are balanced so as to keep the cell's average potential close to threshold.
* More formally, each cell is connected to K others, but sqrt(K) spikes suffice to bring it to threshold.
* In this regime, small fluctuations in the input drive spiking, and the firing pattern is strongly Poisson-like.
* Note that the network's connectivity must be random and sparse (K<<N, the total).

Integrate-and-fire model



Leaky integrate-and-fire neurons with noisy input can fire regularly (A) or irregularly (B). Depends on whether the mean free membrane potential (top) is above or below threshold.

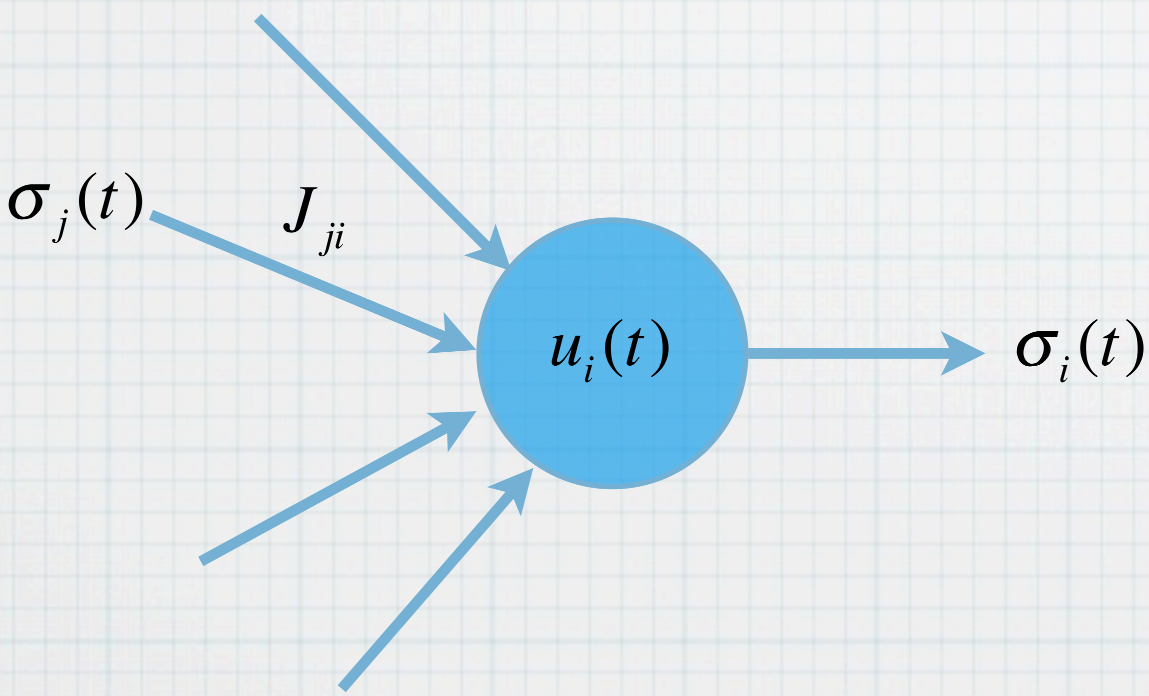
The question is:
"Can balance between excitation and inhibition emerge without fine tuning?"

Balanced network studies

* In networks of binary neurons, balance emerges dynamically through strong negative feedback, which also linearizes the response to external inputs (Van Vreeswijk & Sompolinsky '96, '98).
* In networks of leaky integrate-and-fire neurons with delta synapses, regular and irregular synchronous states exists, in addition to regular and irregular asynchronous states (Brunel '00).
* These four states also exists in networks of cortex-like locally connected random networks with alpha synapses (Mehring et al., 2003).

Binary neurons

- Binary-valued output (0 or 1) is updated by choosing neurons sequentially, in random order.
- Time between consecutive updates of a unit represents the membrane time constant (10ms).



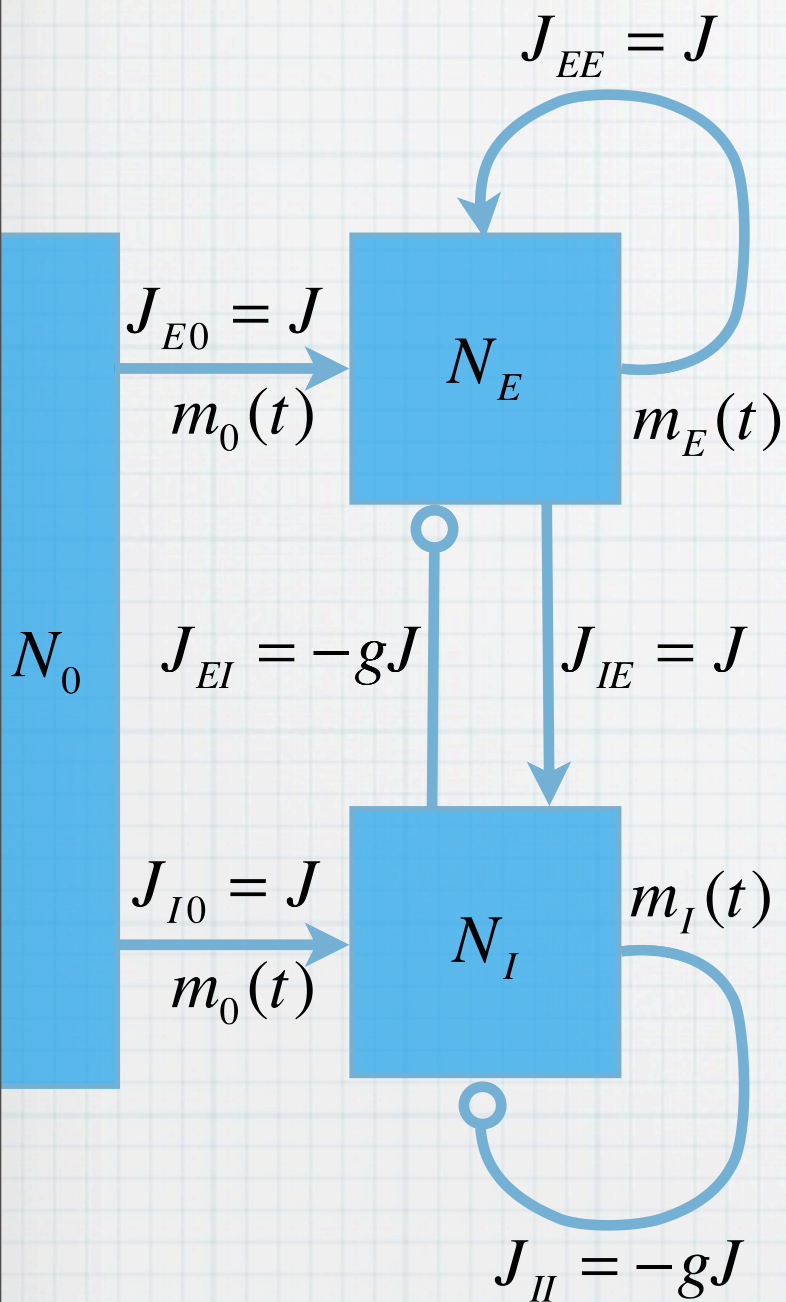
Neuron model

$$\sigma_i(t) = \Theta\big(u_i(t)\big) \text{ where } \Theta(x) \equiv \begin{cases} 1 \text{ if } x > 0 \\ 0 \text{ if } x \le 0 \end{cases}$$

Synapse model

$$u_i(t) = \sum_j J_{ij}\sigma_j(t) + u^0 - \theta$$

Binary neuron network



* Each neuron receives K excitatory, inhibitory, and K external connections, chosen randomly such that $K \ll N_E, N_I, N_0$.
* The threshold θ is chosen such that only √K excitatory inputs are required to cross it.
* The total synaptic current is approximately Gaussian with:

$$\mu_k(t) = K \sum_{l \in E,I,0} J_{kl} m_l(t) \qquad \sigma_k^2(t) = K \sum_{l \in E,I} (J_{kl})^2 m_l(t)$$

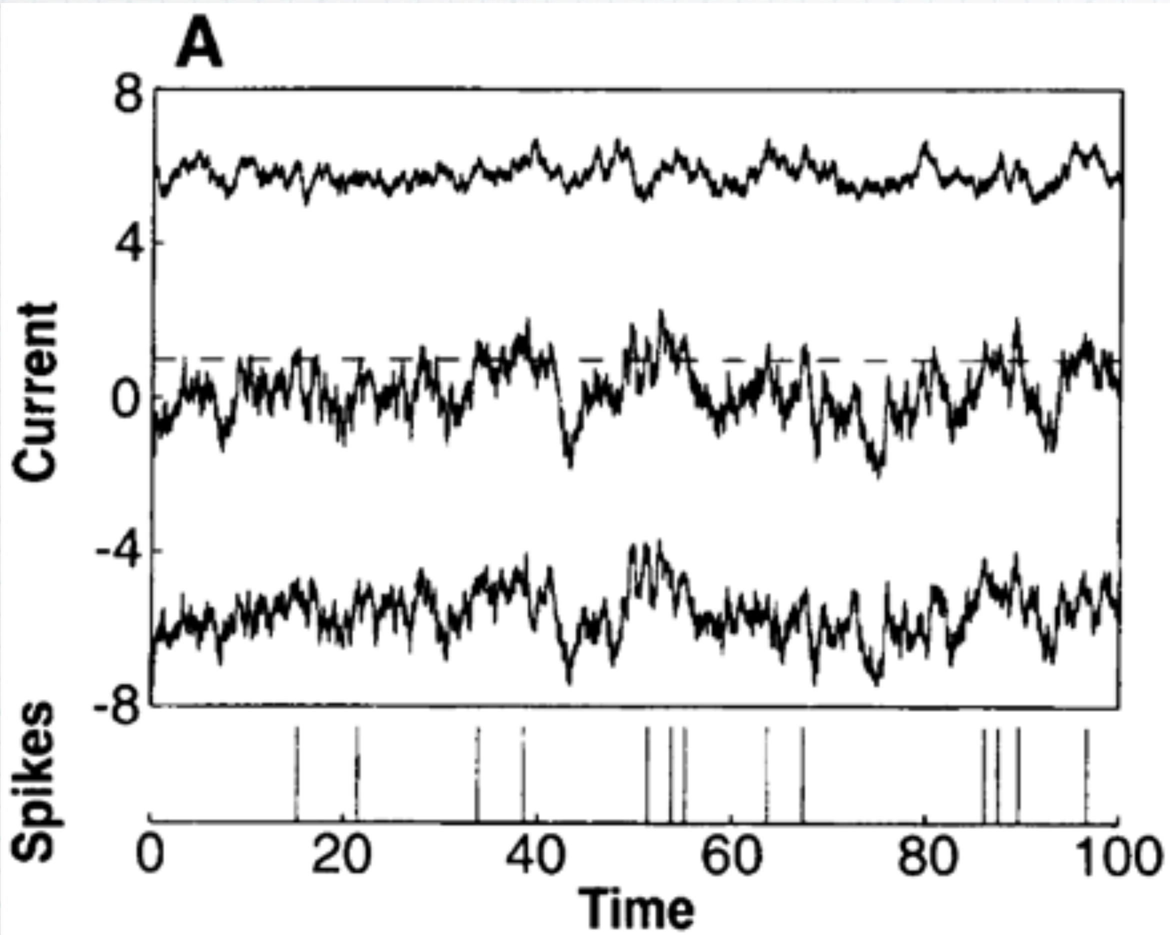
where $m_l(t)$ is the average activity of population l.

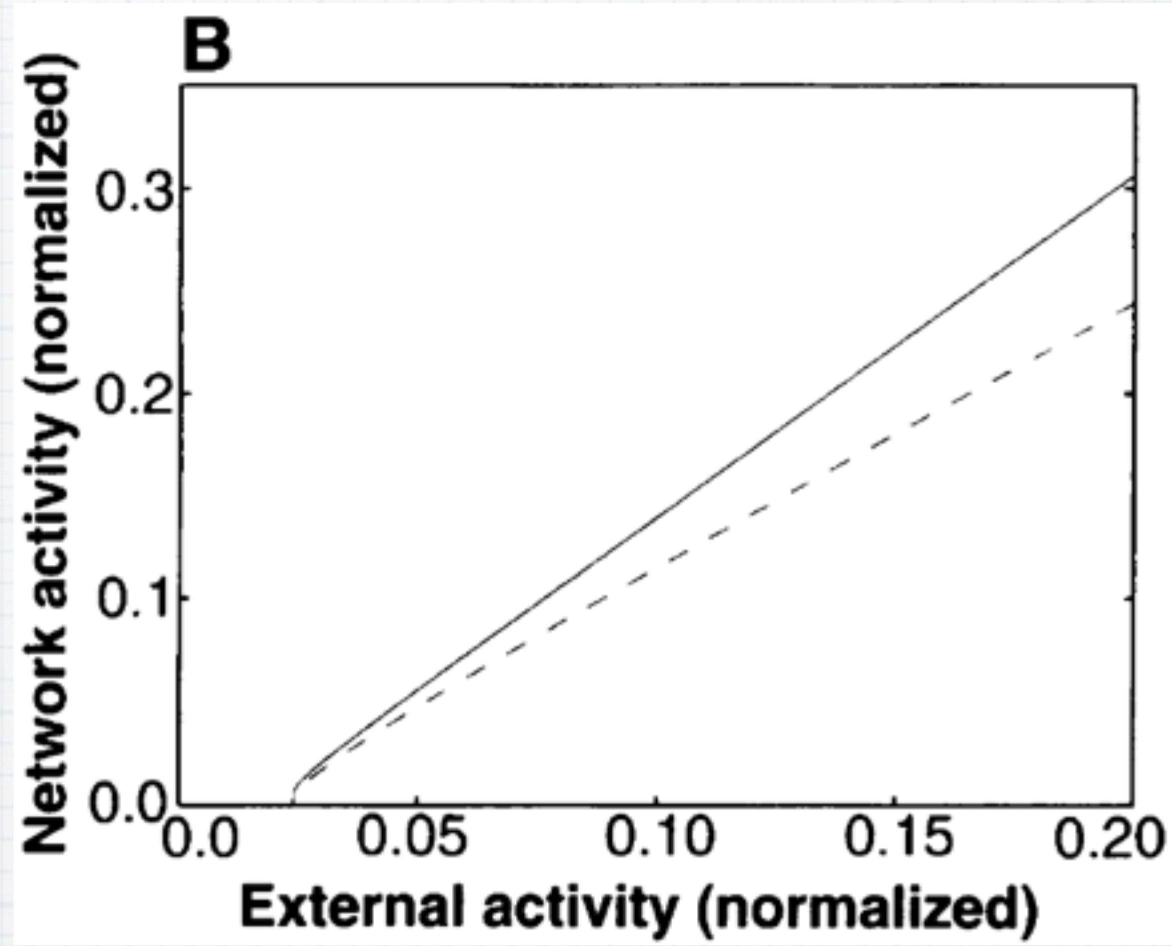
Parameters values

$$J \approx 1, g \approx 2, K = 1000, D = 0.3$$

$$\sqrt{K} < \theta_{E,I} < (1+D)\sqrt{K}$$

Model's balanced state

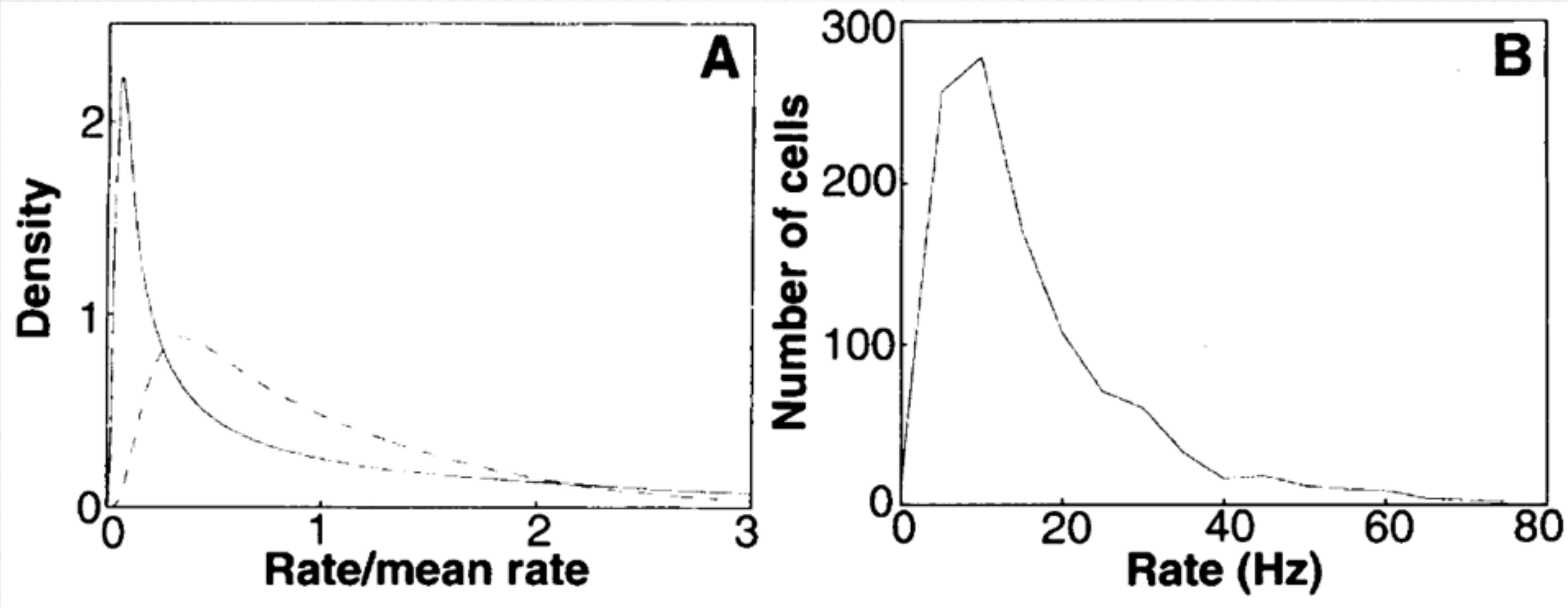




Top to bottom: Total excitatory input (external and feedback), net input, total inhibitory input, and a neuron's activity.

Mean activities of excitatory (solid line) and inhibitory (dashed line) units increase with mean activity of external units.

Firing-rate distribution



Distribution is long-tailed, more so for lower (solid line) than higher (dashed line) population-averaged rates (m_E=0.01,0.03).

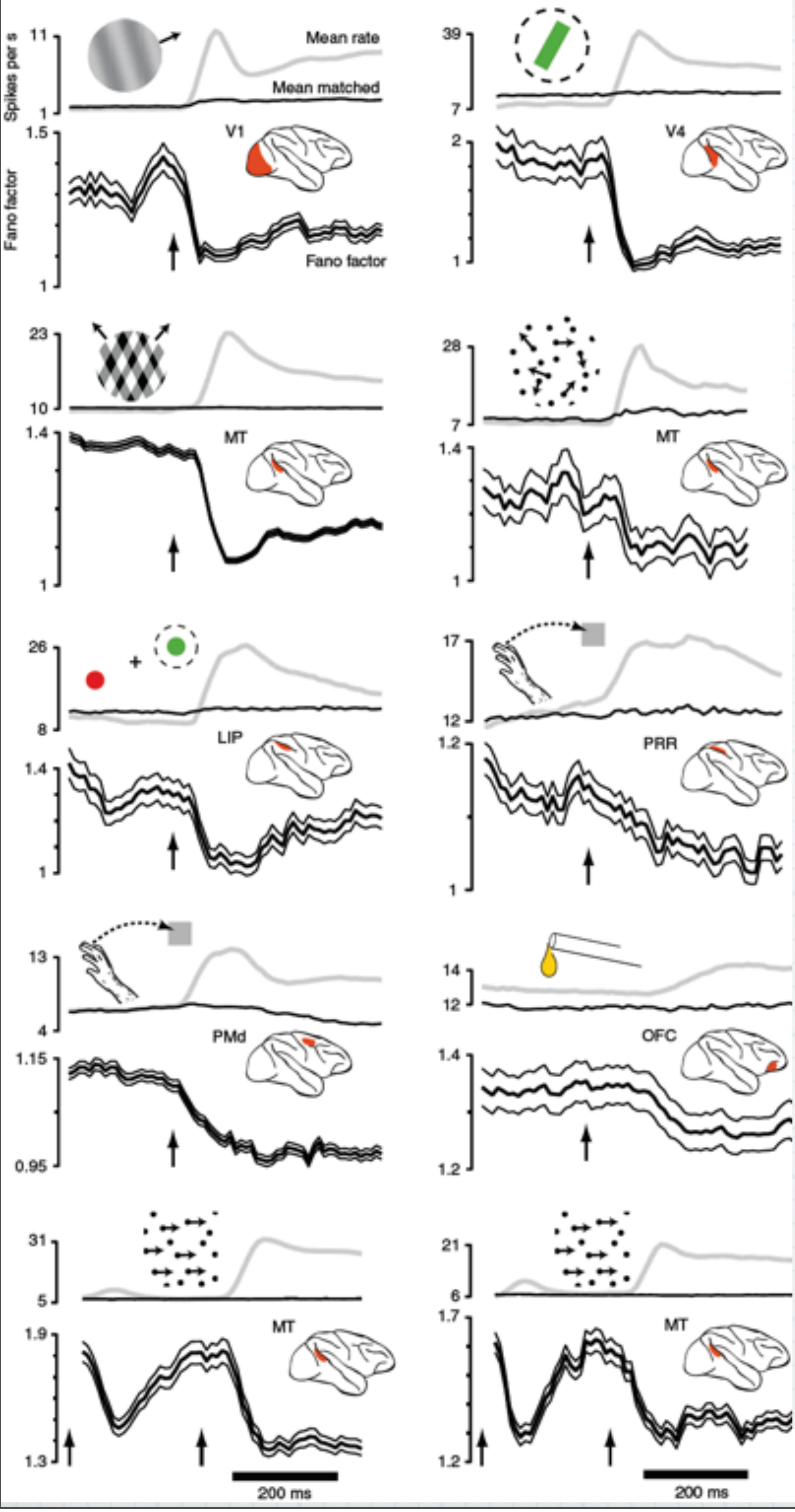
Distribution in prefrontal cortex neurons in a monkey attending to stimuli and executing reaching movements.

Is it fine-tuned?

* How much variation in threshold (relative to the total amount of input) can the model tolerate?

$$\varepsilon = \frac{D\sqrt{K}}{K} \approx \frac{1}{\sqrt{K}}$$

* This is 1% precision for K=10,000, the typical number of inputs a cortical cell receives.

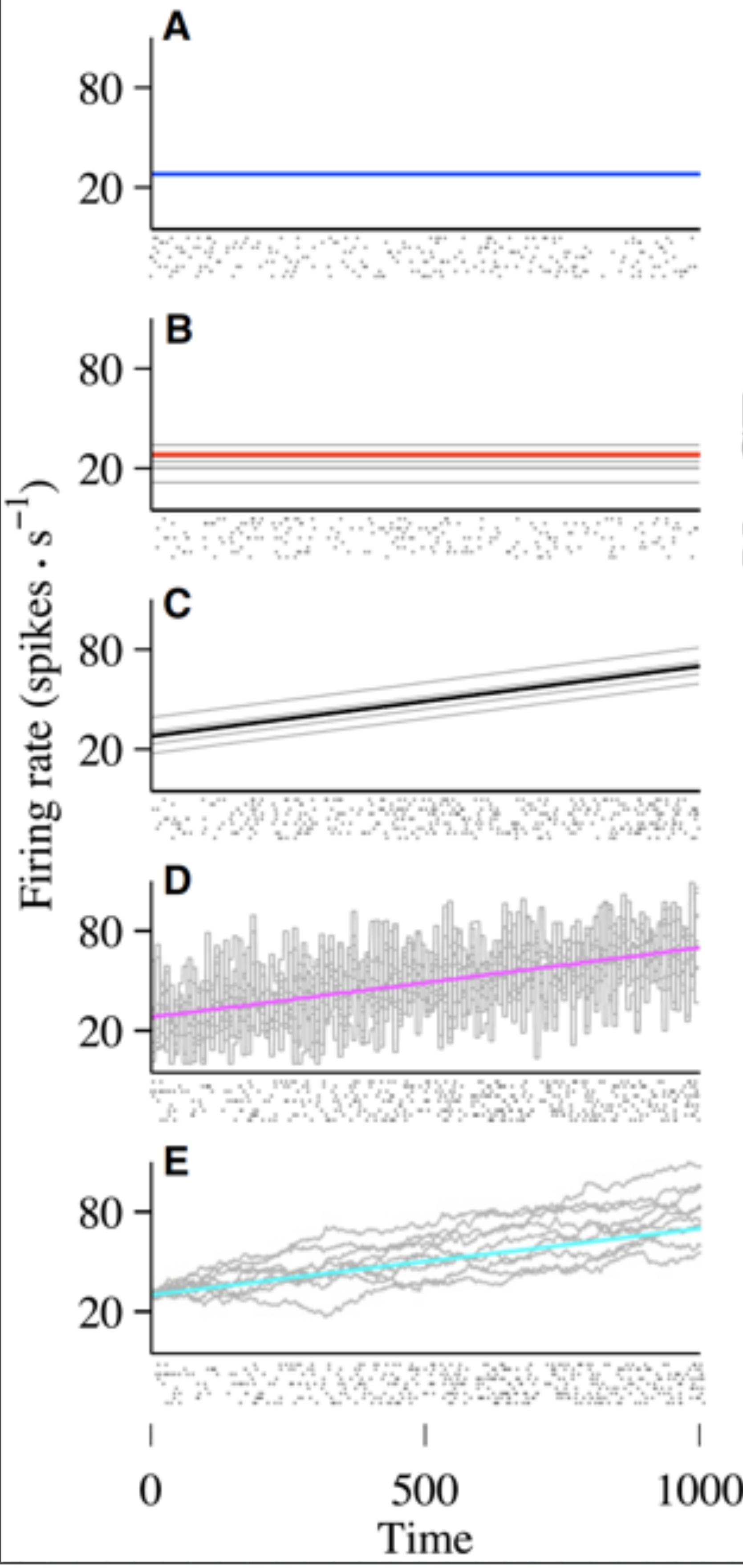


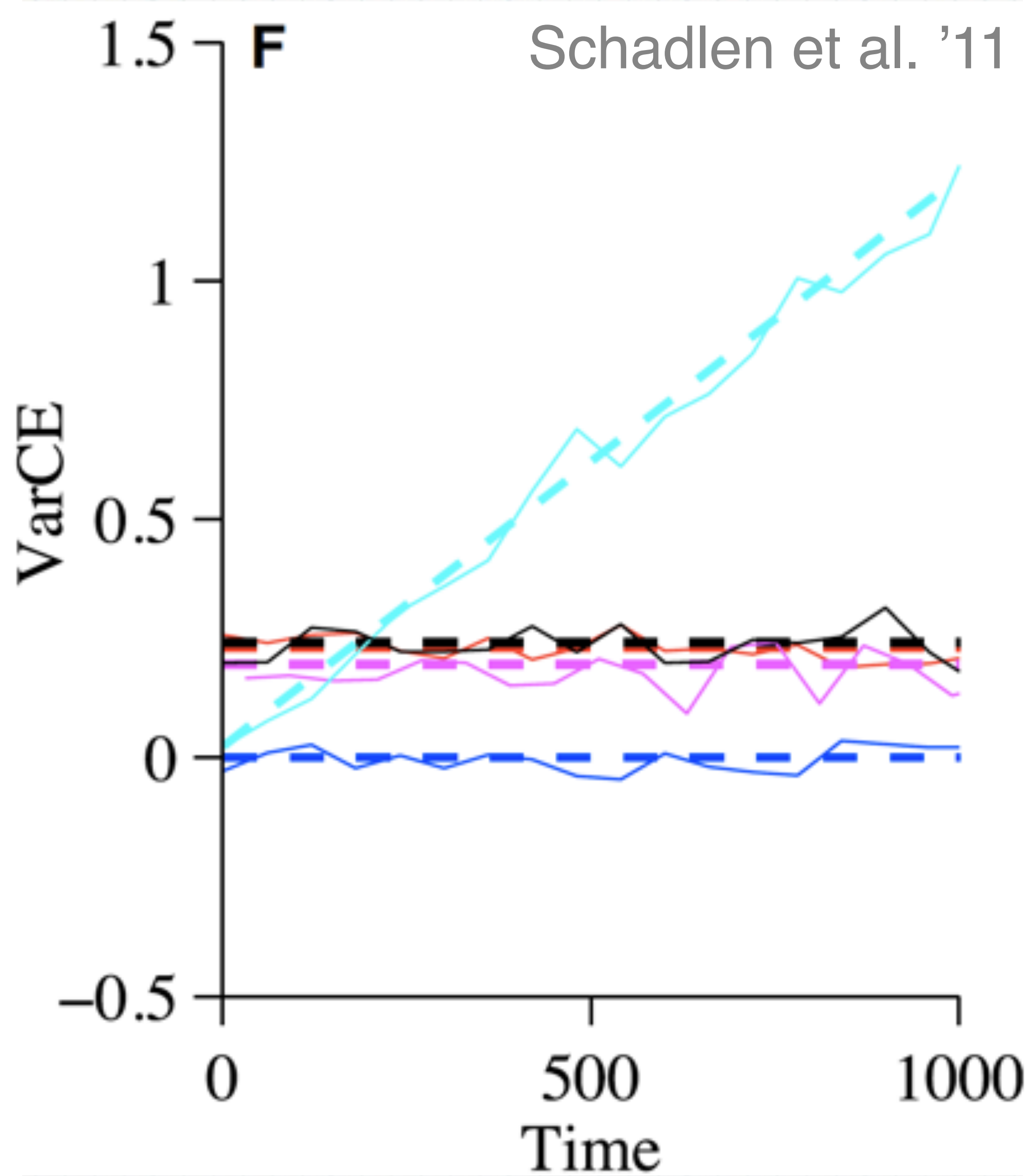
Stimulus onset quenches variability

* Fano factor is greater than one
* Drops to around one when stimulus comes on

Churchland et al. '10

Doubly stochastic process





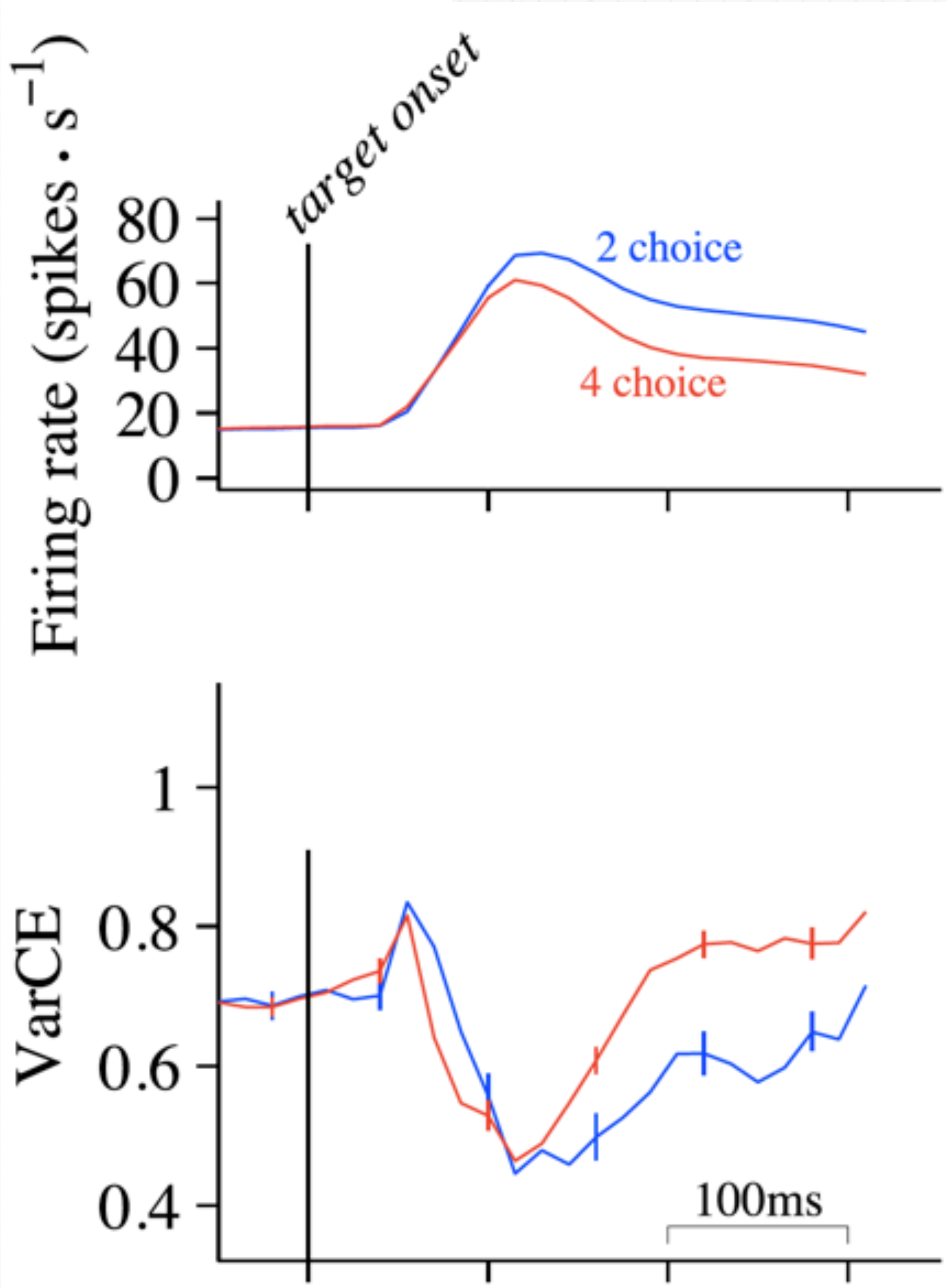
Schadlen et al. ’11

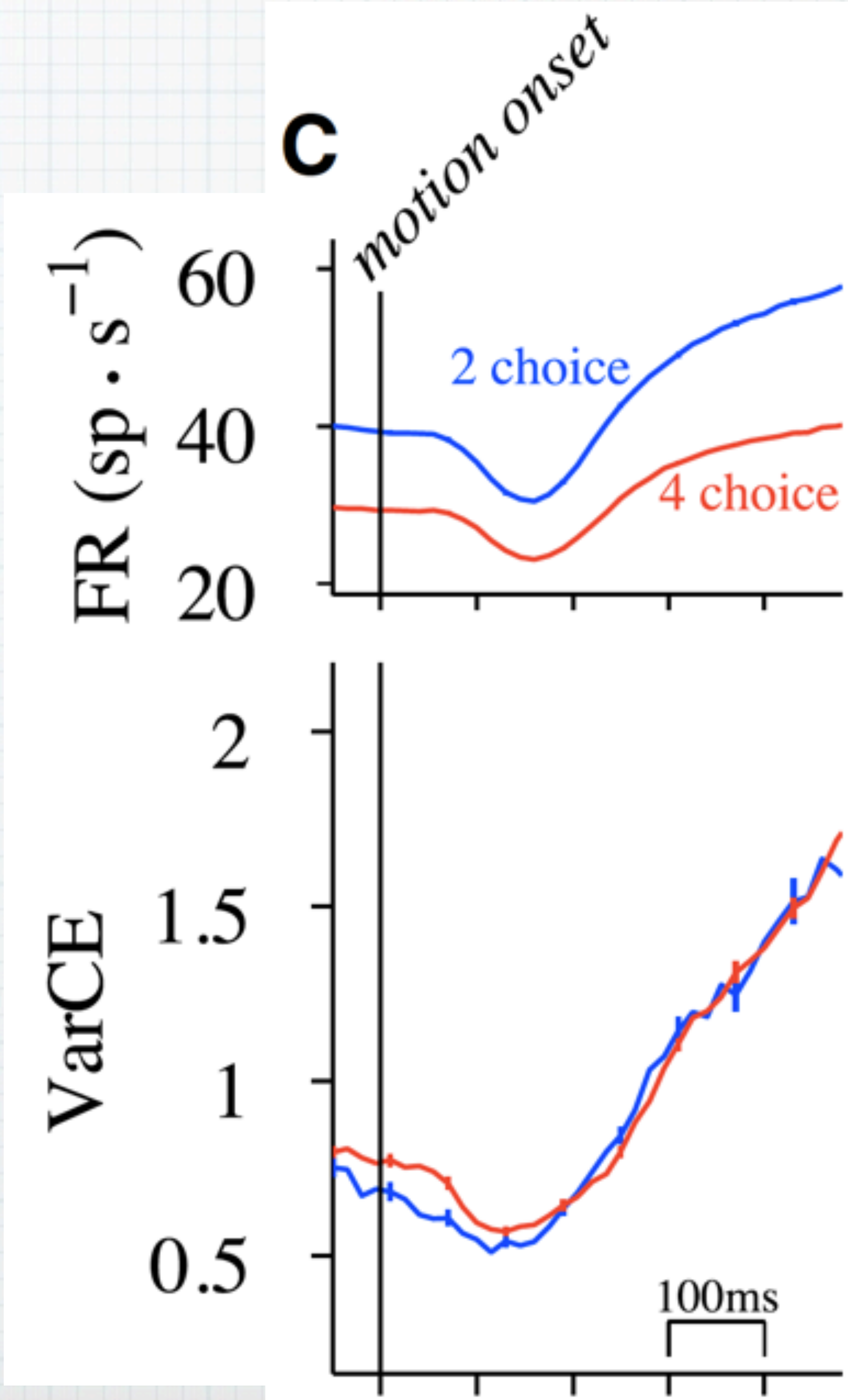
(A) Constant rate without trial-to-trial variation. Spike count variability arises only from the stochastic point process (PPV), hence VarCE = 0.
(B) Constant rate with trial-to-trial variation. A random value perturbs each rate function for the duration of the trial. Gray traces: examples of rate functions used to generate spikes. Total variance comprises PPV and VarCE.
(C) Same as (B) but with time varying rates.
(D) Same as (C) except that a new random perturbation is sampled every 10 ms.
(E) Drift diffusion. Rate is the sum of a deterministic “drift” function (same linear rise as in B and C) plus the cumulative sum of independent, random values drawn from a Normal distribution (mean = 0). Individual rate traces resemble one-dimensional Brownian motion (with drift).
(F) VarCE for the five examples. The VarCE captures the portion of total variance owing to variation in the rate functions across trials. Thick dashed lines show theoretical values ($\sigma^2_{\langle N \rangle}$) of VarCE for doubly stochastic Poisson point processes. Thin solid lines show VarCE estimated by application of Equation 5 to the simulated spike trains ($s^2_{\langle N \rangle}$) assuming $\phi = 1$. Note that in real data, ϕ is not known. Counting window = 60 ms. Line color corresponds to the colors used in (A)–(E).

$$Var[X] = \underbrace{Var[\langle X|Y\rangle]}_{\text{variance of conditional expectation (VarCE)}} + \underbrace{\langle Var[X|Y]\rangle}_{\text{expectation of conditional variance}}$$

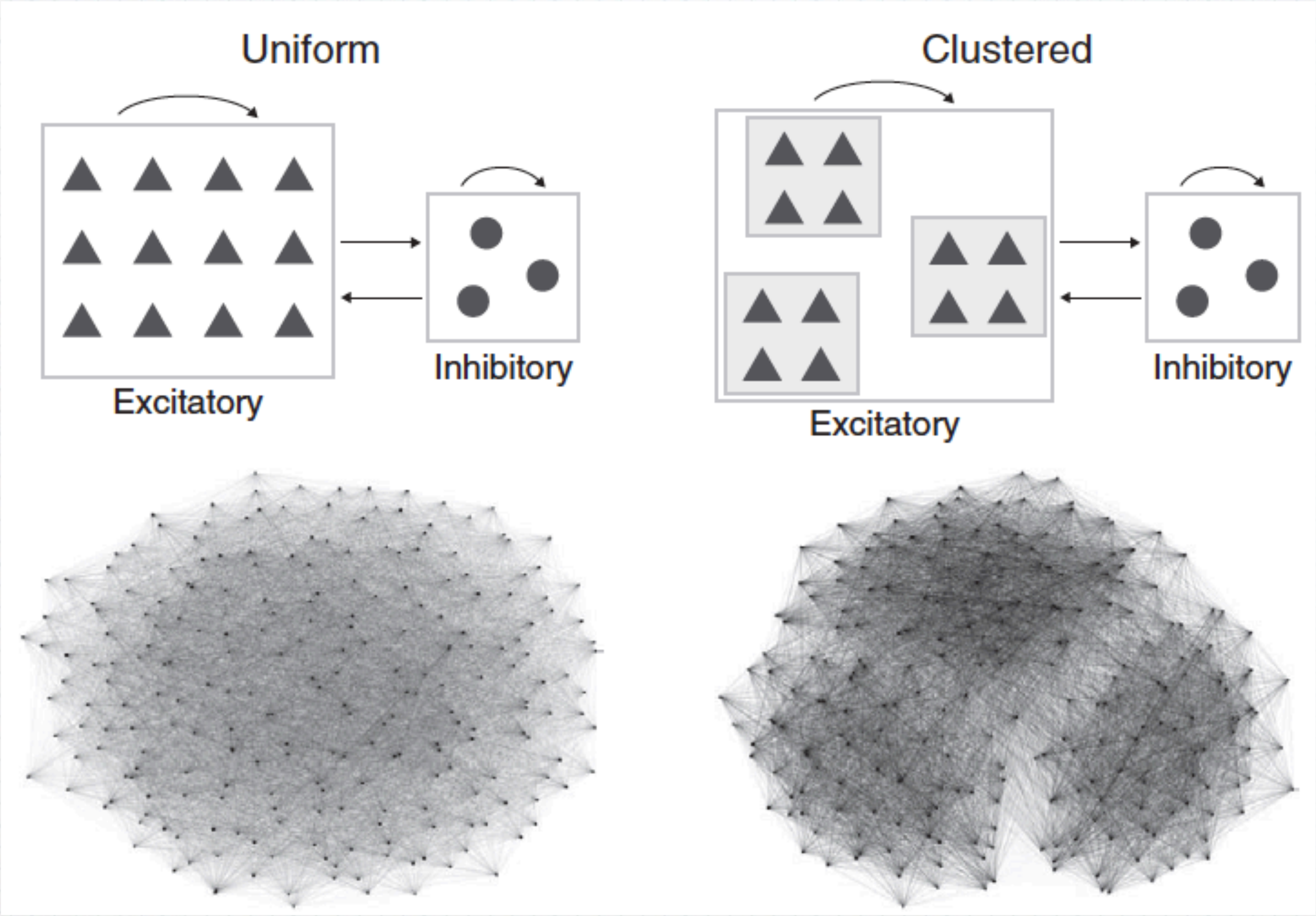
LIP Neurons Making Decision

Schadlen et al. '11

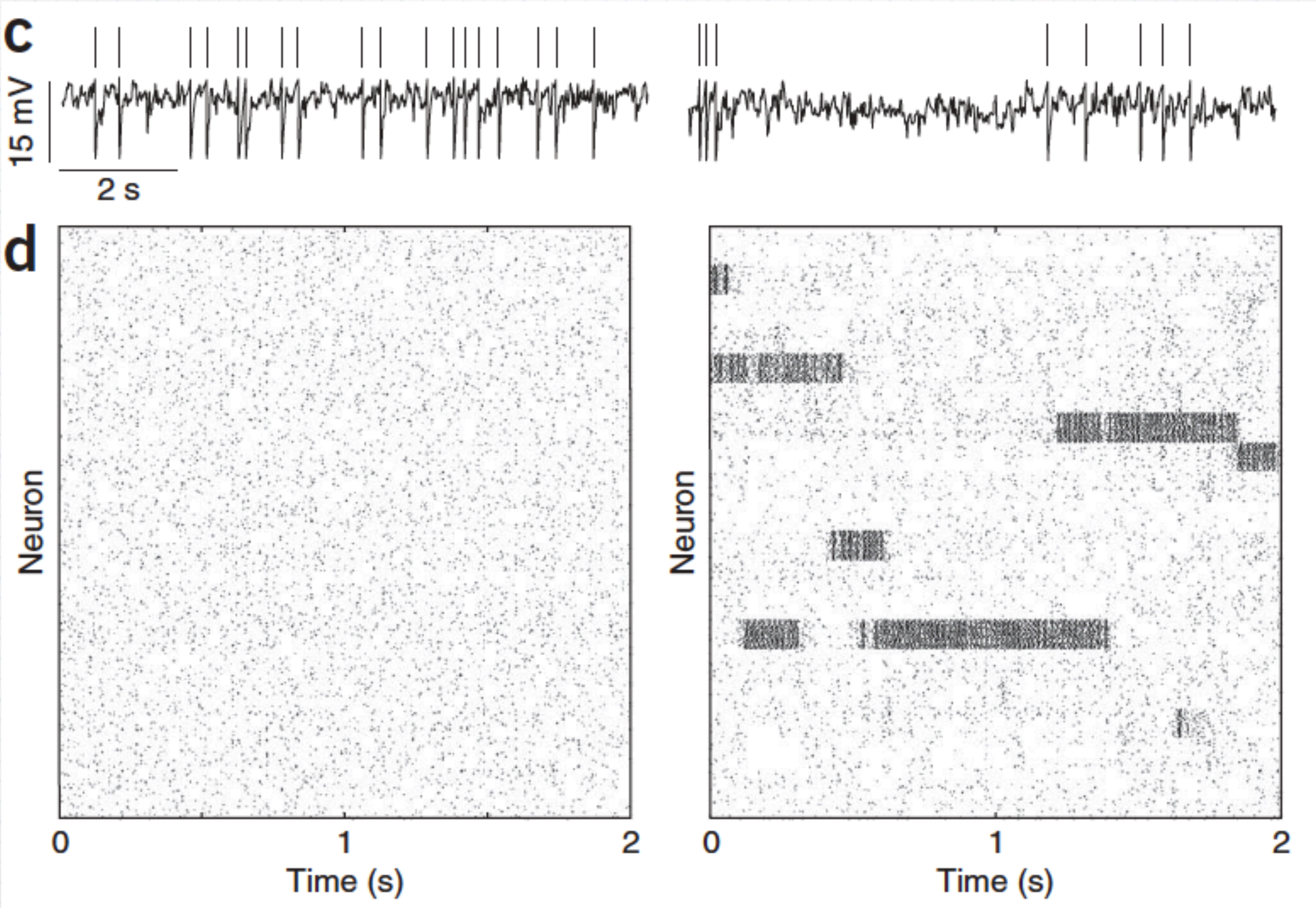




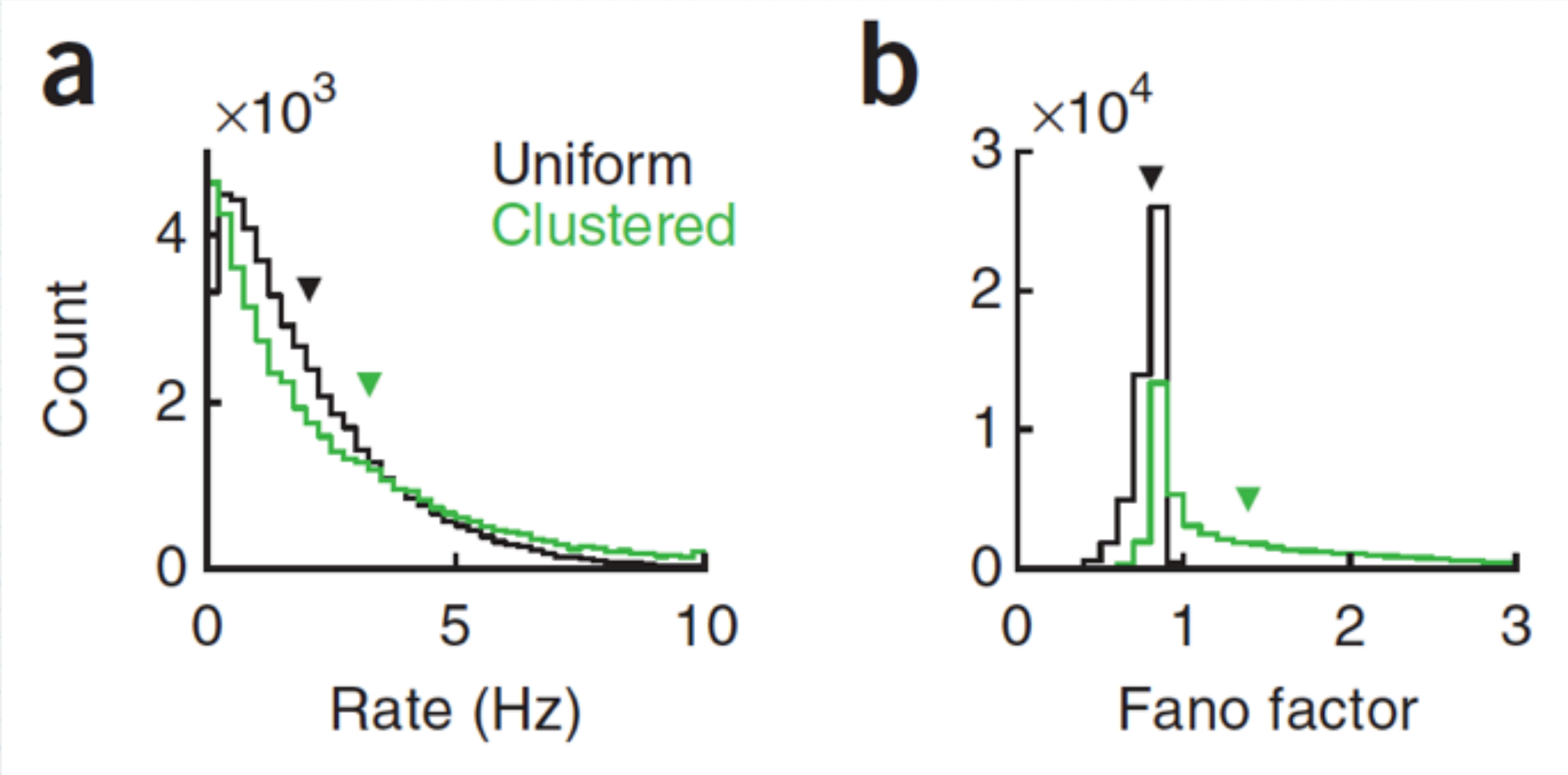
Clustered balanced network



Uniform vs Clustered



Rate and Fano Factor Distribution



Reproduces drop in Fano Factor