Noise-driven adaptation: *in vitro* and mathematical analysis

Liam Paninski, Brian Lau, Alex Reyes
Center for Neural Science, New York University
Contact: liam@cns.nyu.edu;
http://www.cns.nyu.edu/∼liam
Computational Neuroscience Meeting, Chicago
July 22, 2002

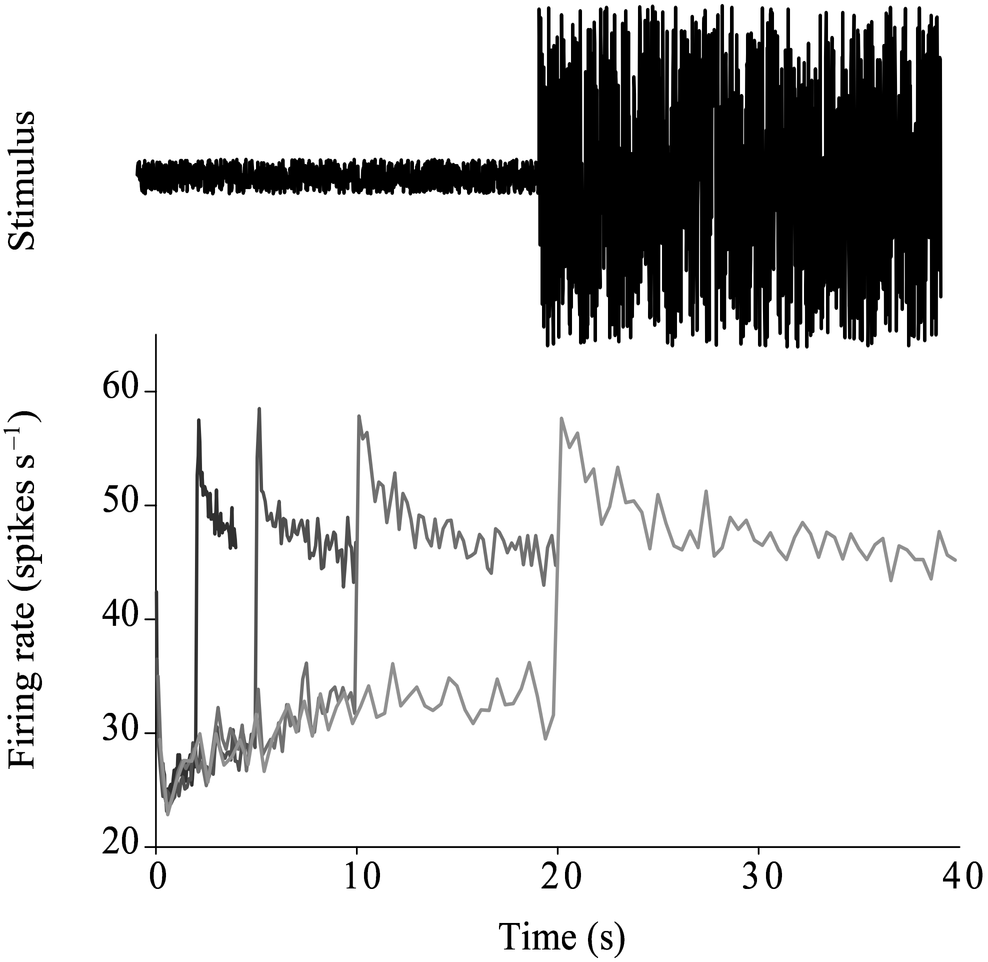
Introduction

Observation: changes in scale (not just mean) of random input can lead to "adaptation" (defined in more depth below) [13, 12, 5]

2 hypotheses:

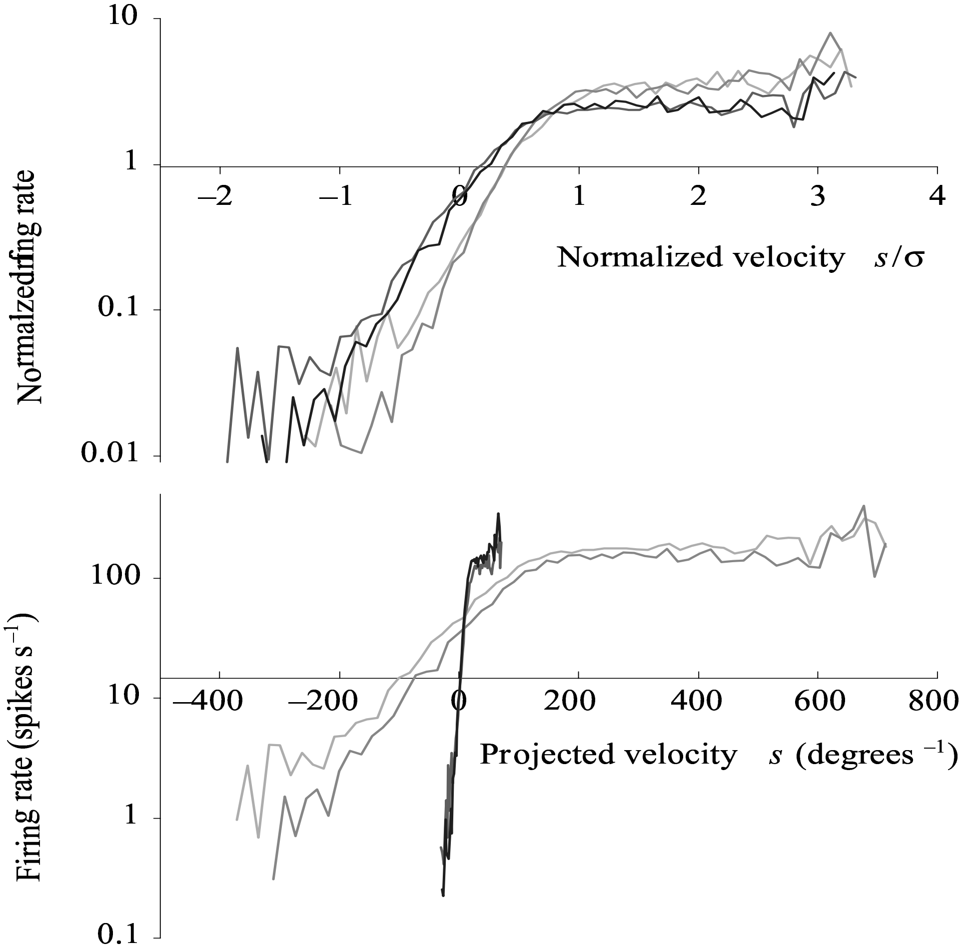
- (physiology) adaptation is at least partially single-cell phenomenon
- (math) adaptation is generic (independent of cellular details)

Results of Fairhall et al. (1)



- firing rate "adapts" to changes in input scale
- adaptation to upward jumps is faster than to downward jumps
- timescale of adaptation depends on timescale of scale changes

Results of Fairhall et al. (2)



- N-function adapts (exact definition below)

Experimental methods

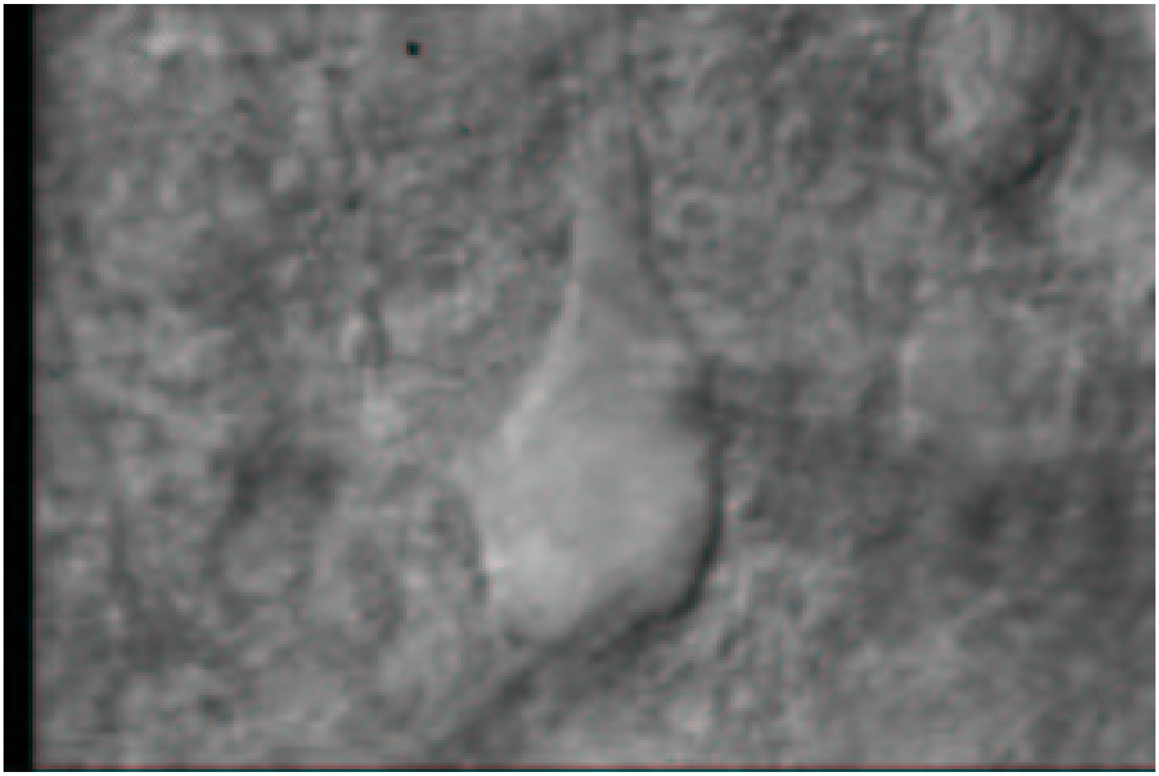
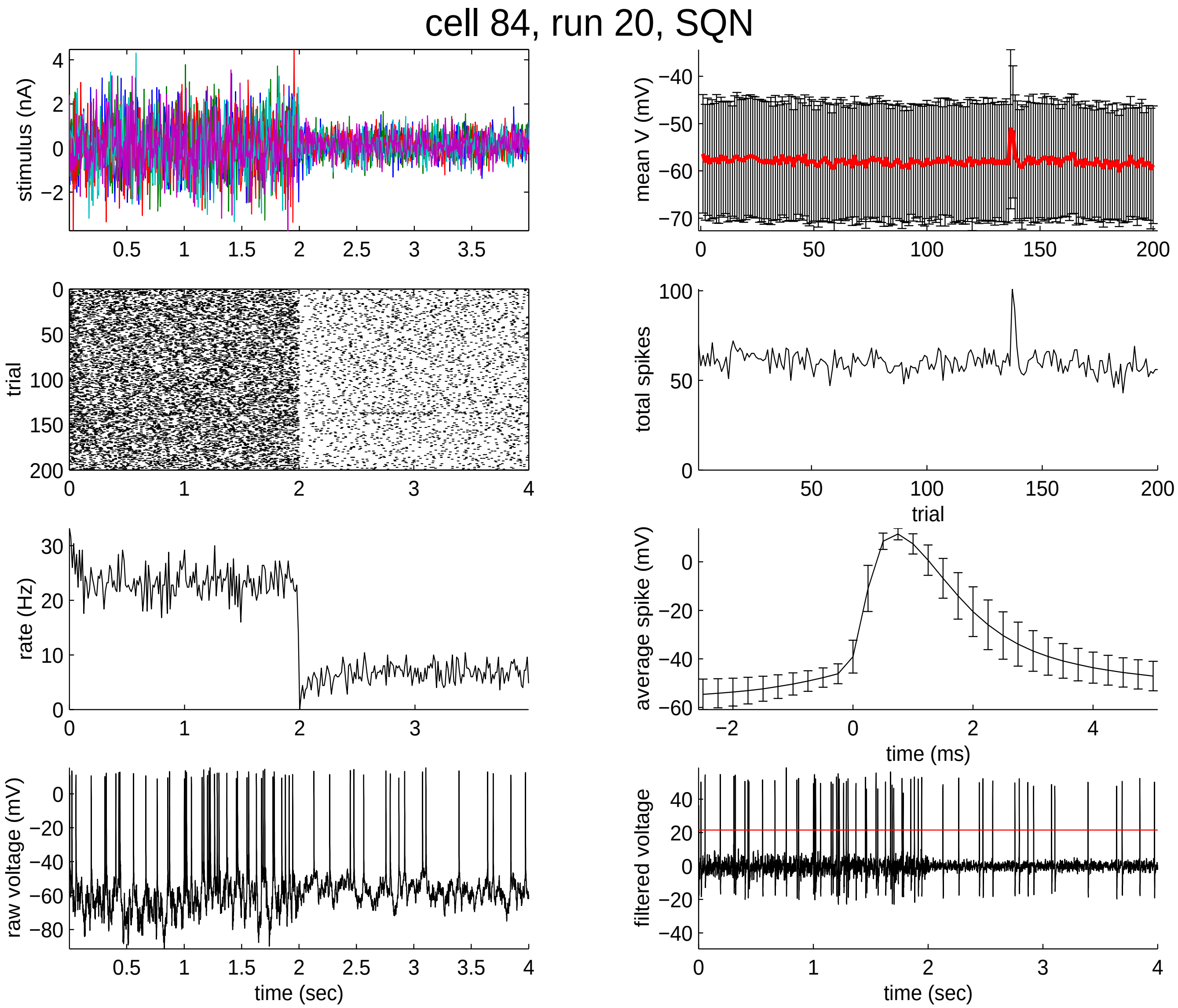
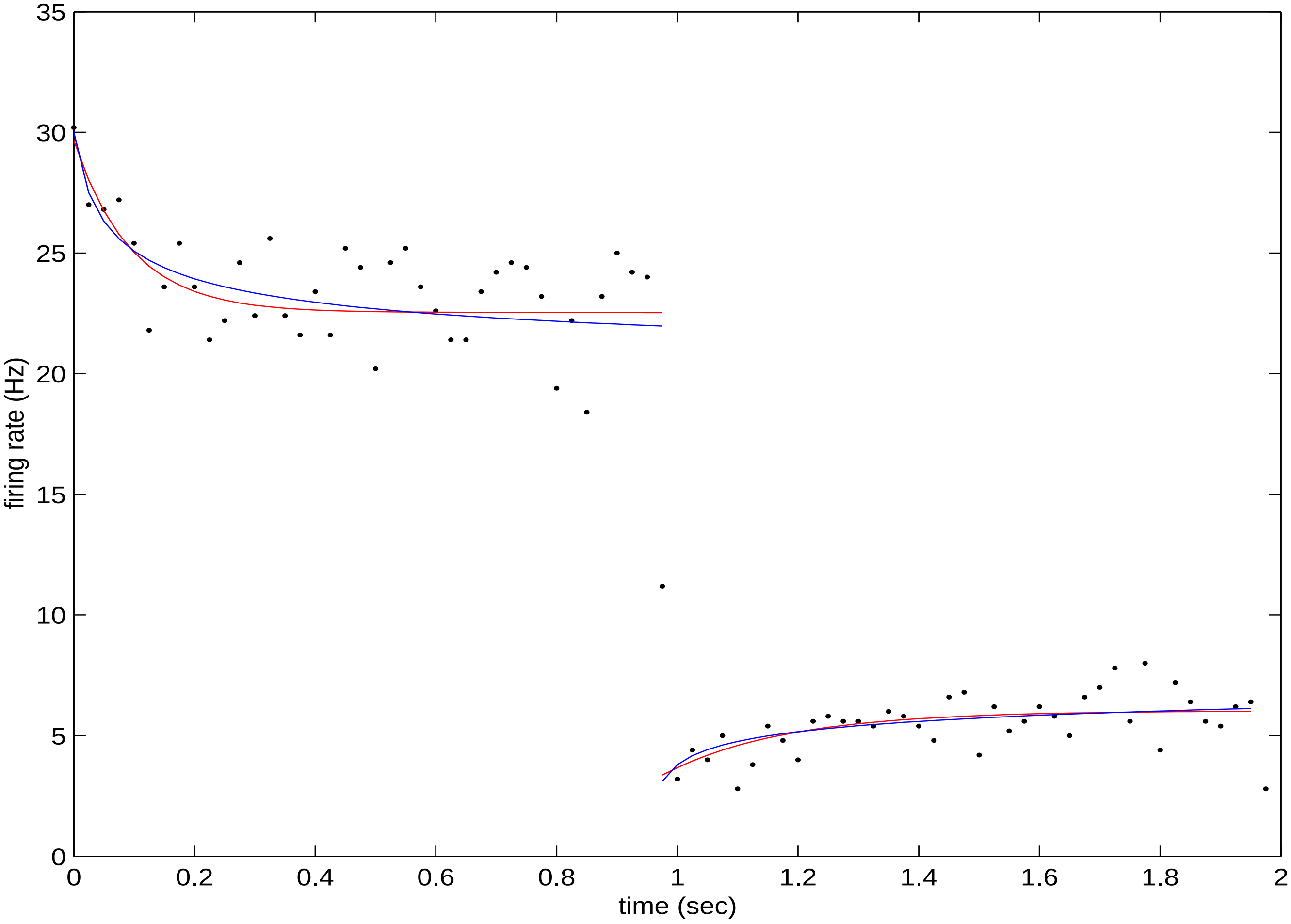


Figure 1: Sagittal slices were prepared from adolescent and adult rats (P14-P24) as described in [10]. Briefly, slices were maintained at 30°C in articificial cerebrospinal fluid consisting of (in mM): 125 NaCl, 2.5 KCl, 25 glucose, 25 $NaHCO_3$, 1.25 NaH_2PO_4, 2 $CaCl_2$, and 1 $MgCl_2$. Cells were visualized using infrared differential interference contrast microscopy with a 40X water immersion objective. Dual-electrode whole-cell recordings were made using pipettes with 5-15 M resistance when filled with (in mM): 100 K-gluconate, 20 KCl, 4 ATP-Mg, 10 phosphocreatine, 0.3 GTP, and 10 HEPES, pH 7.3 (310 mOsm). Recordings were performed in current clamp using Axoclamp 2B amplifiers (Axon Instruments, Foster City, CA), and stimulus presentation and data acquisition was managed using IGOR (Wavemetrics, Lake Oswego, OR). Gaussian noise current stimuli were delivered through one electrode, while voltage was recorded through the other electrode and processed on- and off-line (note that the noise current was not "frozen," that is, a new noise current was drawn i.i.d. for each trial). Panel shows a photograph of a cell with the recording and stimulating electrodes partially visible.

Basic experimental data

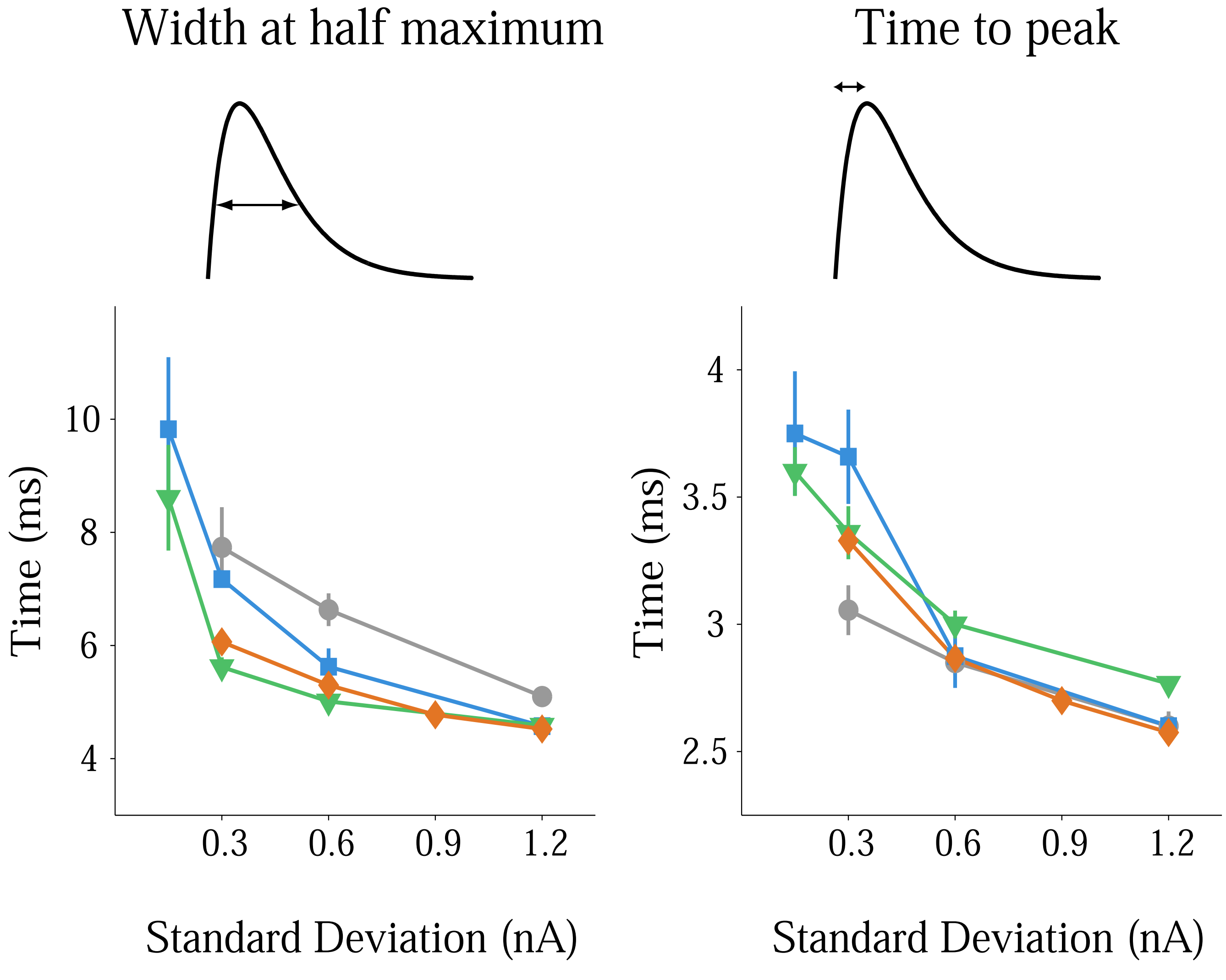


Experimental Result 1: rate adaptation



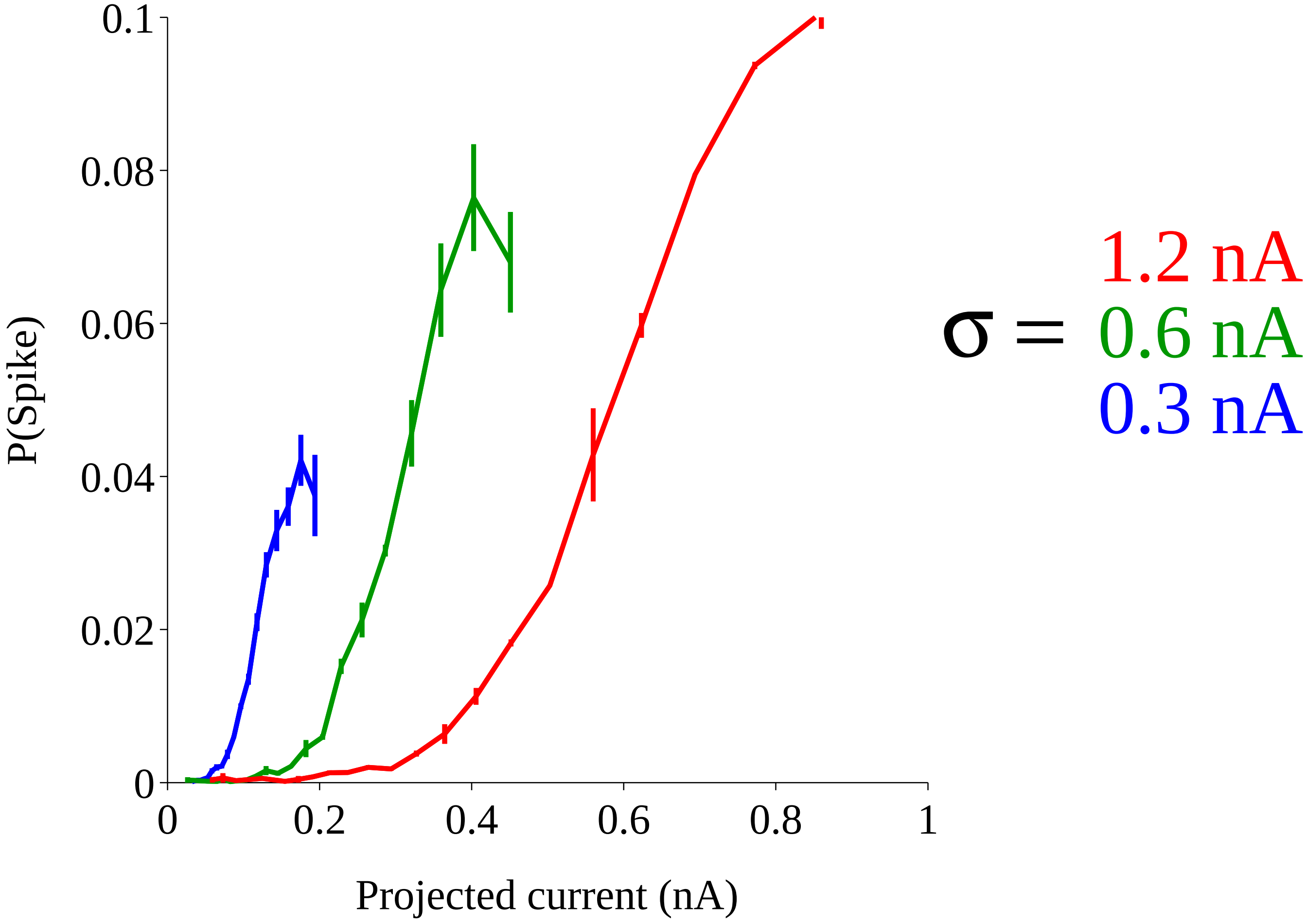
- $\tau_- > \tau_+$
- No oscillations seen
- No period-dependence seen (c.f. Fairhall et al.)

Result 2: changes in spike-triggered average



C.f. [3, 1, 13]

Result 3: adapation of N-function



Definition of N-function

$$N(K\vec{x}) \equiv P(spike|K\vec{x})$$

($\vec{x}$ is stimulus, K is projection onto cell's "linear filter," estimated by spike-triggered average)

$K\vec{x} =$ "projected current"

Theoretical methods: IF model

$$\frac{dV}{dt} = \frac{1}{\tau_m}(V_L - V + R_m I) - (V_{th} - V_{reset})\delta(V - V_{th})$$

τ_m = membrane time constant $\approx$ 20 ms
V_L = leak reversal potential ≈ -70 mV
R_m = membrane resistance $\approx 40M\Omega$
I = input current (white Gaussian noise, fixed DC)
V_{th} = threshold potential ≈ -55 mV
V_{reset} = reset potential ≈ -65 mV

Basic tool: Fokker-Planck equation

Basic idea: instead of modeling single cells, model population [7, 2, 9]

Fundamental object: $P(V)$, probability distribution on voltage

$$\frac{\partial P}{\partial t} = L(P) + F(t)(\delta(V - V_{reset}) - \delta(V - V_{th})),$$

$$L \equiv \frac{\sigma_0^2}{2}\frac{\partial^2 P}{\partial V^2} + \frac{1}{\tau_m}\frac{\partial[(V - V_0)P]}{\partial V};$$

$F(t)$ time-dependent mean firing rate of the cell

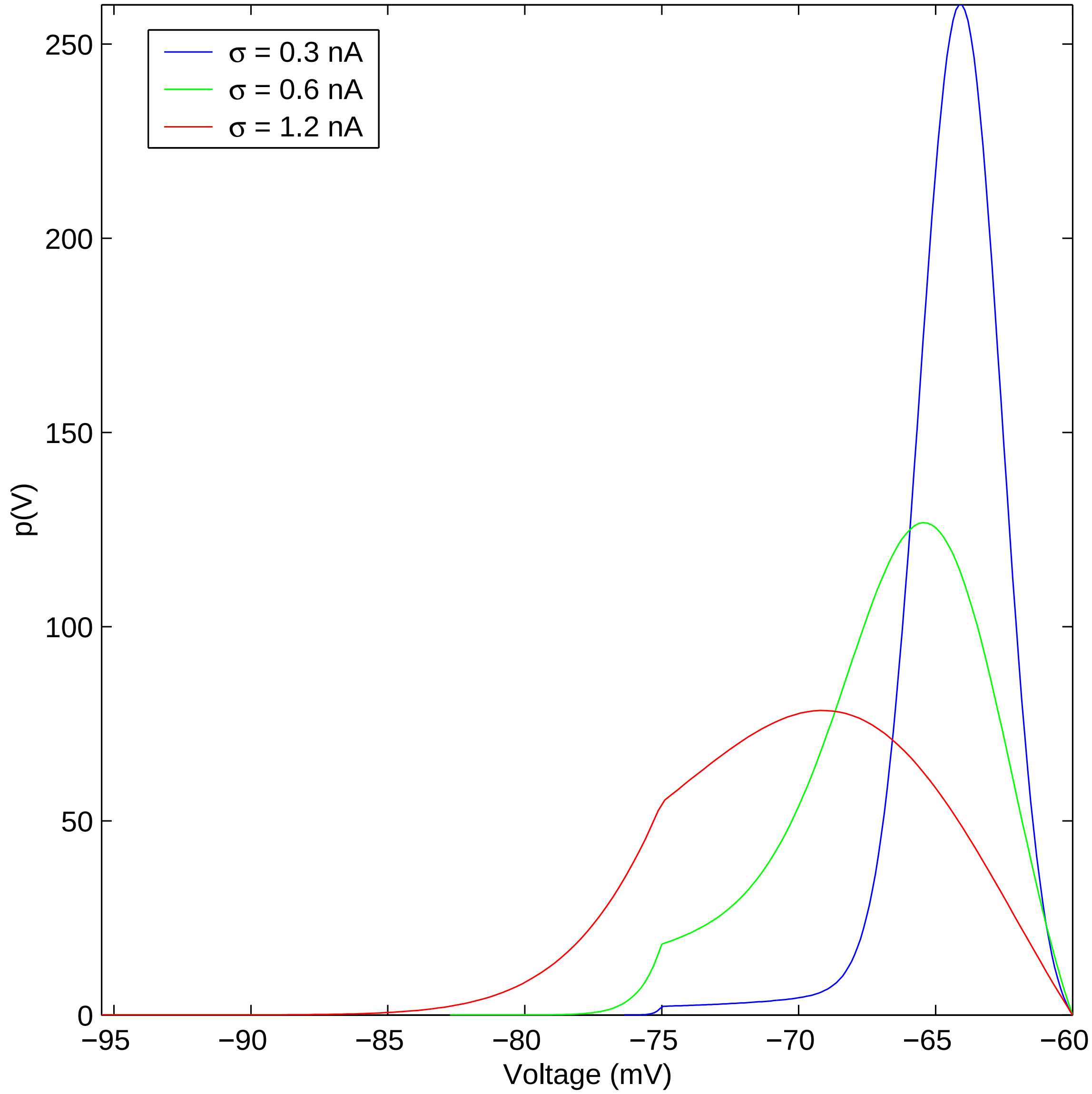
$$\sigma_0 \equiv R_m \sigma / \tau_m$$

$$V_0 \equiv R_m \mu + V_L$$

This equation exact in IF framework — no approximations made

Steady-state solution to FP equation [8, 2]

$$P(V) = \frac{2F}{\sigma_0^2} \int_{\max(V,V_{reset})}^{V_{th}} dV' e^{\frac{(V'-V_0)^2-(V-V_0)^2}{\tau_m \sigma_0^2}}$$



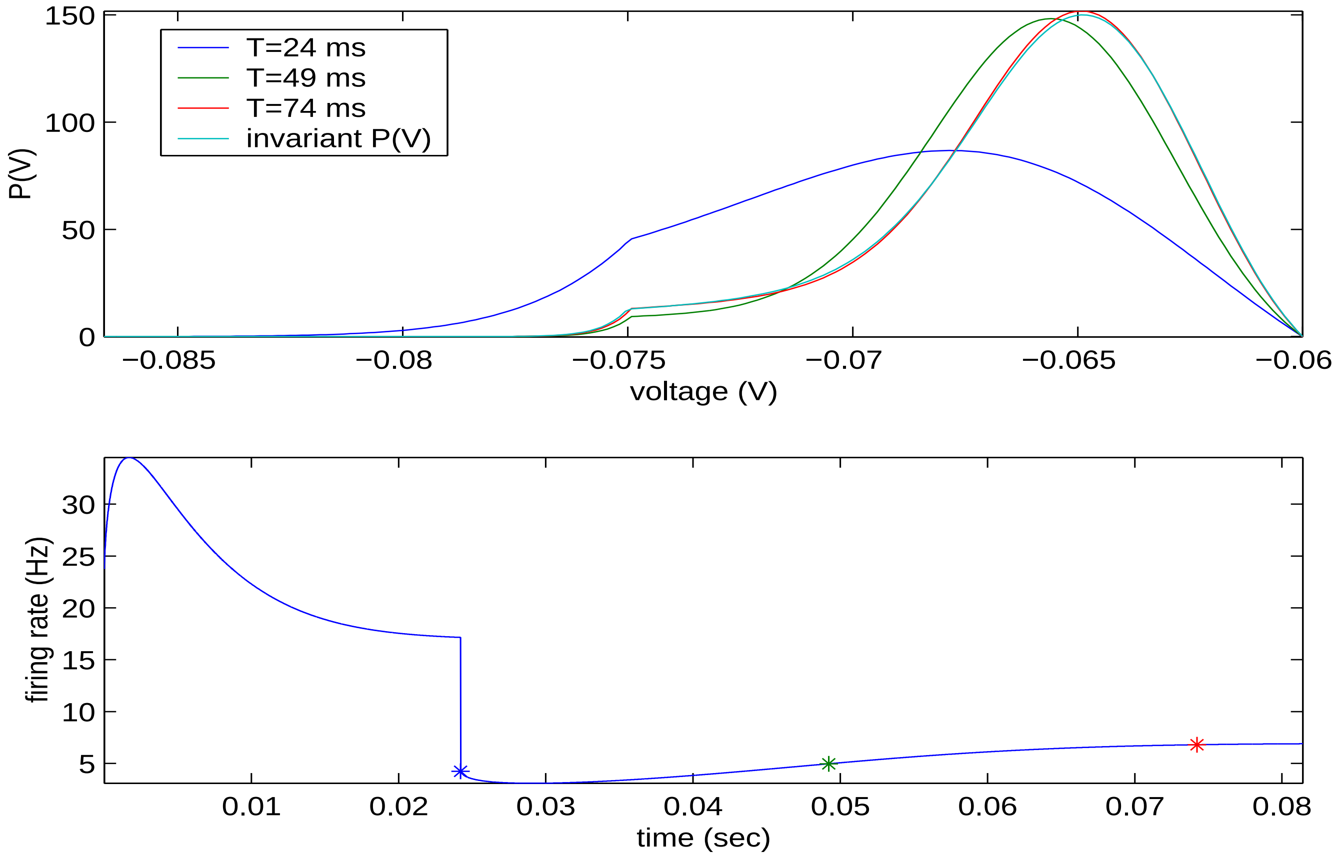
Theoretical result 1: rate adaptation

$$F_\infty = -\frac{\sigma_0^2}{2}\frac{\partial P_\infty(V)}{\partial V}$$

$$F_0 = -\frac{\sigma_0^2}{2}\frac{\partial P_0(V)}{\partial V}$$

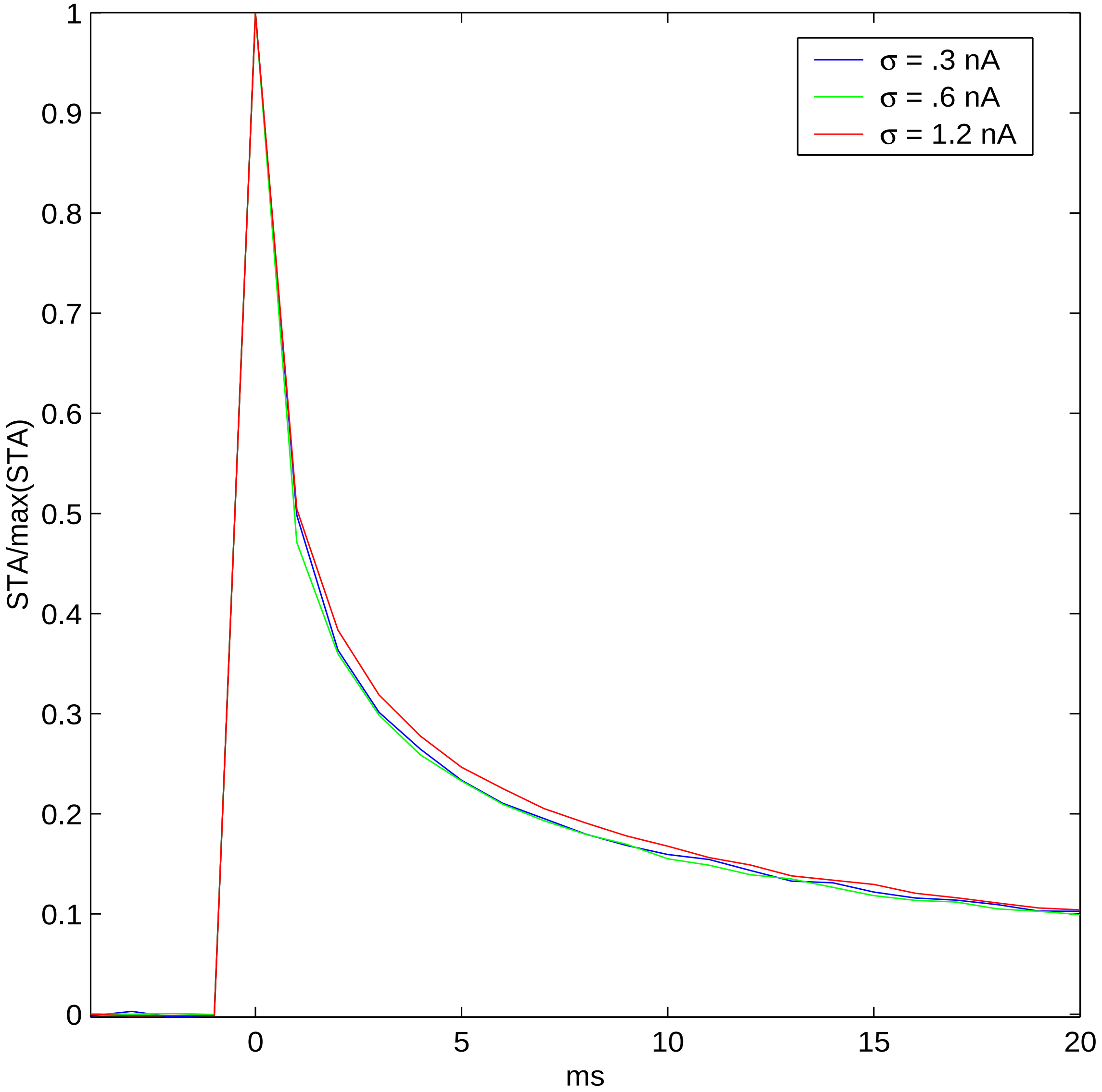
$$\frac{\partial^i F_0}{\partial t^i} = -\frac{\sigma_0^2}{2}\frac{\partial (L^i(P_0))}{\partial V}$$

(but F is not analytic; power series expansion invalid)



Result 2: spike-triggered average

Does not show width scaling behavior seen *in vitro*; different model necessary (see, e.g., [6])



Some exact theory possible, using invariant measure of FP equation; STA scales with σ and (more surprisingly) time step of numerical integration

Result 3: adaptation of three N-functions

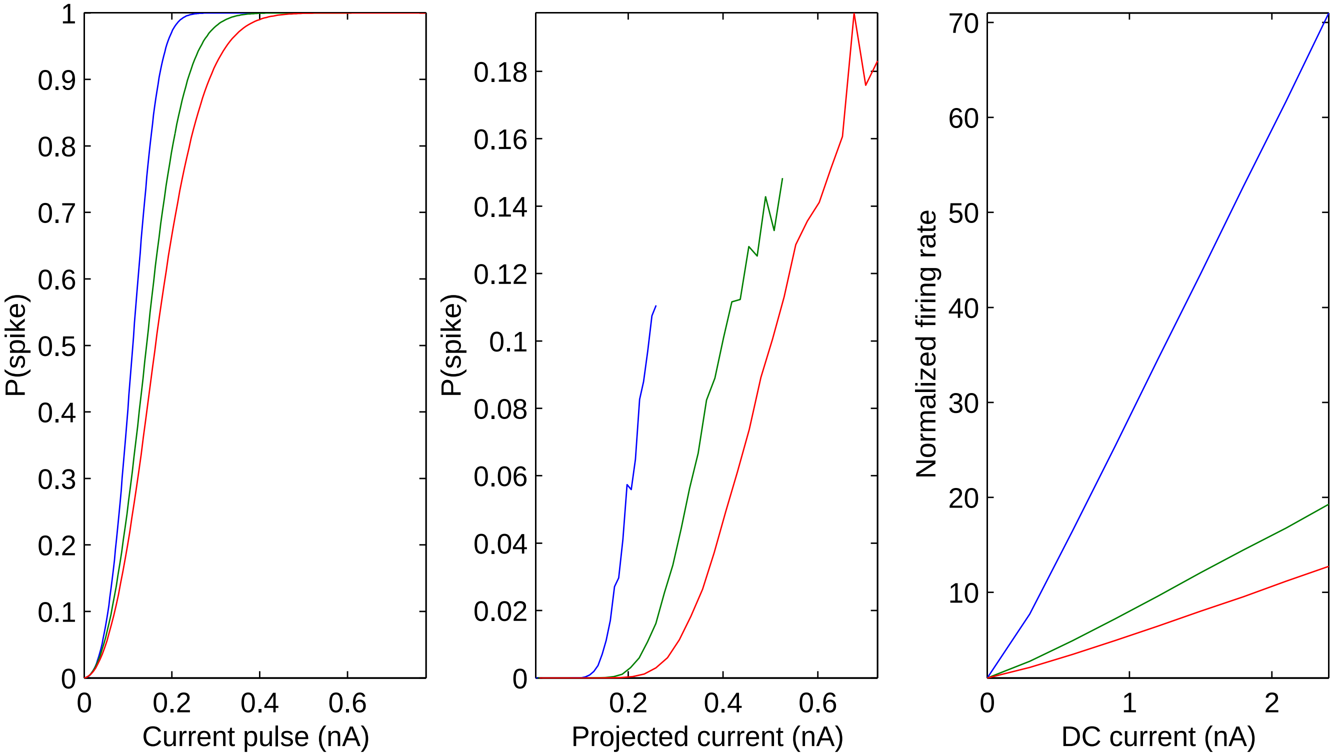


Figure 2: Three "gain functions" for integrate-and-fire cell: middle panel shows N-function, computed by Monte Carlo; left panel is "transient" function $F_0(x, \sigma)$, and right is "long-time" function $F_\infty(x, \sigma)/F_\infty(0, \sigma)$, both computed analytically. (Note that $F_\infty(x, \sigma)/F_\infty(0, \sigma)$ is normalized so that the y-axis is a dimensionless ratio.)

IF gain functions: definitions

Transient gain function:

$$F_0(x,\sigma) \equiv \lim_{dt\to 0}\lim_{T\to 0} P\left(spike \in (-dt,0] \;\middle|\; \int_{-T}^{0} I(t)dt = x\right) = \int_{V_{th}-\frac{xR_m}{\tau_m}}^{V_{th}} P(V)dV,$$

Long-time gain function:

$$F_\infty(x,\sigma) \equiv \lim_{T\to\infty} P\left(spike \in (-dt,0] \;\middle|\; \int_{-T}^{0} I(t)dt = xT\right) \approx -\frac{\sigma_0^2}{2}\frac{\partial P_{\mu+x}(V)}{\partial V}\bigg|_{V=V_{th}} dt,$$

x corresponds to the projected current (x-axis, Fig. 2b).

Conclusions

- Cortical somata display much of the adaptive behavior observed *in vivo*,in various species and preparations
- Much of this behavior is replicated in the simplest possible model [11]
- Different view of adaptive behavior; no efficient coding concepts invoked

Directions

- Dynamics of current-based FP equation
- Conductance-based FP equation (no second-order differential term; instead, jumps, like a delay equation in space).
- Dependence of τ on period in Fairhall et al. data: network effect?

This work was supported by NSF Grant IBN-0079619. LP and BL are supported by HHMI and NDSEG predoctoral fellowships, respectively.

References

[1] Bair, W., Cavanaugh, J. & Movshon, J. NIPS 9: 34-40 (1997).

[2] Brunel, N. & Hakim, V. Neural Computation 11: 1621-1671 (1999).

[3] Bryant, H.L. & Segundo, J.P. Journal of Physiology 260: 279-314 (1976).

[4] Chichilnisky, E. Network 12: 199-213 (2001).

[5] Fairhall, A., Lewen, G., Bialek, W. & de Ruyter, R. Nature 412: 787-792 (2001).

[6] Gerstner, W. Neural Networks 14: 599-610 (2001).

[7] Haskell, E., Nykamp, D. & Tranchina, D. Network 12: 141-174 (2001).

[8] Karlin S. & Taylor, H. A Second Course in Stochastic Processes. Academic Press, New York (1981).

[9] Knight, B., Omurtag, A. & Sirovich, L. Neural Computation 12: 1045-1055 (2000).

[10] Reyes, A. & Sakmann, B. Journal of Neuroscience 19: 3827-3835 (1999).

[11] Rudd, M. & Brown, L. Neural Computation 9: 1047-1069 (1997).

[12] Shapley, R. Current Biology 7: 421-423 (1997).

[13] Smirnakis et al. Nature 386: 69-73 (1997).

[14] Stemmler, M. & Koch, C. Nature Neuroscience 2: 521-527, (1999).