

A universal tradeoff between energy, speed and precision in neural communication



Subhaneil Lahiri, Jascha Sohl-Dickstein and Surya Ganguli Department of Applied Physics, Stanford University, Stanford CA

Background

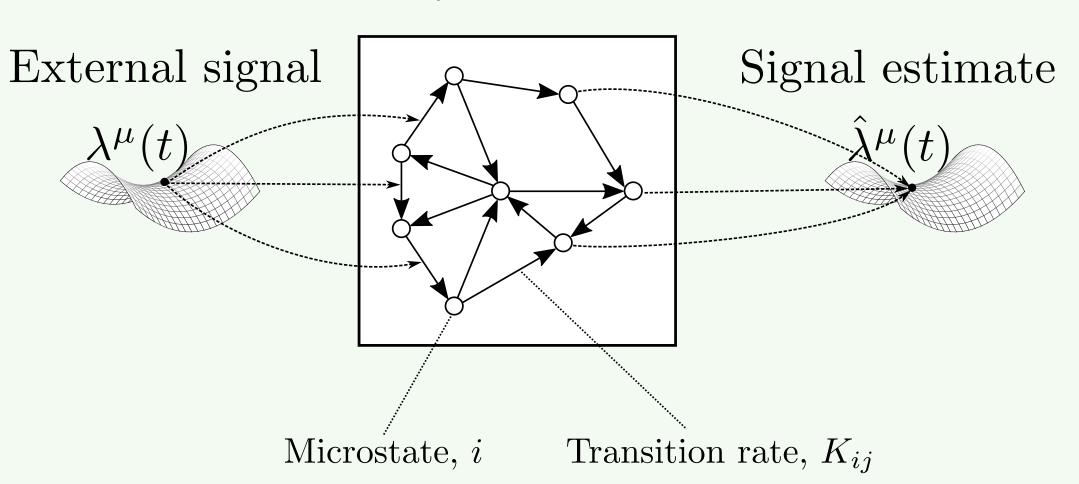
Information theory and thermodynamics provide limits on the accuracy and energy efficiency of physical systems.

However, they assume infinite time / infinitesimal speed.

Can we extend this to systems operating at nonzero speed?

Model of physical signaling substrate

Physical channel

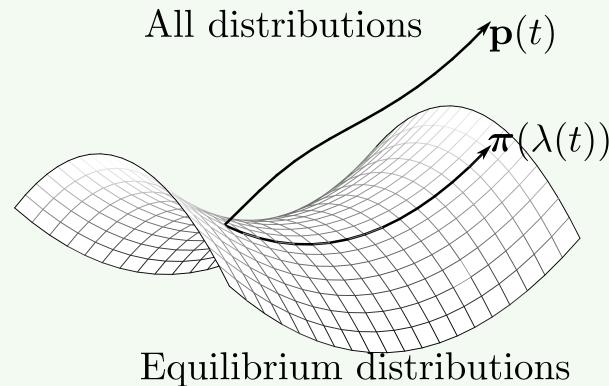


Channel dynamics: arbitrary Markov process.

Signal: control parameters for transition rates & energies. Receiver: estimate λ^{μ} by observing state of channel.

Causes of energy dissipation

Move at nonzero speed \rightarrow out of equilibrium.



 $\mathbf{p}(t)$: current probability distribution, $\pi(\lambda(t))$: equilibrium distribution for

Equilibrium distributions current λ .

Move faster \rightarrow further out of equilibrium \rightarrow more energy. More precision \rightarrow more sensitivity to $\lambda \rightarrow$ more energy.

→ three-way tradeoff between energy, speed and precision.

Previous work

Sensory adaptation: three-way tradeoff between energy, speed and

accuracy for a specific model [1].

Kinetic proofreading: two-way tradeoff between energy and accuracy [2],

or speed and accuracy [3].

Chemosensation: two-way tradeoff between energy and precision [4].

Proof of bound

Dissipation and the friction tensor

When $\dot{\lambda}$ is small on channel dynamics' timescales, dissipation rate is [5]:

$$\mathcal{P}_{\mathsf{ex}} = oldsymbol{g}_{\mu
u}\,\dot{\lambda}^{\mu}\dot{\lambda}^{
u},$$

 $g_{\mu
u}=$ friction tensor:

$$egin{aligned} oldsymbol{g}_{\mu
u} &= oldsymbol{k}_{\mathsf{B}} oldsymbol{T} \int_{0}^{\infty} \mathrm{d}t' \, \left\langle \delta\phi_{\mu}(\mathbf{0}) \delta\phi_{
u}(t')
ight
angle \,, \ \phi_{\mu} &= -eta rac{\partial oldsymbol{E}}{\partial \lambda^{\mu}}, \qquad \delta\phi_{\mu} &= \phi_{\mu} - \left\langle \phi_{\mu}
ight
angle \,. \end{aligned}$$

Riemannian metric on λ manifold \rightarrow thermodynamic distance. Optimal protocol = shortest path.

Friction tensor and Fisher information

We can show that

$$\mathbf{g} = k_{\mathrm{B}}T\sum_{a} \tau_{a}\mathbf{F}^{a},$$

 τ_a = time constant of eigenmode a,

 \mathbf{F}^a = Fisher information projected onto eigenmode a,

$$oldsymbol{\eta}^a \mathbf{K} = - au_a^{-1} oldsymbol{\eta}^a, \qquad oldsymbol{F}_{\mu
u}^a = (oldsymbol{\eta}^a{\cdot}\deltaoldsymbol{\phi}_\mu)(oldsymbol{\eta}^a{\cdot}\deltaoldsymbol{\phi}_
u).$$

Then

$$\mathbf{g} \geq k_{\mathsf{B}} T \, \tau_{\mathsf{min}} \, \mathbf{F},$$

 $\tau_{\min} = \min_a \tau_a$ (only over eigenmodes with $\mathbf{F}^a \not\approx 0$).

Energy-speed-precision bound

Define precision $\Phi = 1/\text{std. error}^2$ of unbiased estimator $\hat{\lambda}$.

Cramér-Rao bound:

$$\Phi \leq F$$

Define $V = \lambda^2$,

$$\Phi V \leq rac{\mathcal{P}_{\mathsf{ex}}}{k_{\mathsf{B}} T \, au_{\mathsf{min}}}.$$

This bound is tightest when

- \bullet λ couples to a narrow range of timescales,
- estimator $\hat{\lambda}$ is efficient.

Dual coordinates for exponential families

We're dealing with Boltzmann distributions: $\pi_i = \frac{e^{-\beta E_i}}{Z}$.

Exponential coordinates: $E = \sum_{\mu} \lambda^{\mu} \mathcal{O}_{\mu}$.

Dual coordinates: $\tilde{\lambda}^{\mu} = \langle \mathcal{O}_{\mu} \rangle \,, \qquad \tilde{\lambda}^{\mu} = \mathcal{O}_{\mu}.$

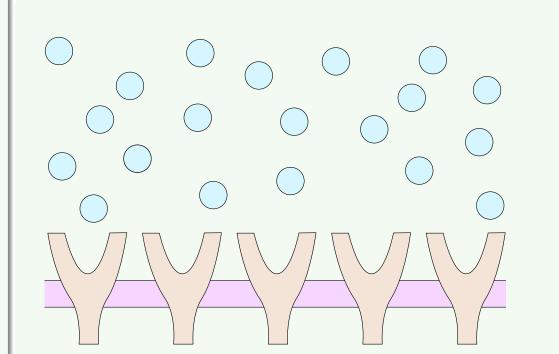
These are the only coordinates that saturate the Cramér-Rao bound [6].

Acknowledgements

We thank Madhu Advani, Gavin Crooks, Dibyendu Mandal and the participants of the Lineq reading group at UC Berkeley for useful discussions. We thank Genentech, the Office of Naval Research, the Burroughs-Wellcome Fund and the Alfred P. Sloan, James S. McDonnell, Simons and McKnight Foundations for support.

Examples

Cooperative receptors



Cooperative receptors can be modeled as an Ising chain [7]

$$E = -h\sum_{n} \sigma_{n} - J\sum_{n} \sigma_{n} \sigma_{n+1}.$$

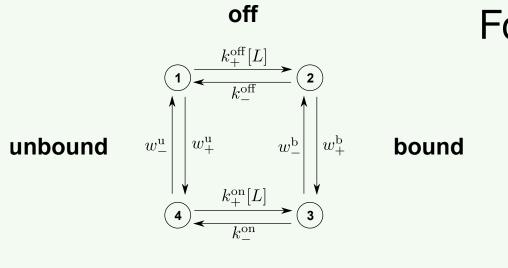
h = function of ligand concentration, J = receptor cooperativity.

Estimate $\tilde{\lambda} = e^{2\beta J} \tanh \beta h$ with $\hat{\tilde{\lambda}} = \frac{\sum_{n} \sigma_{n}}{N}$. At the instant we pass through h = 0, we find:

 $\Phi = N \mathrm{e}^{-2 eta J}, \quad \mathcal{P}_{\mathsf{ex}} = \frac{N \, k_{\mathsf{B}} T \, V \cosh 2 eta J}{2}, \quad au_{\mathsf{min}} = \frac{\mathrm{e}^{2 eta J} \cosh 2 eta J}{2}.$

Saturates bound!

Nonequilibrium receptor



Following [8], define:

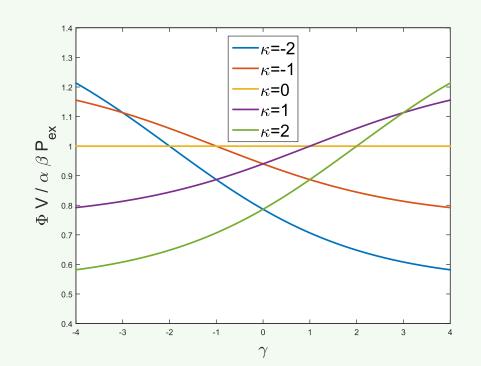
$$egin{aligned} \kappa &= \operatorname{In}rac{\kappa_{-}}{k_{-}^{ ext{on}}}, & \gamma &= \operatorname{In}rac{\kappa_{-} \kappa_{-} \kappa_{-} \kappa_{+}}{k_{+}^{ ext{off}} w_{+}^{ ext{b}} k_{-}^{ ext{on}} \kappa_{+}} & \ \lambda &= \operatorname{In}rac{k_{+}[L]}{(k_{-}^{ ext{off}} k_{-}^{ ext{on}})^{1/2}}, & lpha &= w_{+}^{ ext{u/b}} + w_{-}^{ ext{u/b}}, \end{aligned}$$

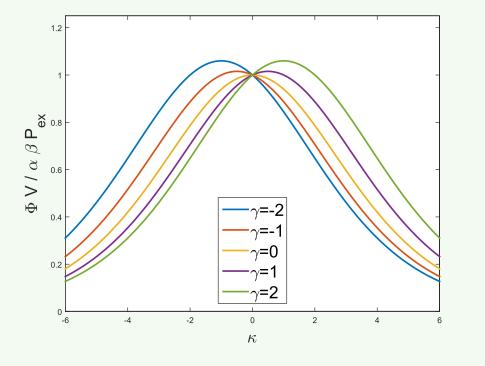
Estimate $\tilde{\lambda}$ with #active — #inactive.

At the instant we pass through $\lambda = 0$, assuming $\alpha \ll k_- = (k_-^{\text{off}} k_-^{\text{on}})^{1/2}$,

$$\Phi = N, \quad \mathcal{P}_{ex} = \frac{N \, k_{\rm B} T \, V \cosh \left(\frac{\kappa - \gamma}{4}\right) \cosh \left(\frac{\kappa}{4}\right)}{\alpha \cosh \left(\frac{\gamma}{4}\right)}, \quad \tau_{\min} = \frac{1}{k_{-}(1 + \mathrm{e}^{|\kappa|/2})}.$$

Satisfies bound, but a long way from saturating it.





References

[1] G. Lan, P. Sartori, S. Neumann, V. Sourjik, and Y. Tu, Nature physics 8 (May, 2012) 422–428.

[2] J. J. Hopfield, *Proc. Natl. Acad. Sci. U.S.A.* **71** (Oct., 1974) 4135–4139; R. R. Freter and M. A. Savageau, *Journal of Theoretical Biology* **85** (July, 1980) 99–123; M. Ehrenberg and C. Blomberg, *Biophysical journal* **31** (Sept., 1980) 333–58; M. A. Savageau and D. S. Lapointe, *Journal of Theoretical Biology* **93** (Nov., 1981) 157–177; H. Qian, *Journal of molecular biology* **362** (Sept., 2006) 387–92; A. Murugan, D. A. Huse, and S. Leibler, *Physical Review X* **4** (Apr., 2014) 021016, arXiv:1312.2286 [cond-mat.stat-mech].

[3] A. Murugan, D. A. Huse, and S. Leibler, *Proc. Natl. Acad. Sci. U.S.A.* **109** (July, 2012) 12034–9.

[4] R. G. Endres and N. S. Wingreen, *Phys. Rev. Lett.* **103** (Oct., 2009) 158101, arXiv:0909.4710 [q-bio.SC]; P. Mehta and D. J. Schwab, *Proc. Natl. Acad. Sci. U.S.A.* **109** (Oct., 2012) 17978–82, arXiv:1203.5426 [q-bio.MN]; A. H. Lang, C. K. Fisher, T. Mora, and P. Mehta, *Phys. Rev. Lett.* **113** (May, 2014) 148103, arXiv:1405.4001 [physics.bio-ph]; A. C. Barato, D. Hartich, and U. Seifert, arXiv:1405.7241 [physics.bio-ph]; C. C. Govern and P. R. Ten Wolde, *Proc. Natl. Acad. Sci. U.S.A.* **111** (Nov., 2014) 17486–17491; P. Sartori, L. Granger, C. Lee,

and J. Horowitz, *PLoS computational biology* 10 (Dec., 2014) e1003974, arXiv:1404.1027 [cond-mat.stat-mech]. [5] D. A. Sivak and G. E. Crooks, *Phys. Rev. Lett.* 108 (May, 2012) 190602, arXiv:1201.4166 [cond-mat.stat-mech].

[6] S.-i. Amari and H. Nagaoka, *Methods of information geometry*, vol. 191. American Mathematical Soc., 2007.

[7] M. Skoge, Y. Meir, and N. S. Wingreen, *Phys. Rev. Lett.* **107** (oct, 2011) 1–5, arXiv:1109.4160 [[q-bio.MN].

[8] M. Skoge, S. Naqvi, Y. Meir, and N. S. Wingreen, *Phys. Rev. Lett.* 110 (June, 2013) 248102, arXiv:1307.2930 [q-bio.MN].