A universal tradeoff between power, precision and speed in physical communication: supplementary material

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Contents

1 Introduction

In this supplement, we provide the details underlying the results of the main text. In Section 2 we show a step-by-step derivation of equation 6 of the main text. Next, Section 3 contains a precise description of the slow signaling limit where the friction tensor used in equation 3 of the main text determines power dissipation. In Section 4, we generalize the power-precision-speed inequality of the main text to multidimensional signals. In Section 5, we further extend these results to channels whose dynamics violate detailed balance (equation 2 of the main text), and therefore have nonequilibrium steady states. Then, Section 6 provides the justification for replacing the Fisher information of the out of equilibrium state of the channel with the Fisher information of the equilibrium distribution in the Cramér-Rao bound (equation 8 of the main text). Following which, Section 7 contains the definition of the dual coordinate system for the signal manifold, which proves to be necessary for finding estimators that can saturate the Cramér-Rao bound. In Section 8, we provide the

details behind the discussion of the example systems in the main text, including the heavily over-damped harmonic oscillator, the Ising ring, which we also extend to the case of multidimensional signals, and a four state receptor that violates detailed balance.

2 Relating friction and information geometry

In this section we provide a detailed derivation of equation 6 of the main text. We introduce an eigenvector basis

$$\mathbf{K}\mathbf{u}^a = -q_a\mathbf{u}^a, \qquad \boldsymbol{\eta}^a\mathbf{K} = -q_a\boldsymbol{\eta}^a, \tag{1}$$

with $q_0 = 0$, $\boldsymbol{\eta}^0 = \boldsymbol{\pi}$ and $\mathbf{u}^0 = \mathbf{e}$, a column vector of ones. If we have detailed balance, then all $q_a, \mathbf{u}^a, \boldsymbol{\eta}^a$ are real and with suitable choice of normalization we have:

$$\boldsymbol{\eta}^a\mathbf{u}^b = \delta^{ab}, \quad \mathbf{K} = -\sum_a q_a\mathbf{u}^a\boldsymbol{\eta}^a, \quad \mathbf{I} = \sum_a \mathbf{u}^a\boldsymbol{\eta}^a, \quad \eta_i^a = \pi_i u_i^a. \tag{2}$$

where the last relation holds element-by-element.

The probability of being in state i at time t and in state j at a later time t' is

$$p_{ij}(t,t') = \pi_i\left[\exp(\mathbf{K}(t'-t))\right]_{ij} = \pi_i\sum_a u_i^a\,\mathrm{e}^{-q_a(t-t')}\,\eta_j^a,$$

assuming that the system is in equilibrium. Then the correlation function in equation 4 of the main text can be written as

$$\begin{aligned}
\langle\delta\phi_\mu(0)\delta\phi_\nu(t')\rangle &= \sum_{ij} p_{ij}(0,t')\delta\phi_\mu^i\delta\phi_\nu^j \\
&= \sum_{ij}\pi_i\left[\exp(\mathbf{K}t')\right]_{ij}\delta\phi_\mu^i\delta\phi_\nu^j \\
&= \sum_{ij}\sum_a \pi_i u_i^a\,\mathrm{e}^{-q_a t'}\,\eta_j^a\,\delta\phi_\mu^i\delta\phi_\nu^j \\
&= \sum_{ij}\sum_a \eta_i^a\,\mathrm{e}^{-q_a t'}\,\eta_j^a\delta\phi_\mu^i\delta\phi_\nu^j \\
&= \sum_{ij}\sum_a \mathrm{e}^{-q_a t'}\left(\eta_i^a\delta\phi_\mu^i\right)\left(\eta_j^a\delta\phi_\nu^j\right).
\end{aligned}$$

Substituting this into equation 4 of the main text and integrating with respect to t' leads to

$$g_{\mu\nu}(\boldsymbol{\lambda}) = k_\mathrm{B}T\sum_a\frac{1}{q_a}\sum_{ij}\left(\eta_i^a\delta\phi_\mu^i\right)\left(\eta_j^a\delta\phi_\nu^j\right).$$

Defining $\tau_a = \frac{1}{q_a}$, this is the first line of equation 6 of the main text.

To derive the last line of equation 6 of the main text, we reverse the process above:

$$\begin{aligned}\sum_a \sum_{ij} \left(\eta_i^a \delta\phi_\mu^i\right)\left(\eta_j^a \delta\phi_\nu^j\right) &= \sum_{ij}\sum_a \eta_i^a \eta_j^a\, \delta\phi_\mu^i \delta\phi_\nu^j \\ &= \sum_{ij}\sum_a \pi_i\, u_i^a \eta_j^a\, \delta\phi_\mu^i \delta\phi_\nu^j \\ &= \sum_{ij} \pi_i\, \delta_{ij}\, \delta\phi_\mu^i \delta\phi_\nu^j \\ &= \sum_i \pi_i\, \delta\phi_\mu^i \delta\phi_\nu^i \\ &= F_{\mu\nu},\end{aligned}$$

where we used the fact that, for the canonical ensemble (equation 1 of the main text), we have $\frac{\partial \ln \pi_i}{\partial \lambda^\mu} = \delta\phi_\mu^i$, so the penultimate line above is identical to equation 7 of the main text.

3 Domain of validity of the slow signal approximation

In this section, we will discuss the regime where the approximations used in the derivation of equation 3 of the main text are valid.

In the original derivation, [1], the linear response approximation was used, which assumes that all changes in the parameters, λ^μ, are small. It was noted in [2] that the same result arises from truncating a derivative expansion at first order. This was made explicit by a systematic derivative expansion in [3].

One can legitimately truncate the derivative expansion at leading order when the functions $\lambda^\mu(t)$ vary slowly relative to the intrinsic timescales of the system. This can be made precise by rewriting all expressions in terms of the Fourier transforms, $\widetilde{\lambda}^\mu(\omega)$.

In the derivative expansion in [3], every time derivative comes with a factor of $\mathbf{K}^{\mathrm{D}}$, the Drazin pseudoinverse of $\mathbf{K}$, which can be defined in terms of the eigenvalues and eigenvectors in (1):

$$\mathbf{K} = -\sum_a q_a \mathbf{u}^a \boldsymbol{\eta}^a \qquad \Leftrightarrow \qquad \mathbf{K}^{\mathrm{D}} = -\sum_{a>0} \tau_a \mathbf{u}^a \boldsymbol{\eta}^a., \tag{3}$$

where $\tau_a = 1/q_a$. Therefore, the eigenvalues of K^{D} are the τ_a.

Using $\Delta\mathbf{p}(t) = \mathbf{p}(t) - \boldsymbol{\pi}(t)$, we can write the Fourier transform of the derivative expansion in [3] as

$$\Delta\mathbf{p}(\omega_0) = \sum_{n=1}^{\infty} \int \frac{\mathrm{d}\omega_1}{2\pi} \cdots \int \frac{\mathrm{d}\omega_n}{2\pi}\, \boldsymbol{\pi}(\omega_n)\, (-\mathrm{i}\omega_n) \mathbf{K}^{\mathrm{D}}(\omega_{n-1} - \omega_n) \cdots (-\mathrm{i}\omega_1) \mathbf{K}^{\mathrm{D}}(\omega_0 - \omega_1). \tag{4}$$

As each power of ω comes with one power of K^{D}, whose eigenvalues are τ_a, the derivative expansion can be thought of as an expansion in $\omega\tau_a$.

We define $\omega_{\max}$ to be the largest ω for which $\lambda^\mu(\omega)$ is significantly nonzero. As $\boldsymbol{\pi}(t)$ and $\mathbf{K}(t)$ inherit their time dependence from $\lambda^\mu(t)$, this will also be of the same order of magnitude as the largest frequency for which $\boldsymbol{\pi}(\omega)$ and $\mathbf{K}^{\mathrm{D}}(\omega)$ are significantly nonzero. Then all integrals over ω will be dominated by regions that satisfy $|\omega| \lesssim \mathcal{O}(\omega_{\max})$. We also define $\tau_{\max} = \max_{a>0} \tau_a$. This means that, provided that

$$\omega_{\max} \tau_{\max} \ll 1, \tag{5}$$

all factors of $\omega\tau_a$ that contribute to $\Delta\mathbf{p}$ will be small and the expansion can be truncated at leading order.

As shown in [3], this expression for $\Delta\mathbf{p}$ can be used to compute the excess power dissipation via

$$\mathcal{P}_{\mathrm{ex}} = T\frac{\mathrm{d}S}{\mathrm{d}t} + k_{\mathrm{B}}T\sum_{ij}\Delta p_i(t)K_{ij}(t)\ln\pi_j(t).$$

Using (4), this can be expressed as an expansion in $\omega\tau_a$ as well. When (5) is satisfied, this expansion can be truncated at leading order, which was shown in [3] to be the $n = 2$ term.

4 Power precision speed tradeoff for multidimensional signals

In this section, we will extend the results of the main text to systems with more than one varying parameter.

Suppose we have several parameters, λ^μ, with a set of unbiased estimators, $\hat{\lambda}^\mu$, for all of them. The Cramér-Rao bound states that the covariance of these estimators, $\mathbf{\Sigma}$, is bounded from below by the inverse Fisher information. This can be rephrased in terms of the precision, $\mathbf{\Phi}$, defined as

$$\Sigma^{\mu\nu} = \left\langle \hat{\lambda}^\mu\hat{\lambda}^\nu \right\rangle - \left\langle \hat{\lambda}^\mu \right\rangle \left\langle \hat{\lambda}^\nu \right\rangle, \qquad \mathbf{\Phi} = \mathbf{\Sigma}^{-1}.$$

Then the Cramér-Rao bound can be written as:

$$\mathbf{\Phi} \leq \mathbf{F}, \tag{6}$$

The diagonal elements of $\mathbf{\Sigma}$ are the squared uncertainties.

We can combine this with equations 3 and 6 of the main text to prove the bound

$$\mathrm{tr}(\mathbf{\Phi}\mathbf{V}) \leq \frac{\mathcal{P}_{\mathrm{ex}}}{(k_{\mathrm{B}}T)\,\tau_{\mathrm{min}}}. \tag{7}$$

Much like equation 9 of the main text, this inequality bounds measures of precision (inverse variance of parameter estimates), $\mathbf{\Phi}$, and speed (squared parameter velocity), $\mathbf{V}$, both desirable properties of a communication channel, in terms of a measure of power use, $\mathcal{P}_{\mathrm{ex}}$, an undesirable property of a channel. This bound also applies to an *arbitrary* physical system.

We can rewrite this bound in a different form for average quantities. In general, there will be an ensemble of signals to be sent, resulting in an ensemble of trajectories for the control parameters, $\lambda^\mu(t)$. This means that, at any instant of time, there will be a probability distribution for the current values of λ^μ and $\dot{\lambda}^\mu$. We can obtain a bound on the instantaneous power dissipation as a function of the current value of λ^μ,

$$\langle\mathcal{P}_{\mathrm{ex}}\rangle \geq (k_{\mathrm{B}}T)\,\tau_{\mathrm{min}}\,\mathrm{tr}(\mathbf{\Sigma}^{-1}\overline{\mathbf{V}}), \qquad \text{where} \quad \overline{\mathbf{V}} = \langle\mathbf{V}\rangle\,,$$

where the averages are over $\dot{\lambda}^\mu$ conditioned on λ^μ. This leads to the inequality

$$\langle\mathcal{P}_{\mathrm{ex}}\rangle\,\mathrm{tr}(\mathbf{\Sigma}\overline{\mathbf{V}}^{-1}) \geq (k_{\mathrm{B}}T)\,\tau_{\mathrm{min}}\,\mathrm{tr}(\mathbf{\Sigma}^{-1}\overline{\mathbf{V}})\,\mathrm{tr}(\mathbf{\Sigma}\overline{\mathbf{V}}^{-1}) \geq n^2(k_{\mathrm{B}}T)\,\tau_{\mathrm{min}}, \tag{8}$$

where n is the number of parameters. We used the fact that $\mathbf{\Sigma}$ and $\overline{\mathbf{V}}$ are positive-definite, therefore $\mathbf{\Sigma}\overline{\mathbf{V}}^{-1}$ is a similarity transform of the positive definite quantity $\overline{\mathbf{V}}^{-1/2}\mathbf{\Sigma}\overline{\mathbf{V}}^{-1/2}$, and therefore has positive eigenvalues. Such matrices satisfy the inequality $\mathrm{tr}(\mathbf{A})\,\mathrm{tr}(\mathbf{A}^{-1}) \geq n^2$, which can be seen by writing the traces as sums of eigenvalues. This is saturated when $\overline{\mathbf{V}} \propto \mathbf{\Sigma}$.

This inequality lower bounds the product of measures of power use, $\mathcal{P}_{\mathrm{ex}}$, imprecision (variance of parameter estimates), $\mathbf{\Sigma}$, and slowness (inverse mean squared parameter velocity), $\overline{\mathbf{V}}^{-1}$, for an *arbitrary* physical system. These are all undesirable properties of a communication system. If we wish to lower any one of these, at least one of the others will necessarily increase for a system that achieves this bound.

5 Communication through channels with non-equilibrium steady states

Here we will show how to extend the bound in equation 7 of the main text to systems that do not satisfy detailed balance. First we will need to define some mathematical quantities.

The natural inner product on the state space of an ergodic Markov process is the $\mathcal{L}^2_{\boldsymbol{\pi}}$ inner product, using the steady state distribution, $\boldsymbol{\pi}$ to weight states:

$$(\mathbf{u}, \mathbf{v}) \equiv \sum_i \pi_i u_i^* v_i = (\mathbf{u}^*)^{\mathrm{T}} \mathbf{\Pi} \mathbf{v}, \tag{9}$$

where $\mathbf{\Pi}$ is a diagonal matrix with $\Pi_{ii} = \pi_i$.

The usual notion of transposing (or hermitian conjugating) vectors and matrices is only appropriate on spaces with an Euclidean inner product. Here we define a different adjoint. For a column vector $\mathbf{u}$, a row vector $\boldsymbol{\xi}$ and a matrix $\mathbf{M}$, the adjoints must satisfy the following relations:

$$\mathbf{u}^\dagger \mathbf{v} = (\mathbf{u}, \mathbf{v}), \qquad (\boldsymbol{\xi}^\dagger, \mathbf{u}) = \boldsymbol{\xi}\mathbf{u}, \qquad (\mathbf{M}^\dagger \mathbf{u}, \mathbf{v}) = (\mathbf{u}, \mathbf{M}\mathbf{v}).$$

The adjoints are given by:

$$\mathbf{u}^\dagger = (\mathbf{u}^*)^{\mathrm{T}} \mathbf{\Pi}, \qquad \boldsymbol{\xi}^\dagger = \mathbf{\Pi}^{-1} (\boldsymbol{\xi}^*)^{\mathrm{T}}, \qquad \mathbf{M}^\dagger = \mathbf{\Pi}^{-1} (\mathbf{M}^*)^{\mathrm{T}} \mathbf{\Pi}. \tag{10}$$

When applied to transition matrices, we see that the adjoint is time-reversal.

In particular, this means that detailed balance is equivalent to the self-adjointness of $\mathbf{K} = \mathbf{K}^\dagger$, which implies that its eigenvalues are real and its eigenvectors can be chosen to be real and orthonormal under the inner product (9). Taking the adjoint of the eigenvector equation (1) then tells us that $\boldsymbol{\eta}^a = (\mathbf{u}^a)^\dagger$ (with suitable choice of normalisation) when detailed balance is satisfied, which implies the last formula in (2).

The transition matrix $\mathbf{K}$ is not invertible, as $\boldsymbol{\pi}$ and $\mathbf{e}$ are left/right null vectors. Instead, we can use the fundamental matrix of the Markov process, defined as [4][1]

$$\mathbf{Z} = \left(\frac{\mathbf{e}\boldsymbol{\pi}}{\tau} - \mathbf{K} \right)^{-1}, \tag{11}$$

where τ is an arbitrary finite positive scalar with units of time. Nothing we calculate will depend on its value. One can show that

$$\boldsymbol{\pi}\mathbf{Z} = \tau\boldsymbol{\pi}, \qquad \mathbf{Z}\mathbf{e} = \tau\mathbf{e}, \qquad \mathbf{Z}\mathbf{K} = \mathbf{e}\boldsymbol{\pi} - \mathbf{I}.$$

[1] The fundamental matrix, $\mathbf{Z}$, is related to the Drazin pseudoinverse in (3) by $\mathbf{K}^{\mathrm{D}} = \tau\mathbf{e}\boldsymbol{\pi} - \mathbf{Z}$.

The fundamental matrix, thus defined, has the same eigenvectors as K

$$\mathbf{Z} = \tau \mathbf{e}\boldsymbol{\pi} + \sum_{a>0} \tau_a \mathbf{u}^a \boldsymbol{\eta}^a.$$

For systems that have no energy function, we can write the "force", ϕ, in terms of the steady state distribution [5, 6]

$$\delta\phi^i_\mu = \frac{\partial \ln \pi_i}{\partial \lambda^\mu}.$$

Its correlation function can be written as

$$\langle \delta\phi_\mu(0)\delta\phi_\nu(t')\rangle = \sum_{ij} p_{ij}(0,t')\delta\phi^i_\mu \delta\phi^j_\nu = -\frac{\mathrm{d}}{\mathrm{d}t'} \sum_{ij} \pi_i \delta\phi^i_\mu \left[Z\mathrm{e}^{Kt'}\right]_{ij} \delta\phi^j_\nu.$$

Then the friction tensor is given by

$$g_{\mu\nu} = k_\mathrm{B}T \int_0^\infty \mathrm{d}t' \ \langle \delta\phi_\mu(0)\delta\phi_\nu(t')\rangle = k_\mathrm{B}T \sum_{ij} \pi_i Z_{ij} \delta\phi^i_\mu \delta\phi^j_\nu.$$

A similar result can be found in [3].

Noting that we need only keep the symmetric part, as the antisymmetric part will not contribute to the dissipation, as it is traced with a symmetric tensor, $\dot\lambda^\mu \dot\lambda^\nu$, in equation 3 of the main text, we can replace this with

$$g_{\mu\nu} = \frac{k_\mathrm{B}T}{2} \sum_{ij} \left(\pi_i Z_{ij} + \pi_j Z_{ji}\right) \delta\phi^i_\mu \delta\phi^j_\nu. \tag{12}$$

Armed with our definition of the adjoint from (10), we can rewrite (12) as

$$g_{\mu\nu} = (k_\mathrm{B}T) \sum_{ij} \pi_i \left(\frac{Z_{ij} + Z^\dagger_{ij}}{2}\right) \delta\phi^i_\mu \delta\phi^j_\nu = (k_\mathrm{B}T) \sum_{ij} \pi_i \widetilde{Z}_{ij} \delta\phi^i_\mu \delta\phi^j_\nu.$$

where we introduced a new matrix $\widetilde{\mathbf{Z}}$[2] with the following eigenmode decomposition:

$$\widetilde{\mathbf{Z}} \equiv \frac{\mathbf{Z} + \mathbf{Z}^\dagger}{2} = \tau \mathbf{e}\boldsymbol{\pi} + \sum_{a>0} \widetilde{\tau}_a \widetilde{\mathbf{u}}^a \widetilde{\boldsymbol{\eta}}^a. \tag{13}$$

where $\tau, \widetilde{\tau}_a$ are the eigenvalues and $\mathbf{e}, \widetilde{\mathbf{u}}^a(\boldsymbol{\pi}, \widetilde{\boldsymbol{\eta}}^a)$ are the right(left) eigenvectors of the self-adjoint matrix $\widetilde{\mathbf{Z}}$. This means that all these quantities are real, orthogonal and $\widetilde{\boldsymbol{\eta}}^a = (\widetilde{\mathbf{u}}^a)^\dagger$.

Note that $\mathbf{Z}(\mathbf{K}^\dagger) = \mathbf{Z}(\mathbf{K})^\dagger$. Therefore, for systems that satisfy detailed balance, the symmetrization in (12) is unnecessary and $\widetilde{\mathbf{Z}} = \mathbf{Z}$. For such systems, the eigenvectors and timescales that appear in (13) are the eigenvectors and timescales of the original transition matrix.

Proceeding in analogy with equation 6 of the main text, we can write

$$g_{\mu\nu} = (k_\mathrm{B}T) \sum_{a>0} \widetilde{\tau}_a \left(\widetilde{\boldsymbol{\eta}}^a \cdot \delta\boldsymbol{\phi}_\mu\right) \left(\widetilde{\boldsymbol{\eta}}^a \cdot \delta\boldsymbol{\phi}_\nu\right) \geq (k_\mathrm{B}T) \widetilde{\tau}_{\min} F_{\mu\nu}. \tag{14}$$

[2]Note that $\widetilde{\mathbf{Z}}$ is not necessarily the fundamental matrix of some Markov process. While the putative transition rate matrix, $\widetilde{\mathbf{K}} = \frac{\mathbf{e}\boldsymbol{\pi}}{\tau} - \widetilde{\mathbf{Z}}^{-1}$, does indeed have zero row sums, we do not know if the off-diagonal elements are nonnegative in general.

The inequality is meant in the operator sense, i.e. the difference between the left and right hand sides is positive semi-definite. This is essentially the same as the case with detailed balance, only now the physical interpretation of $\widetilde{\tau}_{\min}$ is less clear.

If we apply this to the power–precision–speed bounds (equation 9 of the main text, (7) and (8)), we find

$$\begin{aligned} \mathrm{Prec}(\hat{\lambda})\, V &\leq \frac{\mathcal{P}_{\mathrm{ex}}}{(k_{\mathrm{B}}T)\,\widetilde{\tau}_{\min}}, \\ \mathrm{tr}(\mathbf{\Phi V}) &\leq \frac{\mathcal{P}_{\mathrm{ex}}}{(k_{\mathrm{B}}T)\,\widetilde{\tau}_{\min}}, \\ \langle \mathcal{P}_{\mathrm{ex}} \rangle\, \mathrm{tr}(\mathbf{\Sigma}\overline{\mathbf{V}}^{-1}) &\geq n^2 (k_{\mathrm{B}}T)\,\widetilde{\tau}_{\min}. \end{aligned} \tag{15}$$

Now we'll argue that $\widetilde{\tau}_a > 0$ without detailed balance. This guarantees that the friction tensor is positive definite (the authors of [6] were unsure if this was an issue).

The numerical range (a.k.a. field of values) of a matrix $\mathbf{M}$ over a subspace $\mathcal{V}$ is defined as

$$W(\mathbf{M}, \mathcal{V}) = \left\{ \frac{(\mathbf{u}, \mathbf{M}\mathbf{u})}{\|\mathbf{u}\|^2} \,\middle|\, \mathbf{u} \in \mathcal{V}, \mathbf{u} \neq \mathbf{0} \right\},$$

where the norm is computed with the inner product (9). Strictly speaking, we will be using at the closure of this set. Setting $\mathcal{V}$ to the subspace orthogonal to $\mathbf{e}$ under the inner product (9):

$$\widetilde{\tau}_a \in W(\widetilde{\mathbf{Z}}, \mathbf{e}^{\perp}) = \mathbb{R}\mathrm{e}\, W(\mathbf{Z}, \mathbf{e}^{\perp}).$$

From the Cheeger inequality [7], we know that the real part of the numerical range of K is negative:[3]

$$\mathbb{R}\mathrm{e}\, W(\mathbf{K}, \mathbf{e}^{\perp}) < 0.$$

As K is invertible in the space $\mathbf{e}^{\perp}$, we can write $\mathbf{u} = \mathbf{K}\mathbf{v}$, $\mathbf{v} = -\mathbf{Z}\mathbf{u}$ in the following:

$$\begin{aligned} W(\widetilde{\mathbf{Z}}, \mathbf{e}^{\perp}) &= \left\{ \mathbb{R}\mathrm{e}\, \frac{(\mathbf{u}, \mathbf{Z}\mathbf{u})}{\|\mathbf{u}\|^2} \,\middle|\, \mathbf{u} \in \mathbf{e}^{\perp}, \mathbf{u} \neq \mathbf{0} \right\} \\ &= \left\{ -\mathbb{R}\mathrm{e}\, \frac{(\mathbf{K}\mathbf{v}, \mathbf{v})}{\|\mathbf{K}\mathbf{v}\|^2} \,\middle|\, \mathbf{v} \in \mathbf{e}^{\perp}, \mathbf{v} \neq \mathbf{0} \right\} \\ &= \left\{ -\mathbb{R}\mathrm{e}\, \frac{(\mathbf{v}, \mathbf{K}\mathbf{v})}{\|\mathbf{v}\|^2} \frac{\|\mathbf{v}\|^2}{\|\mathbf{K}\mathbf{v}\|^2} \,\middle|\, \mathbf{v} \in \mathbf{e}^{\perp}, \mathbf{v} \neq \mathbf{0} \right\} \\ &> 0 \\ \text{as} \quad & \frac{(\mathbf{v}, \mathbf{K}\mathbf{v})}{\|\mathbf{v}\|^2} \in W(\mathbf{K}, \mathbf{e}^{\perp}) \quad \text{and} \quad \frac{\|\mathbf{v}\|^2}{\|\mathbf{K}\mathbf{v}\|^2} > 0. \end{aligned}$$

This implies that $\widetilde{\tau}_a > 0$, and therefore the friction tensor (14) is positive definite.

[3] For non-normal $\mathbf{K}$ (wrt. the inner product (9)) this condition is stronger than the statement that its spectrum has negative real part. For normal $\mathbf{K}$, the closure of the numerical range is the convex hull of the spectrum and the two statements are equivalent.

6 Corrections to information-precision relations at finite signal speed

The inequality in equation 6 of the main text contains the Fisher information of the equilibrium distribution for the current value of $\lambda^\mu(t)$. However, when we used the Cramér-Rao bound above (6), we should use the actual probability distribution over the system's microstates. This will lag behind the current equilibrium distribution when the parameters change at a nonzero speed. As shown in [3], the correction to the distribution can be expressed as a derivative expansion. The leading term is

$$\begin{aligned} \mathbf{p}(t) &= \boldsymbol{\pi}(t) + \Delta\mathbf{p}(t), \\ \Delta\mathbf{p}(t) &= -\dot{\boldsymbol{\pi}}(t)\mathbf{Z}(t) + \mathcal{O}(\ddot{\lambda}, \dot{\lambda}^2), \end{aligned} \tag{16}$$

where $\mathbf{Z}$ is the fundamental matrix introduced in (11).

We can write the corrected Fisher information as

$$F_{\mu\nu} = \sum_i p_i \frac{\partial \ln p_i}{\partial \lambda^\mu} \frac{\partial \ln p_i}{\partial \lambda^\nu} = F^{\text{eq}}_{\mu\nu} + \Delta F_{\mu\nu}.$$

Using (16), we find

$$\begin{aligned} \Delta F_{\mu\nu} = -\dot{\lambda}^\rho \Bigg\{ \sum_{ij} \pi_i Z_{ij} \Bigg[&(\delta\phi^i_{\mu\rho} + \delta\phi^i_\mu \delta\phi^i_\rho)\delta\phi^j_\nu + (\delta\phi^i_{\nu\rho} + \delta\phi^i_\nu \delta\phi^i_\rho)\delta\phi^j_\mu - \delta\phi^i_\rho \delta\phi^j_\mu \delta\phi^j_\nu \\ &+ \delta\phi^i_\rho \sum_{kl} Z_{kl} \left(\partial_\mu K_{jk} \delta\phi^l_\nu + \partial_\nu K_{jk} \delta\phi^l_\mu \right) \Bigg] \Bigg\} + \mathcal{O}(\ddot{\lambda}, \dot{\lambda}^2), \end{aligned} \tag{17}$$

where $\phi^i_{\mu\nu} = \frac{\partial^2 E_i}{\partial\lambda^\mu \partial\lambda^\nu}$, $\delta\phi^i_{\mu\nu} = \phi^i_{\mu\nu} - \langle\phi_{\mu\nu}\rangle$ and $\partial_\mu K_{ij} = \frac{\partial K_{ij}}{\partial \lambda^\mu}$.

We see that replacing the Fisher information of the equilibrium distribution in equation 6 of the main text with the Fisher information of the current distribution results in corrections that are higher order in $\dot{\lambda}$ than the term that we have kept.

7 Dual coordinates and optimal estimators

When the receiver of the signal attempts to reconstruct it, the aim is to find the correct point on the manifold of control parameters. All coordinate systems on this manifold provide equally good descriptions of that point. However, when it comes to constructing estimators of the coordinates themselves, some coordinate systems are better than others from the point of view of estimator bias and variance.

While the Cramér-Rao bound on the error in estimating the location of this point holds in *any coordinate system*, it may be easier to construct unbiased estimators to saturate this bound in a specific coordinate system. For the exponential family of equilibrium distributions, this privileged coordinate system is the dual coordinate system [8]. If the energy is linearly dependent on the parameters λ^μ, i.e. $E = -\sum_\mu \lambda^\mu \mathcal{O}_\mu$, the dual coordinates are defined by

$$\tilde{\lambda}^\mu = \langle \mathcal{O}_\mu \rangle = -\left\langle \frac{\partial E}{\partial \lambda^\mu} \right\rangle. \tag{18}$$

These are the expectations of the operators coupled to λ^μ. As these quantities are functions of the parameters λ^μ, they provide another coordinate system for the manifold of control parameters. Any linear combination of these parameters would work equally well.

The optimal unbiased estimators for the $\tilde{\lambda}^\mu$ are

$$\hat{\tilde{\lambda}}^\mu = \mathcal{O}_\mu = -\frac{\partial E}{\partial \lambda^\mu}, \tag{19}$$

i.e. the operator to which λ^μ couples in the Hamiltonian. These estimators are unbiased, by comparison to (18). The Fisher information can in the original λ^μ coordinate system can be computed from the second derivatives of the logarithm of the partition function. Due to the fluctuation-dissipation theorem, this quantity is also equal to the covariance of the operators and the susceptibilities (up to factors of $k_\mathrm{B}T$):

$$\frac{\partial^2 \ln \mathcal{Z}}{\partial \lambda^\mu \partial \lambda^\nu} = F_{\mu\nu} = \beta^2 \left\langle \delta\mathcal{O}_\mu \delta\mathcal{O}_\nu \right\rangle = \beta \frac{\partial \left\langle \mathcal{O}_\mu \right\rangle}{\partial \lambda^\nu}.$$

Noting that the third quantity is $\beta^2 \widetilde{\Sigma}_{\mu\nu}$, the covariance of the estimators (19), and the last one is $\frac{\partial \tilde{\lambda}^\mu}{\partial \lambda^\nu}$, the Jacobian matrix for the coordinate change (18), the Fisher information in the new $\tilde{\lambda}^\mu$ coordinate system is given by

$$\widetilde{F}_{\mu\nu} = \frac{\partial \lambda^\rho}{\partial \tilde{\lambda}^\mu} F_{\rho\sigma} \frac{\partial \lambda^\sigma}{\partial \tilde{\lambda}^\nu} = \left[\beta F^{-1} \cdot F \cdot \beta F^{-1}\right]_{\mu\nu} = \beta^2 F^{-1}_{\mu\nu} = \widetilde{\Sigma}^{-1}_{\mu\nu} = \widetilde{\Phi}_{\mu\nu}.$$

Therefore, these estimators saturate the Cramér-Rao bound.

8 Example systems: further details

Here we provide further details for the example systems that were introduced in the main text.

8.1 Heavily over-damped harmonic oscillator

Here we will provide further details for the heavily damped harmonic oscillator presented in the main text. This system is described by the following Langevin equation:

$$\zeta \dot{x} = \kappa(\lambda(t) - x) + \sqrt{2\zeta k_\mathrm{B} T}\xi(t), \tag{20}$$

where $\xi(t)$ is a Gaussian process with $\langle \xi(t) \rangle = 0$ and $\langle \xi(t)\xi(t') \rangle = \delta(t - t')$. The energy of this system is given by:

$$E = \frac{1}{2}\kappa(x - \lambda)^2, \tag{21}$$

with the kinetic energy being neglected in the overdamped limit.

Introducing the quantities $\tau = \frac{\zeta}{\kappa}$ and $\sigma = \sqrt{\frac{k_\mathrm{B}T}{\kappa}}$, the solution of (20) is

$$x(t) = \int_0^\infty \frac{\mathrm{d}t'}{\tau}\, \mathrm{e}^{-t'/\tau} \left(\lambda(t - t') + \sqrt{2\tau}\sigma\xi(t - t')\right). \tag{22}$$

Therefore, $x(t)$ is a Gaussian process with

$$\begin{aligned}\langle x(t)\rangle &= \int_0^\infty \frac{\mathrm{d}t'}{\tau}\,\mathrm{e}^{-t'/\tau}\lambda(t-t') \equiv \mu(t),\\ \langle \delta x(t)\delta x(t')\rangle &= \sigma^2 \mathrm{e}^{-|t-t'|/\tau}.\end{aligned} \tag{23}$$

We can express $\mu(t)$ as a derivative expansion by Taylor expanding $\lambda(t-t')$ in t' to find

$$\mu(t) = \sum_{n=0}^{\infty}\left[-\tau\frac{\mathrm{d}}{\mathrm{d}t}\right]^n \lambda(t) \approx \lambda(t), \tag{24}$$

where the approximation is valid when the timescale over which $\lambda(t)$ varies is much larger than τ. More precisely, looking at the Fourier transforms

$$\mu(\omega) = \frac{\lambda(\omega)}{1-\mathrm{i}\,\omega\tau} = \sum_{n=0}^{\infty}\left(\mathrm{i}\,\omega\tau\right)^n \lambda(\omega). \tag{25}$$

Defining $\omega_{\max}$ as the largest ω for which $\widetilde{\lambda}(\omega)$ is significantly nonzero, when $\omega_{\max}\tau \ll 1$ as in (5), we are justified in neglecting all of the higher order terms in this series.

In this regime, the optimal unbiased estimator of $\lambda(t)$ is

$$\hat{\lambda}(t) = x(t), \qquad \mathrm{Var}(\hat{\lambda}) = \sigma^2, \qquad \mathrm{Prec}(\hat{\lambda}) = \frac{1}{\sigma^2}. \tag{26}$$

The excess power is given by

$$\begin{aligned}\mathcal{P}_{\mathrm{ex}} &= \dot{\lambda}(t)\left\langle\frac{\partial E(t)}{\partial\lambda}\right\rangle\\ &= \kappa\dot{\lambda}(t)\left(\lambda(t)-\mu(t)\right)\\ &= \kappa\dot{\lambda}(t)\int_0^\infty \mathrm{d}t'\,\mathrm{e}^{-t'/\tau}\dot{\lambda}(t-t')\\ &= \zeta\dot{\lambda}(t)\sum_{n=0}^{\infty}(-\tau)^n\frac{\mathrm{d}^{n+1}\lambda(t)}{\mathrm{d}t^{n+1}}.\end{aligned} \tag{27}$$

By the same logic used when making the approximation $\mu(t)\approx\lambda(t)$, in the regime where timescale over which $\lambda(t)$ varies is much larger than τ we can neglect the higher order terms to find

$$\mathcal{P}_{\mathrm{ex}} \approx \zeta\dot{\lambda}(t)^2. \tag{28}$$

To calculate $\tau_{\min}$, we need to look at the Fokker-Planck equation associated with (20):

$$\frac{\partial P(x,t)}{\partial t} = \frac{\partial}{\partial x}\left[\frac{(x-\lambda)P(x,t)}{\tau}\right] + \left[\frac{\sigma^2}{\tau}\right]\frac{\partial^2 P(x,t)}{\partial x^2}. \tag{29}$$

The eigenfunctions of the operator on the right are

$$\begin{aligned}\eta^n(x) &= \frac{\mathrm{e}^{-(x-\lambda)^2/2\sigma^2}}{\sqrt{2^{n+1}\pi n!}\sigma}H_n\left(\frac{x-\lambda}{\sqrt{2}\sigma}\right),\\ u^n(x) &= \frac{1}{\sqrt{2^n n!}}H_n\left(\frac{x-\lambda}{\sqrt{2}\sigma}\right),\\ \tau_n &= \frac{\tau}{n},\end{aligned} \tag{30}$$

where $H_n(x)$ are Hermite polynomials.

The "force" dual to λ is given by

$$\delta\phi(x) = -\beta\left(\frac{\partial E}{\partial\lambda} - \left\langle\frac{\partial E}{\partial\lambda}\right\rangle\right) = \frac{x-\lambda}{\sigma^2} = \frac{u^1(x)}{\sigma}. \tag{31}$$

Therefore, the coupling between λ and the eigenmodes is

$$\int \mathrm{d}x\, \eta^n(x)\delta\phi(x) = \frac{\delta_{n,1}}{\sigma}. \tag{32}$$

As λ only couples to the first mode, we have $\tau_{\min} = \tau$.

8.2 Ising ring

Here we provide the details underlying the calculations summarized in the main text for the Ising model and extend them to the construction of estimators and varying J. The Hamiltonian of this system is

$$H = -h\sum_n \sigma_n - J\sum_n \sigma_n\sigma_{n+1}.$$

The sender of the signal will vary h and J and the receiver will observe the spins. We will perform all computations at the instant when we pass through $h = 0$, although $\dot{h}$ is not necessarily zero. It will be convenient to use the notation

$$\theta = \tanh\beta h, \qquad \gamma = \tanh 2\beta J, \qquad \xi = \tanh\beta J.$$

This system undergoes Glauber dynamics [9], i.e. the rate at which spin n flips is given by

$$w_n = \frac{\alpha}{2}\left[1 - \theta\,\sigma_n + \frac{\gamma}{2}(\theta - \sigma_n)(\sigma_{n-1} + \sigma_{n+1})\right],$$

where α is an overall rate. These dynamics satisfy detailed balance.

When h and θ are zero, the relevant correlation functions have been computed [9, 10]:

$$\begin{aligned}
\langle\delta\phi_h(0)\delta\phi_h(t)\rangle &= N\beta^2\mathrm{e}^{2J}\left(\frac{1-\xi^N}{1+\xi^N}\right)\mathrm{e}^{-\alpha(1-\gamma)t},\\
\langle\delta\phi_J(0)\delta\phi_J(t)\rangle &= \beta^2\sum_{m=0}^{N-1}\frac{2(1-\gamma^2)\sin^2 q_m}{\nu(q_m)^2}\,\mathrm{e}^{-2\alpha\nu(q_m)t},\\
&\text{where}\quad \nu(q) = 1-\gamma\cos q\\
&\text{and}\quad q_m = \frac{2\pi}{N}\left(m+\frac{1}{2}\right).
\end{aligned} \tag{33}$$

All off-diagonal components vanish at $h = 0$ by symmetry. This is sufficient to compute the dissipation rate when $\dot{h}$ and $\dot{J}$ are nonzero at the instant when $h = 0$, but not for computing finite distances away from that line.

In the large N limit, the friction tensor and Fisher information are given by

$$\begin{aligned}
g_{hh} &= \frac{N\beta\mathrm{e}^{2\beta J}}{\alpha(1-\gamma)}, \quad g_{JJ} = \frac{N\beta(1+\xi^2)}{\alpha},\\
F_{hh} &= N\beta^2\mathrm{e}^{2\beta J}, \quad F_{JJ} = N\beta^2(1-\xi^2).
\end{aligned}$$

The timescales of the eigenmodes were given in [9]. They are

$$\frac{1}{\tau_a} = \sum_r \alpha\nu(q_r).$$

These can be loosely thought of multi-particle states, with each particle a plane-wave superposition of single spin flips, q_r their (distinct) momenta and $\alpha\nu(q)$ the dispersion relation. The shortest of these timescales is $\frac{1}{\alpha N}$. If we used this as $\tau_{\min}$ we would have a very loose bound. Instead, if we look at the timescales that appear in the correlation functions (33), we see that these parameters only couple to a subset of the eigenmodes. The magnetic field, h, only couples to the mode with one particle of zero momentum. The ferromagnetic interaction, J, couples to modes with two particles of equal and opposite momenta. Finding the shortest of these timescales gives

$$\tau_{\min} = \frac{1}{2\alpha(1+|\gamma|)} = \frac{\mathrm{e}^{-2\beta|J|}\cosh 2\beta J}{2\alpha}.$$

It is difficult to construct unbiased estimators for h and J. Instead, in the large N limit, we will use estimators for the following dual parameters (see (18))

$$\tilde{\lambda}^1 = \frac{\theta(1+\xi)}{(1+\zeta)(1-\xi)}, \qquad \hat{\tilde{\lambda}}^1 = \frac{\sum_n \sigma_n}{N},$$
$$\tilde{\lambda}^2 = \frac{\xi + (1-\xi)\left(\frac{\theta^2}{1+\zeta} - \frac{\zeta}{2}\right)}{1 + (1-\xi)\frac{\zeta}{2}}, \quad \hat{\tilde{\lambda}}^2 = \frac{\sum_n \sigma_n\sigma_{n+1}}{N},$$
$$\text{where} \quad \zeta = \sqrt{1 + \frac{4\theta^2\xi}{(1-\xi)^2}} - 1.$$

For small h, $\tilde{\lambda}^1 \approx \mathrm{e}^{2\beta J}\tanh\beta h$ and $\tilde{\lambda}^2 \approx \tanh\beta J$. When $h = 0$, the covariance of these estimators is

$$\Sigma^{11} = \frac{\mathrm{e}^{2\beta J}}{N}, \qquad \Sigma^{22} = \frac{\operatorname{sech}^2\beta J}{N},$$

and the friction tensor in these coordinates is

$$g_{11} = \frac{N(k_{\mathrm{B}}T)\cosh 2\beta J}{\alpha},$$
$$g_{22} = \frac{N(k_{\mathrm{B}}T)\cosh 2\beta J\cosh^2\beta J}{\alpha}.$$

These quantities can be used to investigate the power–precision–speed bound (7):

$$\frac{\mathrm{tr}(\mathbf{\Phi V})}{\mathcal{P}_{\mathrm{ex}}} = \frac{\alpha\beta}{\cosh 2\beta J}\frac{\mathrm{e}^{-2J}(\dot{\tilde{\lambda}}^1)^2 + \cosh^2\beta J(\dot{\tilde{\lambda}}^2)^2}{(\dot{\tilde{\lambda}}^1)^2 + \cosh^2\beta J(\dot{\tilde{\lambda}}^2)^2}. \tag{34}$$

This is maximized either when $\dot{\tilde{\lambda}}^1 = 0$ or when $\dot{\tilde{\lambda}}^2 = 0$, leading to

$$\frac{\mathrm{tr}(\mathbf{\Phi V})}{\mathcal{P}_{\mathrm{ex}}} \leq \frac{\alpha\beta}{\mathrm{e}^{2\beta[J]_-}\cosh 2\beta J} = \frac{\frac{1}{2}\mathrm{e}^{-2\beta[J]_+}}{(k_{\mathrm{B}}T)\,\tau_{\min}}, \tag{35}$$

We can also compute the mean power use,

$$\beta \langle \mathcal{P}_{\text{ex}} \rangle \operatorname{tr}(\boldsymbol{\Sigma}\overline{\mathbf{V}}^{-1}) = \frac{\left(\overline{V}^{11} + \overline{V}^{22}\cosh^2\beta J\right)\left(\overline{V}^{11} + \overline{V}^{22}\mathrm{e}^{2\beta J}\cosh^2\beta J\right)}{\alpha \operatorname{sech} 2\beta J \cosh^2\beta J \left(\overline{V}^{11}\overline{V}^{22} - \overline{V}^{12}\overline{V}^{21}\right)}. \tag{36}$$

This is minimized when $\overline{V}^{12} = \overline{V}^{21} = 0$ and $\frac{\overline{V}^{11}}{\overline{V}^{22}} = \mathrm{e}^{\beta J}\cosh^2\beta J$, leading to

$$\beta \langle \mathcal{P}_{\text{ex}} \rangle \operatorname{tr}(\boldsymbol{\Sigma}\overline{\mathbf{V}}^{-1}) \geq \frac{\cosh 2\beta J(1+\mathrm{e}^{\beta}J)^2}{\alpha} = \frac{\mathrm{e}^{2\beta|J|}(1+\mathrm{e}^{\beta J})^2}{2} \cdot 4\tau_{\min}. \tag{37}$$

So our bounds, (7) and (8), are tighter at weak coupling/high temperature but very loose at strong coupling/low temperature. However, the looseness of this bound does not scale with the size of the system, N, as one might have worried based on the proof of the inequality equation 6 of the main text. This is another illustration of the importance of computing the coupling of the parameters to the eigenmodes when computing $\tau_{\min}$.

If we only allow h to vary and only estimate $\tilde{\lambda}^1$, we only include the mode that h couples to when calculating $\tau_{\min}$:

$$\tau_{\min} = \frac{\mathrm{e}^{2\beta J}\cosh 2\beta J}{\alpha}.$$

In this case, we have

$$\mathcal{P}_{\text{ex}} = \frac{N(k_{\text{B}}T)\,\dot{\tilde{\lambda}}^2 \cosh 2\beta J}{\alpha}, \qquad \operatorname{Prec}\left(\hat{\tilde{\lambda}}\right) = N\mathrm{e}^{-2\beta J}.$$

We can then investigate the bound in equation 9 of the main text

$$\frac{\operatorname{Prec}(\hat{\lambda})\,V}{\mathcal{P}_{\text{ex}}} = \frac{\alpha}{(k_{\text{B}}T)\,\mathrm{e}^{2\beta J}\cosh 2\beta J} = \frac{1}{(k_{\text{B}}T)\,\tau_{\min}},$$

which saturates the bound.

8.3 A non-equilibrium four-state receptor

As an example of a system that does not satisfy detailed balance, we will study the four-state model of a single receptor in [11, Fig.1a], as shown in Figure 1. we will be treating this system as a Markov process rather than a chemical reaction. The control parameter will be the external ligand concentration, so the physical interpretation of the source of the work is unclear.

Following [11], we will assume that $k_+^{\text{on}} = k_+^{\text{off}} = k_+$. We will use the following notation

$$k_- = \sqrt{k_-^{\text{off}} k_-^{\text{on}}}, \quad \kappa = \ln \frac{k_-^{\text{off}}}{k_-^{\text{on}}}, \quad \lambda = \ln \frac{k_+[L]}{k_-}. \tag{38}$$

Activation and inactivation are described by heat bath kinetics

$$w_{\pm}^{\text{u/b}} = \frac{\alpha}{1+\mathrm{e}^{\pm\beta\Delta\mathcal{E}^{\text{u/b}}}}, \qquad \alpha \ll k_-. \tag{39}$$

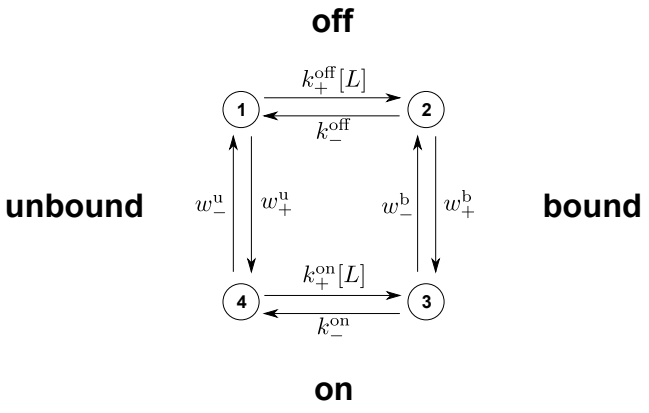

Figure 1: Single four-state receptor, adapted from [11, Fig.1a]. Arrows are labelled with transition rates. Ligand concentration is indicated by $[L]$. In states 2 and 3, the receptor is bound to a ligand molecule. In states 3 and 4, the receptor is in an activated state.

The thermodynamic driving force, which is a measure of the violation of detailed balance, is given by

$$\mathrm{e}^{-\gamma} = \frac{k_+^{\rm off} w_+^{\rm b} k_-^{\rm on} w_-^{\rm u}}{k_-^{\rm off} w_-^{\rm b} k_+^{\rm on} w_+^{\rm u}}, \qquad \Longrightarrow \qquad \beta(\Delta\mathcal{E}^{\rm u} - \Delta\mathcal{E}^{\rm b}) = \kappa - \gamma. \tag{40}$$

Following [11], we make the choice

$$\Delta\mathcal{E}^{\rm u} = -\Delta\mathcal{E}^{\rm b} = \frac{k_{\rm B}T}{2}\,(\kappa - \gamma), \tag{41}$$

At the point $\lambda = 0$, the eigenvectors and eigenvalues of the matrix $\widetilde{Z}$ that appears in (13) can be computed perturbatively in the small parameter $\frac{\alpha}{k_-}$.

$$\begin{aligned}
\widetilde{\tau}_1 &= \frac{1}{k_-(1+\mathrm{e}^{\kappa/2})} + \mathcal{O}\!\left(\frac{\alpha}{k_-^2}\right), \\
\widetilde{\tau}_2 &= \frac{1}{k_-(1+\mathrm{e}^{-\kappa/2})} + \mathcal{O}\!\left(\frac{\alpha}{k_-^2}\right), \\
\widetilde{\tau}_3 &= \frac{\cosh\left(\frac{\kappa-\gamma}{4}\right)\cosh\left(\frac{\kappa}{4}\right)}{\alpha\cosh\left(\frac{\gamma}{4}\right)} + \mathcal{O}\big(k_-^{-1}\big)\,.
\end{aligned} \tag{42}$$

The couplings to the parameter λ are

$$\begin{aligned}
\widetilde{\boldsymbol{\eta}}^1\cdot\delta\boldsymbol{\phi}_\lambda &= \frac{\operatorname{sech}\left(\frac{\kappa}{4}\right)}{2\sqrt{2}} + \mathcal{O}\!\left(\frac{\alpha}{k_-}\right), \\
\widetilde{\boldsymbol{\eta}}^2\cdot\delta\boldsymbol{\phi}_\lambda &= \frac{\operatorname{sech}\left(\frac{\kappa}{4}\right)}{2\sqrt{2}} + \mathcal{O}\!\left(\frac{\alpha}{k_-}\right), \\
\widetilde{\boldsymbol{\eta}}^3\cdot\delta\boldsymbol{\phi}_\lambda &= \frac{\tanh\left(\frac{\kappa}{4}\right) - \tanh\left(\frac{\gamma}{4}\right)}{2} + \mathcal{O}\!\left(\frac{\alpha}{k_-}\right).
\end{aligned} \tag{43}$$

As in the case of the Ising ring, these are sufficient to compute the dissipation rate when $\dot{\lambda}$ is nonzero at the instant when $\lambda = 0$, but not at a finite distance from that point.

We can use these to compute the friction tensor and Fisher information:

$$g_{\lambda\lambda} = \frac{(k_B T)\cosh\left(\frac{\kappa-\gamma}{4}\right)\sinh^2\left(\frac{\kappa-\gamma}{4}\right)}{16\alpha\cosh^3\left(\frac{\gamma}{4}\right)\cosh\left(\frac{\kappa}{4}\right)} + \mathcal{O}\big(k_-^{-1}\big)\,,$$
$$F_{\lambda\lambda} = \frac{\cosh\left(\frac{\kappa-2\gamma}{4}\right)}{16\cosh^2\left(\frac{\gamma}{4}\right)\cosh\left(\frac{\kappa}{4}\right)} + \mathcal{O}\left(\frac{\alpha}{k_-}\right).$$

From (42), we see that $\widetilde{\tau}_{\min} = \frac{1}{k_-(1+e^{|\kappa|/2})}$, so generically the bound (14) is loose by a factor $\mathcal{O}(k_-/\alpha)$. This is because the system has one very long timescale, $\widetilde{\tau}_3$, and two very short timescales, $\widetilde{\tau}_1$ and $\widetilde{\tau}_2$, all of which couple to the parameter λ.[4] At the special parameter values $\gamma = \kappa$, the parameter does not couple to the slowest timescale and the bound is only loose by a factor of $\frac{1}{2}(1 + e^{|\kappa|/2})$. However, this is the point where $\Delta\mathcal{E}^{\mathrm{u}} = \Delta\mathcal{E}^{\mathrm{b}}$ (see (40)), so the relative occupation of the on/off states contains no information about $[L]$.

Defining an observable σ that is +1 in the on states and -1 in the off states, we can use it as an unbiased estimator for the dual parameter $\tilde{\lambda}$ (see (18))

$$\tilde{\lambda} = \frac{\sinh\left(\frac{\kappa-\gamma}{4}\right)\sinh\lambda}{\cosh\left(\frac{\kappa-\gamma}{4}\right)\cosh\lambda + \cosh\left(\frac{\kappa+\gamma}{4}\right)},$$
$$\mathrm{Var}\Big(\hat{\tilde{\lambda}}\Big) = 1 - \tilde{\lambda}^2 + \mathcal{O}\left(\frac{\alpha}{k_-}\right),$$
$$\mathrm{Prec}\Big(\hat{\tilde{\lambda}}\Big) = \frac{1}{1-\tilde{\lambda}^2} + \mathcal{O}\left(\frac{\alpha}{k_-}\right).$$

This estimator is more sensible when we consider many independent receptors.This will scale down the estimator variance by $1/N$ and scale up the power consumption by N. The parameter will only couple to the eigenmodes with timescales $\widetilde{\tau}_{1,2,3}$, so $\widetilde{\tau}_{\min}$ will be unchanged.

With this parameterization, the friction tensor is

$$g_{\tilde{\lambda}\tilde{\lambda}} = \frac{(k_B T)\cosh\left(\frac{\kappa-\gamma}{4}\right)\cosh\left(\frac{\kappa}{4}\right)}{\alpha\cosh\left(\frac{\gamma}{4}\right)} + \mathcal{O}\big(k_-^{-1}\big)\,,$$

We can then compute all quantities in the bound (15) to find

$$\frac{\mathrm{Prec}(\hat{\lambda})\,V}{\mathcal{P}_{\mathrm{ex}}} = \frac{\alpha\beta\cosh\left(\frac{\gamma}{4}\right)}{\cosh\left(\frac{\kappa-\gamma}{4}\right)\cosh\left(\frac{\kappa}{4}\right)} + \mathcal{O}\big(k_-^{-1}\big) \ll \frac{1}{(k_B T)\,\widetilde{\tau}_{\min}}. \tag{44}$$

We see that the thermodynamic driving force, γ, has no effect on the right hand side of this bound. What it does is allow us to get closer to the bound by reducing the timescale of the slowest mode, as shown in Figure 2.

When $|\kappa|$ is large, the coupling to the two fastest modes becomes very small, as seen in (43). In this regime, one could neglect these two modes and set $\widetilde{\tau}_{\min} = \widetilde{\tau}_3$. In this case, the bound (15) would be saturated.

We see in Figure 2, that at fixed κ it is always helpful to increase γ (with the same sign as κ). However, at fixed γ this is minimized at $\kappa = \frac{\gamma}{2}$. Note that we made a number of assumptions in the choice of parameters in (38), (39) and (41), following [11], as well

[4] This appears to still be true away from the special point $\lambda = 0$, but the algebra is much more complicated.

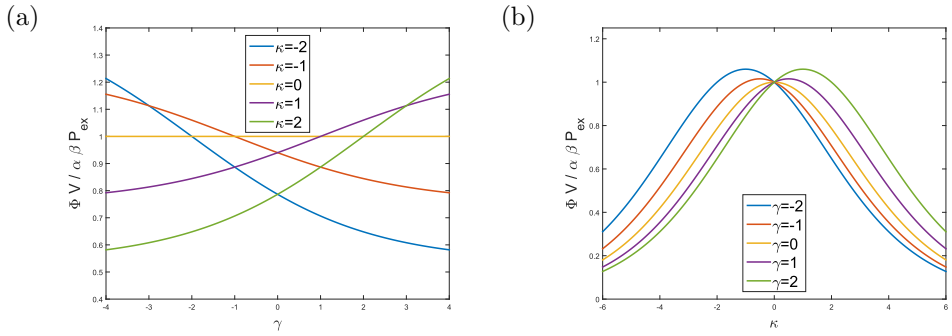

Figure 2: Power-precision-speed trade-off as a function of (a) non-equilibrium parameter, γ, and (b) log unbinding ratio, κ.

as working in the regime where the ligand concentration varies slowly compared to the intrinsic timescales of the system and neglecting receptor cooperativity. In addition, we only computed excess power, neglecting the power consumed to maintain the non-equilibrium steady state. Furthermore, the levels of ATP, etc. are needed to support many other cellular processes. Therefore, the special value $\gamma = 2\kappa$ should not be taken too seriously as a prediction. Note that for $\kappa < \gamma$, the occupation of the on states is anticorrelated with $[L]$.

References

[1] D. A. Sivak and G. E. Crooks, "Thermodynamic Metrics and Optimal Paths," *Phys. Rev. Lett.* **108** (May, 2012) 190602, `arXiv:1201.4166 [cond-mat.stat-mech]`.

[2] P. R. Zulkowski, D. A. Sivak, G. E. Crooks, and M. R. Deweese, "Geometry of thermodynamic control," *Phys. Rev. E* **86** (Oct., 2012) 041148, `arXiv:1208.4553 [cond-mat.stat-mech]`.

[3] D. Mandal and C. Jarzynski, "Analysis of slow transitions between nonequilibrium steady states," `arXiv:1507.06269 [cond-mat.stat-mech]`.

[4] J. Kemeny and J. Snell, *Finite markov chains*. Springer, 1960.

[5] T. Hatano and S.-i. Sasa, "Steady-State Thermodynamics of Langevin Systems," *Phys. Rev. Lett.* **86** (Apr., 2001) 3463–3466, `arXiv:cond-mat/0010405 [cond-mat.stat-mech]`.

[6] P. R. Zulkowski, D. A. Sivak, and M. R. DeWeese, "Optimal control of transitions between nonequilibrium steady states.," *PloS one* **8** (Jan., 2013) e82754, `arXiv:1303.6596 [cond-mat.stat-mech]`.

[7] G. F. Lawler and A. D. Sokal, "Bounds on the L^2 Spectrum for Markov Chains and Markov Processes: A Generalization of Cheeger's Inequality," *Transactions of the American Mathematical Society* **309** (1988) no. 2, 557–580.

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

[9] R. J. Glauber, "Time-Dependent Statistics of the Ising Model," *Journal of Mathematical Physics* **4** (Dec., 1963) 294.

[10] P. Mayer and P. Sollich, "General solutions for multispin two-time correlation and response functions in the Glauber-Ising chain," *Journal of Physics A: Mathematical and General* **37** (Jan., 2004) 9–49, `arXiv:cond-mat/0307214 [cond-mat.stat-mech]`.

[11] M. Skoge, S. Naqvi, Y. Meir, and N. S. Wingreen, "Chemical Sensing by Nonequilibrium Cooperative Receptors.," *Phys. Rev. Lett.* **110** (June, 2013) , `arXiv:1307.2930 [q-bio.MN]`.