Nonequilibrium cooperative sensing

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While cellular sensing relies on both cooperation between receptors and energy consumption to suppress noise, their combined effect is not well understood. Here we introduce a minimal model of interacting sensors which allows for the detailed exploration of signal statistics and cooperation strategies in the context of optimal sensing. For two sensors we show that the sensing strategy which maximizes the mutual information between the signal and the sensors depends both on the noise level and the statistics of the signals. For signals on a single sensor, nonequilibrium, asymmetric couplings result in maximum information gain in the noise-dominated limit while for joint, correlated signals, the improvement is greatest in the low-noise limit. In particular we show that optimal sensing does not always require energy consumption. We detail the difference in mechanism behind nonequilibrium improvement for univariate and correlated signals and our results provide insight into the principles of optimal sensor design.

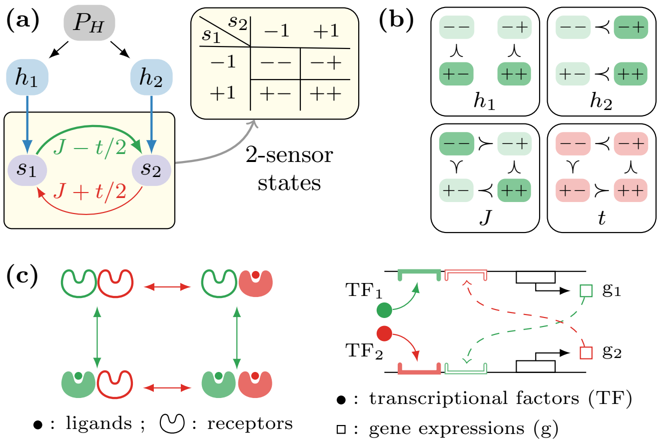
INTRODUCTION

Cells are surrounded by chemical cocktails which carry important information such as the number of other cells in the vicinity, the presence of foreign cells and the locations of food sources or toxins. The ability to reliably measure chemical concentrations is therefore essential to cellular functions. Indeed cells can exhibit extremely high sensitivity in chemical sensing, for example our immune response can be triggered by only one foreign ligand [1] and *Escherichia coli* chemotaxis responds to nanomolar changes in chemical concentration [2]. This sensitivity raises important questions about the design principles behind the underlying cellular machinery.

Although cellular sensing remains an active area of research [3, 4], one important component is the ability to suppress noise that originates from stochasticity in ligand diffusions, ligand-receptor binding-unbinding and downstream biochemical networks. In general noise reduction involves two mechanisms — receptor cooperativity [5–7] and energy consumption [8–11] — both of which are far from fully understood [3, 4]. While it is well known that receptor cooperativity can increase chemical sensitivity in steady state [5], it is independent receptors that maximize the signal-to-noise ratio when a finite signal integration time is taken into account [12]. Even when receptor interactions are coupled to energy consumption, cooperative sensing, which is now nonequilibrium, offers only a modest improvement on separate receptors [13]. In these studies however, the effects of stochasticity in signal integration are largely ignored, resulting in an underestimation of the noise. Although energy consumption can suppress noise in downstream networks [10, 14], signal integration is a long way from noiseless. If downstream networks cannot reduce noise, can cooperativity enhance sensing performance? Does energy consumption allow further improvement?

We consider a simple system of two information processing units (sensors), an abstraction of a pair of coupled chemoreceptors or two transcriptional regulations with cross-feedback [Fig. 1(c)]. The sensor states depend on noises, signals (e.g., chemical changes) and sensor interactions, which can couple to energy consumption. Instead of the signal-to-noise ratio which relies on signal integration, we use the mutual information between the signals and the states of the system as the measure of sensing performance, Physically, the mutual information corresponds to the reduction in the uncertainty (entropy) of the signal (input) once the system state (output) is known. The mutual information between the signals and sensors is also the maximum information the system can learn about the signals as noisy downstream networks can only further degrade the signals. However computing mutual information requires the knowledge of the prior distribution of the signals. Importantly the prior encodes some of the information about the signal, e.g., signals could be more likely to take certain values or drawn from a set of discrete values. Although the signal prior in cellular sensing is generally unknown, one simple, physically plausible choice is the Gaussian distribution, which is the least informative distribution for a given mean and variance.

In the following we first introduce a general model for nonequilibrium coupled binary sensors. Specializing to the case of two sensors, we obtain the steady-state distribution of the two-sensor states for a specified signal. We then determine sensing strategy that maximizes the mutual information for a given noise level and signal prior. Finally we show that depending on whether the signal is present at both sensors, the optimal sensing strategy



$s_1 \backslash s_2$	-1	$+1$
-1	$--$	$-+$
$+1$	$+-$	$++$

FIG. 1. A minimal model of a sensory complex which includes both external signals and interactions between the sensors. (a) Model schematic. Each sensor is endowed with binary states $s_1 = \pm 1$ and $s_2 = \pm 1$, so that the sensor complex admits four states: $--$, $-+$, $+-$ and $++$. A signal H is drawn from the prior distribution P_H and couples to each sensor via the local fields h_1 and h_2. The coupling between the sensors is described by $J_{12} = J + t/2$ and $J_{21} = J - t/2$, and can be asymmetric so in general $J_{12} \neq J_{21}$. (b) The field h_i favors the states with $s_i = +1$ (top row); the coupling J favors the correlated states $--$ and $++$ (bottom left); and the nonequilibrium drive t generates a cyclic bias (bottom right). (c) Physical examples of a sensor system with two interacting sensors: a pair of chemoreceptors with receptor coupling (left) and a pair of transcriptional regulations of gene expressions with cross-feedback (right).

— particularly the mechanisms behind nonequilibrium performance improvement — can be very different.

MODEL

We provide an overview of our model in Fig. 1(a). Here a sensor complex is a network of interacting sensors, each endowed with binary states $s = \pm 1$, e.g., whether a receptor or gene regulation is active. The state of each sensor depends on that of the others through interactions, and on the local bias fields generated by a signal; for example, an increase in ligand concentration favors the occupied state of a chemoreceptor. Due to noise, the sensor states are not deterministic so that the probability of every state is finite. We encode the effects of signals, interactions and intrinsic noise in the inversion rate — the rate at which a sensor switches its state. For the sensor i, we define the inversion rate as follows

$$\Gamma^i_{S|H} \equiv \mathcal{N}_H \exp\left[-\beta\left(h_i s_i + \sum_j^{j\neq i} J_{ij} s_i s_j\right)\right], \qquad (1)$$

where $S = \{s_i\}$ denotes the present state of the sensor system, $H = \{h_i\}$ the signal, J_{ij} the interactions, and β the sensor reliability (i.e., the inverse intrinsic noise level). The normalization $\mathcal{N}_H$ sets the overall timescale but drops out in steady state.

Given an input signal H, the conditional probability of the states of the sensor complex in steady state $P_{S|H}$ is obtained by balancing the probability flows into and out of each state while conserving the total probability $\sum_S P_{S|H} = 1$,

$$\sum_i \left[P_{S^i|H}\Gamma^i_{S^i|H} - P_{S|H}\Gamma^i_{S|H}\right] = 0, \qquad (2)$$

where S^i is related to S by the inversion $s_i \to -s_i$.

In equilibrium, detailed balance imposes an additional constraint forbidding net probability flow between any two states,

$$P^{\mathrm{eq}}_{S^i|H}\Gamma^{i,\mathrm{eq}}_{S^i|H} - P^{\mathrm{eq}}_{S|H}\Gamma^{i,\mathrm{eq}}_{S|H} = 0, \qquad (3)$$

and this condition can only be satisfied by symmetric interactions $J_{ij} = J_{ji}$. Thus in equilibrium we define the free energy

$$F_{S|H} = -\sum_i h_i s_i - \sum_{i,j}^{i<j} J_{ij} s_i s_j, \qquad (4)$$

such that the inversion rate depends on the initial and final states of the system only through the change in free energy

$$\Gamma^{i,\mathrm{eq}}_{S|H} = \mathcal{N}_H \exp\left[-\tfrac{1}{2}\beta\left(F_{S^i|H} - F_{S|H}\right)\right]. \qquad (5)$$

Together with the detailed balance condition [Eq. (3)], this equation leads directly to the Boltzmann distribution $P^{\mathrm{eq}}_{S|H} = e^{-\beta F_{S|H}}/\mathcal{Z}^{\mathrm{eq}}_H$ with the partition function $\mathcal{Z}^{\mathrm{eq}}_H$.

Asymmetric interactions $J_{ij} \neq J_{ji}$ break detailed balance, resulting in a nonequilibrium steady state. For concreteness, we specialize to the case of two coupled sensors $S = (s_1, s_2)$, belonging to one of the four states: $--$, $-+$, $++$ and $+-$ [Fig. 1(a)]. For convenience we introduce two new variables, the coupling J and nonequilibrium drive t, and parametrize J_{12} and J_{21} such that $J_{21} = J - t/2$ and $J_{12} = J + t/2$ [Fig. 1(a)]. The effects of the bias fields (h_1, h_2), coupling J and nonequilibrium drive t are summarized in Fig. 1(b). Compared to the equilibrium inversion rate [Eq .(5)], a finite nonequilibrium drive leads to a modification of the form

$$\Gamma^i_{S|H} = \begin{cases} e^{\frac{1}{2}\beta t}\Gamma^{i,\mathrm{eq}}_{S|H} & \text{for cyclic } S \to S^i, \\ e^{-\frac{1}{2}\beta t}\Gamma^{i,\mathrm{eq}}_{S|H} & \text{for anticyclic } S \to S^i, \end{cases} \qquad (6)$$

where $S \to S^i$ is cyclic if it corresponds to one of the transitions in the cycle $-- \to -+ \to ++ \to +- \to --$, and anticyclic otherwise. Recalling that a probability flow vanishes in equilibrium, it is easy to see that, depending on whether t is positive or negative, the nonequilibrium inversion rates result in either cyclic or anticyclic steady state probability flow.

A net probability flow in steady state leads to power dissipation. By analogy with Eq. (5), we write down the effective change in free energy of a transition $S \to S^i$,

$$\Delta F^{\text{eff}}_{S\to S^i} = \Delta F^{\text{eq}}_{S\to S^i} - \begin{cases} t & \text{for cyclic } S \to S^i, \\ -t & \text{for anticyclic } S \to S^i. \end{cases}$$

That is, the system loses energy of $4t$ per complete cycle. To conserve total energy, the sensor complex must consume the same amount of energy it dissipates to the environment. The nonequilibrium drive also modifies the steady state probability distribution. Solving Eq. (2), we have

$$P_{S|H} = \exp\left[-\beta\left(F_{S|H} + \delta F_{S|H}\right)\right]/\mathcal{Z}_H, \tag{7}$$

where $F_{S|H}$ denotes the free energy in equilibrium [Eq. (4)]. The nonequilibrium effects are encoded in the effective, noise-dependent energy shift

$$\delta F_{S|H} = -\frac{1}{\beta}\ln\left[e^{\frac{1}{2}\beta t s_1 s_2}\frac{\cosh[\beta(h_1 - t s_2)]}{\cosh\beta h_1 + \cosh\beta h_2} + e^{-\frac{1}{2}\beta t s_1 s_2}\frac{\cosh[\beta(h_2 + t s_1)]}{\cosh\beta h_1 + \cosh\beta h_2}\right], \tag{8}$$

and note that $\delta F_{S|H} \to 0$ as $t \to 0$.

MUTUAL INFORMATION

We quantify sensing performance through the mutual information between the signal and sensor complex $I(S;H)$, which measures the reduction in the uncertainty (entropy) in the signal H once the system state S is known and vice versa. For convenience we introduce the "output" and "noise" entropies where output entropy is the entropy of the two-sensor state distribution $\mathcal{S}[P_S] = \mathcal{S}[\sum_H P_H P_{S|H}]$ whereas the noise entropy is defined as the average entropy of the conditional probability of sensor states $\sum_H P_H \mathcal{S}[P_{S|H}]$. Here P_H is the prior distribution from which a signal is drawn and the entropy of a distribution is defined by $\mathcal{S}[P_X] = -\sum_X P_X \log_2 P_X$. In terms of the output and noise entropies, the mutual information is given by

$$I(S;H) = \underbrace{\mathcal{S}[\textstyle\sum_H P_H P_{S|H}]}_{\text{Output entropy}} - \underbrace{\textstyle\sum_H P_H \mathcal{S}[P_{S|H}]}_{\text{Noise entropy}}, \tag{9}$$

and we seek the sensing strategy (the coupling J and nonequilibrium drive t) that maximizes the mutual information for given reliability β and signal priors P_H.

UNIVARIATE SIGNALS

We consider univariate signals $H = (h, 0)$ drawn from a Gaussian distribution with zero mean and unit variance $P_H = e^{-h^2/2}/\sqrt{2\pi}$. In this case the signal couples

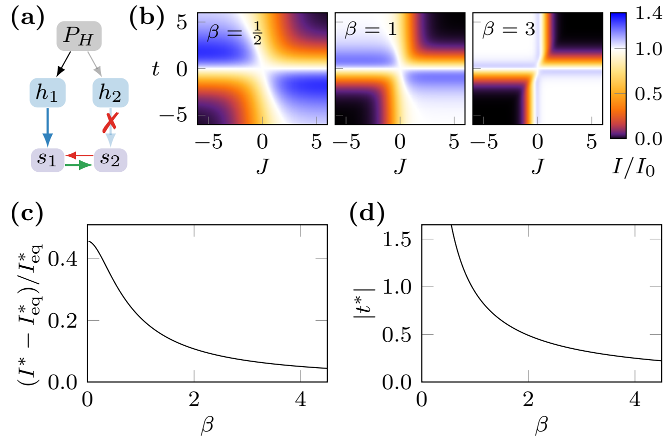


FIG. 2. Nonequilibrium strategies produce large gains in the maximum mutual information for the noise-dominated regime of univariate Gaussian signals. (a) We assume that the signal directly influences only one sensor so that $H = (h, 0)$ with prior distribution $P_H = e^{-h^2/2}/\sqrt{2\pi}$. (b) Mutual information in the parameter space of the coupling J and nonequilibrium drive t. I_0 is the mutual information of a noninteracting system and is colored in white. The mutual information is maximum at finite J and t; the optimal sensing strategy is always nonequilibrium. For an equilibrium strategy, the mutual information is insensitive to sensor coupling as illustrated by the white band $I = I_0$ along the line $t = 0$. (c) The nonequilibrium gain as a function of sensor reliability β. With increasing β, the fractional difference between the maximum mutual information for equilibrium and nonequilibrium sensors (I^*_{eq} and I^*, respectively) decreases from the maximum of 46% at $\beta = 0$, suggesting that the nonequilibrium enhancement results from the ability to suppress intrinsic noise. (d) The magnitude of the optimal nonequilibrium drive $|t^*|$ decreases with β.

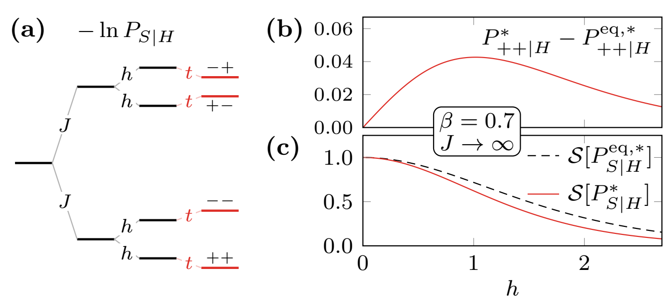


FIG. 3. For univariate signals, the nonequilibrium improvement relies on the reduction of intrinsic noises in sensor kinetics. (a) The splitting of the effective free energy as the coupling J, bias field h and nonequilibrium drive t are turned on successively. The nonequilibrium drive t modifies the energy gaps originally split by h [Eq. (10)]. By letting $|J| \to \infty$, the system can select the pair of states that exhibits a wider energy gap. Thus, compared to equilibrium sensing, nonequilibrium sensors can be more deterministic as manifest in both (b) the conditional probability distribution and (c) the corresponding entropy. As the output entropy is fixed at one bit in this effective two-level system, the reduction in noise entropy (the entropy of the conditional probability averaged over the prior) leads to higher mutual information [Eq. (9)].

directly to the s_1 sensor and affects s_2 only through interactions [see Fig. 2(a)], and could arise, for example, from two receptors that respond to different ligands. For equilibrium sensing, we maximize the mutual information under the constraint $t = 0$. We find that the mutual information is completely insensitive to the sensor coupling, as illustrated by the white color, which indicates the mutual information in a noninteracting system, along the line $t = 0$ in Fig. 2(b). This is because although cooperativity can reduce noise entropy, the output entropy decreases by the same amount since the coupling J favors the same outputs ($++$ and $--$ for $J > 0$ and $+-$ and $-+$ for $J < 0$) regardless of signals.

When we maximize the mutual information in the full J-t parameter space [Fig. 2(b)] we see that an improvement on equilibrium sensing at all reliability $\beta > 0$,with a maximum gain of 46% in the noise-dominated limit, Fig. 2(c). Although the nonequilibrium gain is finite for completely unreliable sensors ($\beta = 0$), the mutual information vanishes for both equilibrium and nonequilibrium sensing as expected [15]. In the absence of intrinsic noise ($\beta \to \infty$), both equilibrium and nonequilibrium sensing yields a maximum mutual information of one bit [15], suggesting that the nonequilibrium improvement relies on the reduction of the intrinsic noise at the sensors. Unlike the equilibrium case, the maximum mutual information depends on both the coupling J and the nonequilibrium drive t and we find that the optimal sensing corresponds to an infinite J and a finite t [Fig. 2(d)]. The signs of the optimal parameters J^* and t^* are opposite [Fig. 2(b)], meaning that the influence of s_1 over s_2 is stronger($|J_{21}| - |J_{12}| = |t| > 0$) and this is an expected result since only s_1 is directly coupled to the signal.

To understand the mechanism behind the nonequilibrium improvement, we expand the nonequilibrium energy shift δF [Eq. (8)] to the linear order in t,

$$\delta F = -\frac{1}{2}\tanh^2\left(\frac{\beta h}{2}\right) t s_1 s_2 + \tanh\left(\frac{\beta h}{2}\right) t s_2 + \mathcal{O}(t^2). \tag{10}$$

The first term of the expansion provides an effective sensor coupling while the second generates an effective bias field on s_2. This results in an adjustment of the free energy gaps, originally split by the external bias field, Fig. 3(a). As the sign of this adjustment depends on the correlation between the individual sensor states, the system can eliminate the pair of states that exhibits a narrower gap by letting $|J| \to \infty$. Due to a wider gap, a nonequilibrium system can be more deterministic compared to an equilibrium one. The feature is clearly visible in both the conditional probability distribution and the corresponding entropy, Fig. 3(b)&(c). As the output entropy is fixed at one bit in a two-level system, the reduction in noise entropy (the entropy of the conditional probability averaged over the prior) leads directly to higher mutual information [Eq. (9)].

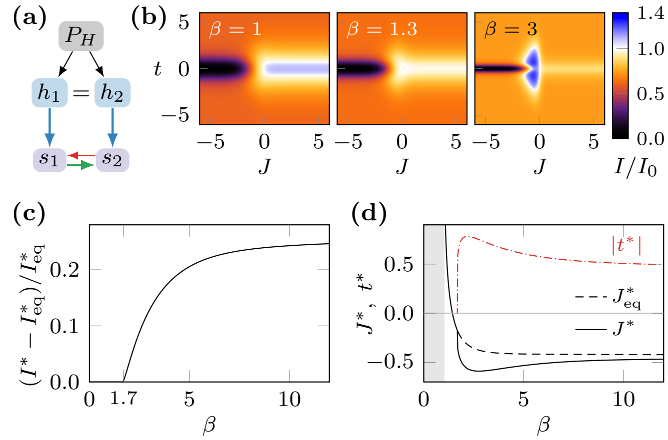


FIG. 4. The nonequilibrium information gain is largest in the noiseless limit for perfectly correlated Gaussian signals. (a) We consider a sensor complex driven with signal $H = (h, h)$ with $P_H = e^{-h^2/2}/\sqrt{2\pi}$. (b) The mutual information in units of noninteracting-sensor mutual information I_0 as a function of the coupling J and nonequilibrium drive t. A nonequilibrium drive increases the maximum mutual information only when the intrinsic noise is low, i.e., large β. (c) The nonequilibrium gain as a function of sensor reliability β. The gain grows from zero at $\beta = 1.7$ and increases with β, suggesting that the enhancement results from the ability to distinguish additional signal features. (d) Optimal sensing strategy for varying noise levels. For $\beta < 1$ (shaded), the mutual information is maximized by an equilibrium system ($t^* = 0$) with infinitely strong coupling. The equilibrium strategy remains optimal for $\beta < 1.7$ with a coupling J^* (solid) that decreases with β and exhibits a sign change at $\beta = 1.4$. At bigger β, the optimal coupling in the equilibrium case (dashed) continues to decreases but equilibrium sensing becomes suboptimal. For $\beta > 1.7$, the mutual information is maximized by a finite nonequilibrium drive (dot-dashed) and negative coupling.

PERFECTLY CORRELATED SIGNALS

In the case of perfectly correlated Gaussian signals, the direct coupling of the bias fields to both sensors leads to a completely different sensing strategy Fig. 4(b), even as the signal distribution is identical to the univariate example. When we maximize the mutual information in the J-t parameter space we find that nonequilibrium sensing allows further improvement only for $\beta > 1.7$ and that the nonequilibrium gain remains finite as $\beta \to \infty$ [Fig. 4(c)]. In Fig. 4(d), we show the optimal parameters for both equilibrium and nonequilibrium sensing. The optimal coupling diverges for sensors with $\beta < 1$, decreases with increasing β and exhibits a sign change at $\beta = 1.4$. For $\beta > 1.7$, the nonequilibrium drive is finite and the couplings are distinct $J^* \neq J^*_{eq}$.

To reveal the mechanisms behind optimal sensing, we compare the output and noise entropies of equilibrium and nonequilibrium sensing at optimal with that of noninteracting sensors for a representative $\beta = 4$, Fig. 5(a). Here, anticooperativity ($J^*_{eq} < 0$) enhances mutual infor-

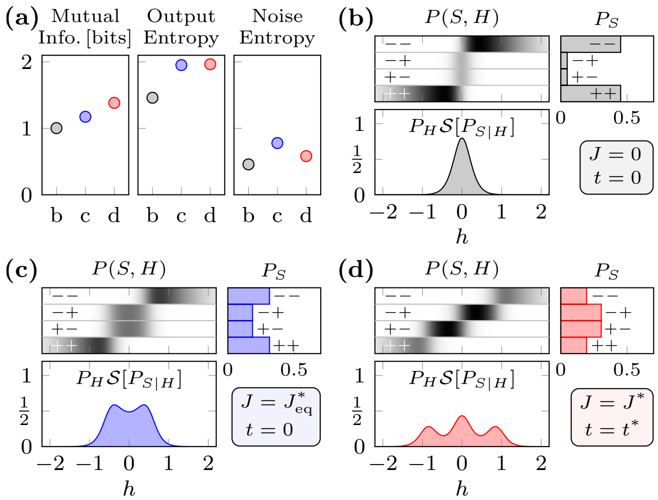


FIG. 5. For perfectly correlated Gaussian signals, in the low noise limit, sensor anticooperativity ($J < 0$) increases the mutual information by maximizing the output entropy while nonequilibrium drive ($t \neq 0$) provides further improvement by suppressing noise entropy. (a) We compare the mutual information, output and noise entropies for three sensing strategies at $\beta = 4$: (b, grey) noninteracting, (c, blue) equilibrium and (d, red) nonequilibrium cases. For each case we find the configuration that maximizes the mutual information under the respective constraints. (b)-(d) Signal-sensor joint probability distribution $P(S, H)$, output distribution P_S, and the "signal-resolved noise entropy" $P_H \mathcal{S}[P_{S|H}]$. Note that the noise entropy is the area under the signal-resolved curve. As the optimal coupling is negative ($J < 0$) at $\beta = 4$ (see Fig. 4(d)), the states $-+$ and $+-$, which are heavily suppressed in a noninteracting system (b), become more probable in the interacting cases, resulting in a more even output distribution (c,d) and thus a larger output entropy (a). However anticooperativity also increases noise entropy in the equilibrium case (a) since the states $-+$ and $+-$ are degenerate (c). By lifting this degeneracy (d), a nonequilibrium system can suppress the noise entropy and further increase mutual information (a).

mation in equilibrium sensing by maximizing the output entropy whereas nonequilibrium drive produces further improvement by lowering noise entropy. Compared to the noninteracting case Fig. 5(b), optimal equilibrium sensing distributes the probability of the output states, P_S, more evenly [Fig. 5(c)], resulting in higher output entropy. This is because a negative coupling $J < 0$ favors the states $+-$ and $-+$, which are much less probable than $++$ and $--$ in a noninteracting system [Fig. 5(b)]. However this also leads to higher noise entropy since the states $+-$ and $-+$ are equally likely for a given signal [Fig. 5(c)]. By lifting the degeneracy between the states $+-$ and $-+$, nonequilibrium sensing suppresses the noise entropy while maintaining a relatively even distribution of output states, Fig. 5(d).

Although anticooperativity increases output entropy more than noise entropy at $\beta = 4$, it is not the optimal strategy for $\beta < 1.4$. For noisy sensors, a positive coupling $J > 0$ yields higher mutual information, Fig. 4(d). This is because when the noise level is high, the output entropy is nearly saturated and an increase in mutual information must result primarily from the reduction of noise entropy by suppressing some output states — in this case, the states $+-$ and $-+$ are suppressed by $J > 0$.

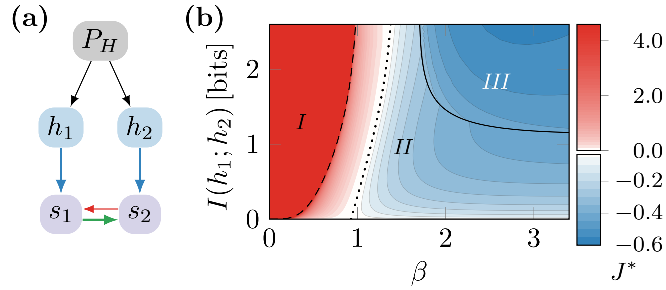


FIG. 6. Nonequilibrium sensing is optimal in the low-noise limit for correlated Gaussian signals. (a) We assume that the signal directly influences both sensors with varying correlation, Eq. (11). (b) The optimal coupling J^* as a function of sensor reliability β and the mutual information between the signals $I(h_1, h_2)$. The optimal coupling diverges $J^* \to \infty$ at small β (region *I*, left of the dashed curve) and decreases with larger β. Between the dashed and solid curves (region *II*), the mutual information is maximized by equilibrium sensors with a finite J^* that changes from cooperative (red) to anticooperative (blue) at the dotted line. Nonequilibrium sensing is the optimal strategy for signals with relatively high correlations in the low noise limit (region *III*, above the solid curve).

CORRELATED SIGNALS

The bias fields at two sensors are generally different, for example chemoreceptors with distinct ligand specificity or exposure, and we consider signals $H = (h_1, h_2)$, drawn from a correlated bivariate Gaussian distribution [Fig. 6(a)],

$$P_H = \frac{1}{2\pi\sqrt{1-\alpha^2}} \exp\left(-\frac{h_1^2 - 2\alpha h_1 h_2 + h_2^2}{2(1-\alpha^2)}\right), \quad (11)$$

where $\alpha \in [-1, 1]$ is the correlation between h_1 and h_2. Similarly to the case of perfectly correlated signals ($\alpha = 1$), at small β we find that the mutual information is maximized by an equilibrium system ($t^* = 0$). In Fig. 6(b), we show that the optimal strategy is cooperative ($J > 0$) at small β and switches to anticooperative ($J < 0$) around $\beta \sim 1$. Below a certain value of β, the optimal coupling diverges $J^* \to \infty$. In addition, sensor cooperativity is less effective for less correlated signals because while more information is encoded in a less correlated prior, the information capacity of a sensor complex decreases as a cooperative strategy relies on output suppression (which reduces both noise and output entropies).

As sensors become less noisy, the optimal strategy is nonequilibrium ($t^* \neq 0$) only when the signal correlation is relatively high. To understand this, we recall that for perfectly correlated signal ($\alpha = 1$), nonequilibrium sensing suppress noise entropy by lifting the degeneracy between output states (Fig. 5). As α approaches zero, the states of a sensor complex are less likely to be degenerate (since the probability that $h_1 \approx h_2$ is smaller) and a nonequilibrium strategy allows no further improvement.

CONCLUSION

We introduced and analyzed a minimal model of a sensor complex that encapsulates both sensor interactions and energy consumption. For correlated signals we find that sensor interactions can increase sensing performance of two binary sensors, as measured by the steady-state mutual information between the signal and the states of the sensor complex. The nature of the optimal sensor coupling does not always reflect the correlation in the signal; for positively correlated signals, the optimal sensing strategy changes from cooperativity to anticooperativity as the noise level decreases, see also Ref. [16]. Surprisingly we find that energy consumption leads to further improvement only when the noise level is low and the signal correlation high. Our results offer a new insight into an optimal design principle for sensors in the low noise regime.

When the signal generates a bias field at only one sensor, the mutual information is maximized by an infinitely strong sensor coupling but only when energy consumption is allowed; otherwise, the sensing performance is independent of sensor interactions. Indeed, previous work showed that energy consumption can increase the sensitivity and the signal-to-noise ratio in a single four-state receptor [13, 17]. For this sensing scenario our model is equivalent to the four-state model when the states of the two sensors are identified with the vacant, occupied states and binary conformal states.

Our analysis does not rely on the specific Gaussian form of the prior distribution. Indeed for correlated signals the nonequilibrium improvement in the low-noise, high-correlation limit is generic for most continuous priors and our results for univariate signals hold also for discrete priors [15].

Although we considered a simple model here, our approach provides a general framework for understanding collective sensing strategies across different biological systems from chemoreceptors to transcriptional regulation to a group of animals in search of mates or food. In particular, possible future investigations include the mechanisms behind collective sensing strategies in more complex, realistic models, perhaps with downstream signal integration, non-binary sensors, adaptation, and generalization to a larger number of sensors. It would also be interesting to study the channel capacity in the parameter spaces of both the sensor couplings and the signal prior, an approach that has already led to major advances in the understanding of gene regulatory networks [18]. Finally, the existence of optimal collective sensing strategies necessitates a characterization of the learning rules that gives rise to such strategies.

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Nonequilibrium cooperative sensing: Supplemental Material

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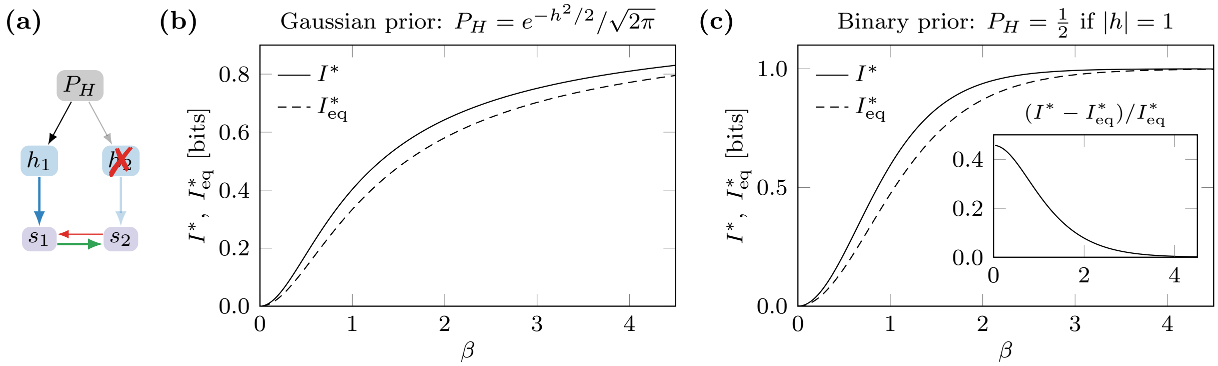

FIG. S1. (a) When the signal couples to only one sensor, the mutual information is maximized by nonequilibrium sensing strategy for both (b) continuous and (c) discrete signal priors. (b)&(c) The maximum mutual information in equilibrium (solid) and nonequilibrium (dashed) systems for (b) a continuous Gaussian prior, $P_H = e^{-h^2/2}/\sqrt{2\pi}$, and (c) a discrete binary prior, $P_H = 1/2$ if $|h| = 1$ and $P_H = 0$ otherwise. The inset of (c) depicts the nonequilibrium gain for the binary prior example. Similarly to the Gaussian prior case [Fig. 2(c)], the nonequilibrium improvement is maximum at 45 per cent in the noise-dominated limit and decreases with sensor reliability, suggesting the reduction of intrinsic noise as the mechanism behind the improvement.

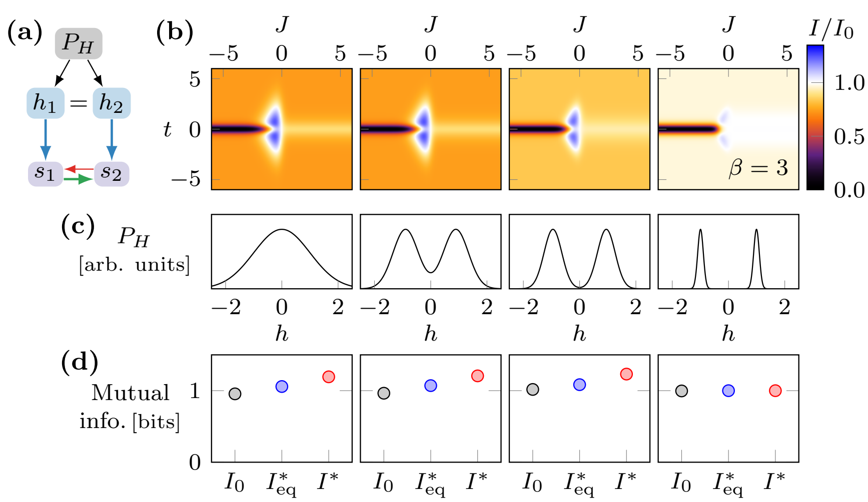

FIG. S2. For highly correlated signals, the nonequilibrium improvement in the low-noise limit does not rely on the specific Gaussian prior. (a) We assume that two sensors are driven by the same bias field $h \equiv h_1 = h_2$. (b) The mutual information at sensor reliability of $\beta = 3$ for four different prior distributions with a zero mean and unit variance, shown in (c). For all priors considered, the optimal nonequilibrium drive t^* is clearly finite, suggesting that the nonequilibrium enhancement is robust for most continuous priors. The dependence of the mutual information on J and t remains qualitatively unchanged. This means the mechanism behind the nonequilibrium enhancement is likely to be identical to the one for a Gaussian prior, as described in the main text. (d) The maximum mutual information — I_0, $I^*_{\rm eq}$ and I^* — for noninteracting, equilibrium and nonequilibrium sensors, respectively. The nonequilibrium enhancement is visible in all cases except for the most binary-like one (far right).