

Resource limitations induce phase transitions in biological information processing

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Biological information processing exhibits remarkable diversity across different organisms, which is presumably shaped by evolutionary optimization under limited resources. Starting from simple memoryless responses, more complex memory-based strategies may have evolved as resources became more available. In this Letter, we investigate minimal models of biological information processing under resource limitations by applying an optimal control technique proposed in [Tottori and Kobayashi, *Phys. Rev. Res.* **7**, 043048 (2025)]. We find that resource limitations such as sensing reliability, intrinsic stochasticity, and energy cost induce discontinuous phase transitions between memoryless and memory-based strategies, even though the minimal models fall within the standard linear-quadratic-Gaussian class. Moreover, these transitions can be nonmonotonic: Optimal information processing initially shifts from memoryless to memory-based strategies as sensing reliability increases, but then reverts to memoryless strategies if it increases further. Our results suggest that the complexity of biological information processing may be an evolvable trait that can switch back and forth between distinct strategies in a punctuated manner.

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Introduction. Biological systems process environmental information to estimate external conditions and control their internal states to adapt to changing environments. Recent applications of estimation and control theories have revealed that such information processing is optimized not only in humans [1–3] but also in simple bacteria [4–10]. Despite such optimization, the complexity of information processing varies widely across organisms. In light of bounded rationality [11–14], this diversity may stem from the limited resources that organisms can allocate for information processing. For example, our brain works by assembling billions of neurons and consuming 20% of body energy [15–17], whereas *Escherichia coli* optimally senses ligand gradients using a small number of noisy chemical reactions and limited energy [18–21]. These observations suggest that the complexity of biological information processing has evolved with resource availability. Although several pioneering studies have addressed this issue individually [22–37], a unified theoretical framework is still lacking, making it difficult to answer a simple yet fundamental question: “Do optimal information processing strategies progress in a gradual or punctuated manner as resources expand?”

This gap partly arises from the fact that conventional estimation and control theories [38–42] cannot take into account resource limitations inherent in biological systems. These

theories, originally developed in the context of engineering rather than biology, have been widely applied to analyze the optimality of biological information processing [8–10,43–52]. However, they are designed for artificial systems and typically assume idealized conditions such as sufficient memory capacity, precise internal computation, and negligible energy consumption, which do not hold in biological systems.

To address this issue, the accompanying full paper [53] has developed a theoretical framework for optimal estimation and control under such resource limitations. In this Letter, we apply that framework to minimal models of biological information processing and analyze how their optimal strategies change depending on resource limitations. We find that resource limitations such as sensing reliability, intrinsic stochasticity, and energy cost induce discontinuous and nonmonotonic phase transitions between simple memoryless and complex memory-based strategies, even though the minimal models are linear quadratic Gaussian (LQG). These findings suggest that the complexity of biological information processing may evolve in a punctuated and nonmonotonic manner depending on resource availability.

Model. In this Letter, we consider a minimal model of biological information processing under resource limitations (Fig. 1). Let $x_t \in \mathbb{R}$ denote an environmental state, such as ligand concentration, which evolves by the following Ornstein-Uhlenbeck process [Fig. 1(a)]:

$$dx_t = -x_t dt + \sqrt{D} d\omega_t, \quad (1)$$

where $\omega_t \in \mathbb{R}$ is a standard Wiener process and $D \geq 0$ is the diffusion constant. The mean of x_t is rescaled to 0 without loss of generality [8,23–25]. The noisy observation of the state, such as receptor activity, is denoted by $y_t \in \mathbb{R}$ [Fig. 1(b)], which follows a Gaussian distribution with mean x_t and

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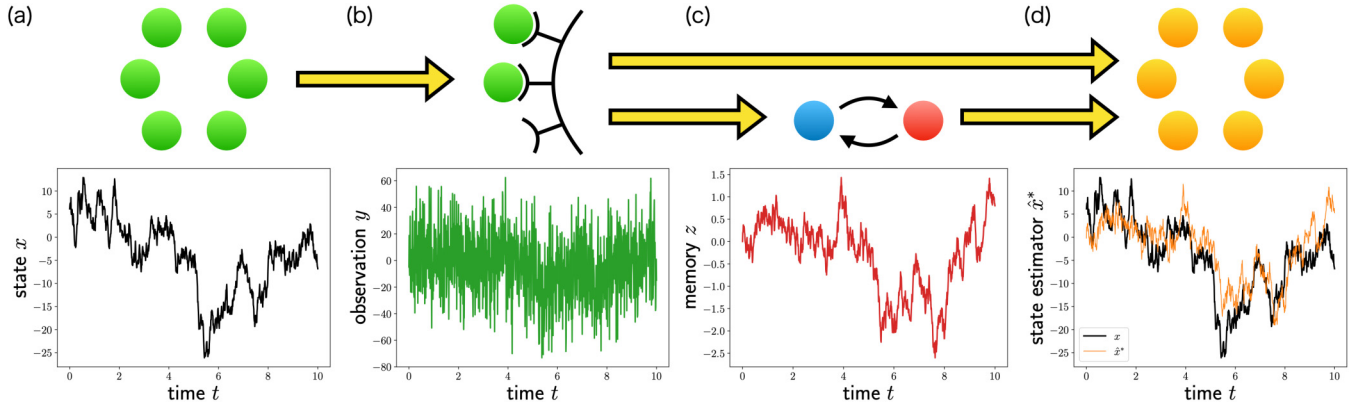


FIG. 1. Schematic diagram of a minimal model of cellular information processing. (a) Stochastic dynamics of environmental state $x_t \in \mathbb{R}$, e.g., the fluctuation in ligand concentration, which the cell senses for adaptation. (b) Noisy receptor activity $y_t \in \mathbb{R}$, which conveys the environmental information into the cell. (c) Intracellular memory dynamics $z_t \in \mathbb{R}$, which encodes and accumulates the receptor observations for further information processing. (d) Downstream molecules utilize both instantaneous receptor observation y_t and intracellular memory z_t to generate optimal estimate $\hat{x}_t^*$ (orange curve) of the current environmental state x_t (black curve). The parameters are $D = 100$, $E = 500$, $F = 1$, $Q = 10$, and $M = 1$.

variance $E \geq 0$:

$$y_t \sim \mathcal{N}(y_t | x_t, E). \quad (2)$$

The conventional Bayesian theory focuses on the posterior distribution $p(x_t | y_t, \dots, y_0)$ [38–40], but its dynamics are infinite dimensional and deterministic [54]. Furthermore, it does not account for the energy cost required to compute the posterior distribution. These properties may not align with biological systems that process information under limited memory capacity, intrinsic stochasticity, and energetic constraints [18–37].

To address this issue, we explicitly introduce the finite-dimensional intracellular memory $z_t \in \mathbb{R}$, whose dynamics are modeled by the following stochastic differential equation (SDE) [Fig. 1(c)] [53]:

$$dz_t = v(y_t, z_t)dt + \sqrt{F}d\xi_t, \quad (3)$$

where $\xi_t \in \mathbb{R}$ is a standard Wiener process representing intrinsic noise with intensity $F \geq 0$. The dynamics of z_t is regulated by observation y_t and self-feedback through control $v(y_t, z_t) \in \mathbb{R}$. We then derive the optimal control $v(y_t, z_t)$ under resource limitations by minimizing the objective function

$$J[v, \hat{x}] := \lim_{T \rightarrow \infty} \frac{1}{T} \mathbb{E} \left[\int_0^T (Mv_t^2 + Q(x_t - \hat{x}_t)^2) dt \right], \quad (4)$$

where $M > 0$ and $Q > 0$ are weighting parameters. The first term is the quadratic cost of memory control, penalizing costly memory dynamics. The second term represents the estimation error of the environmental state x_t , where $\hat{x}_t = \hat{x}(y_t, z_t)$ is a readout function that converts current observation y_t and memory z_t into an estimate of state x_t [Fig. 1(d)]. The optimal memory control v^* is obtained together with the optimal state estimator $\hat{x}^*$ by solving the joint optimization problem:

$$v^*, \hat{x}^* := \arg \min_{v, \hat{x}} J[v, \hat{x}]. \quad (5)$$

This minimal model considers the linear and Gaussian dynamics of the state, observation, and memory [Eqs. (1)–(3)]

and the quadratic objective function [Eq. (4)], which corresponds to an LQG problem. The accompanying full paper [53] shows that LQG structures approximately emerge when systems fluctuate around their stable fixed points. Therefore, the insights obtained from this model may apply not only to cellular information processing but also to other biological phenomena, such as brain computations [36,55–60]. The accompanying full paper [53] also demonstrates that this minimal model can be approximately described by a push-pull network in cellular information processing [21–26].

Optimal solution. While the formulation is straightforward, solving this optimization problem is technically non-trivial. Using the framework developed in the accompanying full paper [53], the optimal memory control v^* and state estimator $\hat{x}^*$ are obtained semi-analytically as

$$v^*(y, z) = -M^{-1} \Pi_{zx} \hat{x}^*(y, z) - M^{-1} \Pi_{zz} z, \quad (6)$$

$$\hat{x}^*(y, z) = \mathbb{E}_{p(x|y,z)}[x] = K_{xy}y + K_{xz}z, \quad (7)$$

where the control gains, Π_{zx} and Π_{zz} , and the estimation gains, K_{xy} and K_{xz} , are nonlinear functions of the parameters D, E, F, M , and Q . For a given set of these parameters, the gains are obtained by jointly solving the Hamilton-Jacobi-Bellman (HJB) and Fokker-Planck (FP) equations [53]. Figure 1(c) illustrates the memory dynamics under optimal control $v^*(y, z)$, and Fig. 1(d) demonstrates that optimal estimator $\hat{x}^*(y, z)$ aligns with the true state x_t .

It should be noted that our framework can accommodate general nonlinear dynamics and nonquadratic costs, which result in nonlinear forms of $v^*(y, z)$ and $\hat{x}^*(y, z)$ [53]. However, in this Letter, we focus on the linear dynamics and the quadratic cost to demonstrate that the observed transitions stem purely from resource limitations, without any unnecessary nonlinearities that can be a potential source of transitionlike behaviors. Moreover, this simplified setup allows us to investigate various parameters owing to efficient computation, which is computationally prohibitive in more general settings.

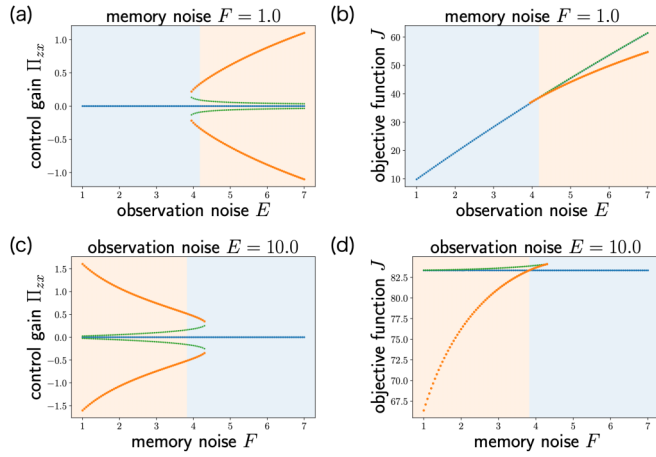


FIG. 2. Π_{zx} and J as functions of E [panels (a) and (b)] and F [panels (c) and (d)]. Blue, green, and orange dots correspond to the solutions of the HJB-FP equations that locally minimize or maximize J . Details of how these solutions are obtained are provided in the associated full paper [53]. The zero memory control gains (blue dots) are optimal in the blue region, while the stronger ones (orange dots) are optimal in the orange region. The weaker memory control gains (green dots) are never optimal because they correspond to local maxima of J [53]. The remaining parameters are $D = 100$, $Q = 10$, and $M = 1$.

Phase transition. We investigate how $v^*(y, z)$ varies with resource availability, such as sensory noise E , intrinsic noise F , and control cost M , by focusing on optimal control gain Π_{zx} [Eq. (6)]. In cellular information processing, the values of E , F , and M are determined by the number of receptors, the number of intracellular molecules, and the energy dissipation of intracellular reactions, respectively [53], all of which have been highlighted as key resources in previous studies [22–26].

If $\Pi_{zx} = 0$, then $v^*(y_t, z_t)$ does not depend on y_t , meaning that memory z_t does not accumulate past observations at all. In this case, $\hat{x}^*(y_t, z_t)$ reduces to being only responsive, i.e., the optimal estimator $\hat{x}^*(y_t, z_t)$ depends only on instantaneous observation y_t . In contrast, if $\Pi_{zx} \neq 0$, then z_t accumulates past observations and the optimal estimator $\hat{x}^*(y_t, z_t)$ integrates observation y_t and memory z_t to estimate the environment.

Figures 2(a) and 2(b) show the control gain and the objective function as functions of sensory noise E . When E is small, i.e., sensing is reliable, $\Pi_{zx} = 0$ holds and the responsive strategy is optimal. As sensing becomes less reliable (E increases), a locally optimal solution with finite $\Pi_{zx} \neq 0$ emerges discontinuously, while the responsive behavior, i.e., $\Pi_{zx} = 0$, remains globally optimal. As E increases further, the global optimum switches from the responsive strategy to the memory-dependent one, while the responsive solution remains as a locally optimal but globally suboptimal solution. We find similar discontinuous transitions when memory z_t becomes more reliable or less costly, i.e., when intrinsic noise F is decreased [Figs. 2(c) and 2(d)] or when control cost M is reduced [53].

This result, obtained under the minimal LQG setting, suggests that discontinuity may underlie transitions in optimal information processing strategies as a function of

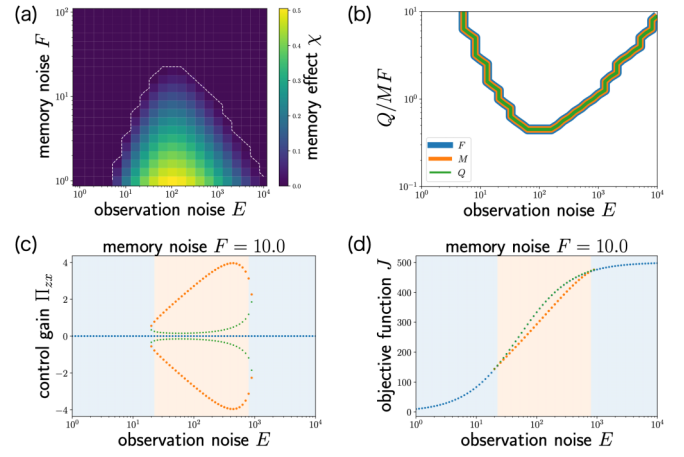


FIG. 3. (a) A phase diagram of χ for E and F . χ is defined by $(J_{\text{without memory}}^* - J_{\text{with memory}}^*)/J_{\text{without memory}}^*$, which quantifies the relative contribution of memory. $J_{\text{with/without memory}}^*$ is the minimum value of the objective function with/without memory. (b) Phase boundaries as a function of E and Q/MF . Blue, orange, and green curves change only F , M , and Q , respectively. (c), (d) Π_{zx} and J as functions of E for $F = 10$, demonstrating the forward and reverse transitions between responsive and memory-dependent strategies. The color codes and the rest of the parameters are the same as in Fig. 2.

resource availability. Such discontinuity qualitatively impacts the evolutionary scenario of information processing strategies because small mutational perturbations of the control gain around $\Pi_{zx} = 0$ cannot generate advantageous mutants even if the responsive strategy is no longer globally optimal. To overcome the gap between suboptimal and optimal strategies, a large mutational perturbation or systematic accumulation of mutations is required, which would make the evolution of information processing strategies punctuated rather than gradual as the change in resource availability. Our results also suggest the possibility of hysteresis: Once a particular strategy becomes established, it may remain locally optimal even after a different strategy becomes globally optimal. In such cases, biological systems may not immediately adopt the newly optimal strategy, resulting in a delayed transition.

To scrutinize the interrelation between different resource-related parameters, we computed the phase diagram for observation noise E and intrinsic noise F [Fig. 3(a)]. From this diagram, we identify the critical intrinsic noise intensity $F^\dagger$, above which memory usage is no longer encouraged for any value of E . In addition, for a fixed intensity of intrinsic noise $F < F^\dagger$, the transition from responsive to memory-dependent strategies is accompanied by its reverse transition as observation noise E increases [Figs. 3(c) and 3(d)], meaning that memory is advantageous only when observations are moderately noisy. Furthermore, the optimal observation noise level $E^*(F)$ exists for each fixed $F < F^\dagger$, at which the memory performance is maximal [Fig. 3(a)]. This nonmonotonic dependence appears not only for observation noise E but also for state noise D , whereas the memory performance changes monotonously with respect to intrinsic noise F , control cost M , and estimation error Q [53]. Thus, extrinsic noise such as observation and state noise may contribute to evolution

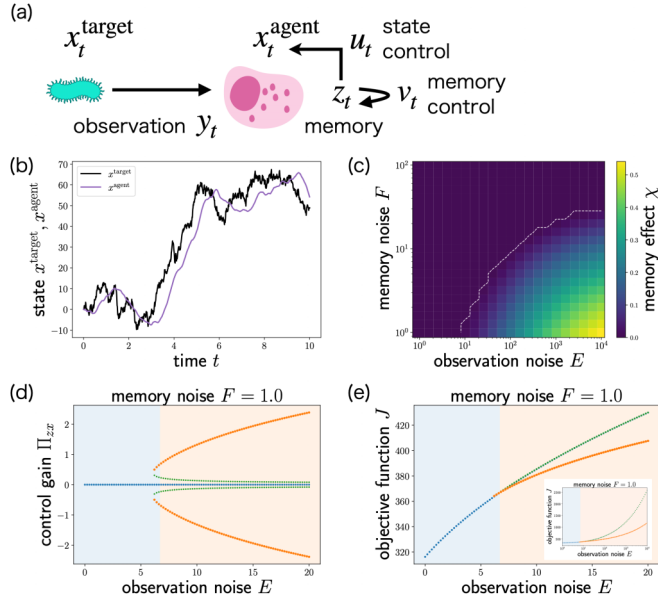


FIG. 4. (a) Schematic diagram of a target tracking problem. An agent estimates the position of the target x_t^{target} from observation y_t and memory z_t , and tracks it by controlling its own position x_t^{agent} through state control u_t . Memory control v_t compresses past observation history $y_{t-dt}, \dots, y_0$ into memory z_t . (b) The trajectories of x_t^{target} and x_t^{agent} for $E = 500$ and $F = 1.0$. (c) Phase diagram of χ as a function of E and F . (d), (e) Π_{zx} and J as functions of E . The color codes are the same as in Fig. 2. The rest of the parameters are $D = 100$, $Q = 10$, $R = 1$, and $M = 1$.

of information processing in a more complex manner than intrinsic noise and cost parameters: As extrinsic noise increases, organisms may transition from simple to complex strategies and then back to simpler ones. This nonmonotonic pattern aligns with recent experimental findings in human decision-making [35], which suggest that complex information processing strategies are most beneficial at intermediate levels of extrinsic noise. We also find that the phase boundaries for F , M , and Q are nearly identical when plotted against Q/MF [Fig. 3(b)], suggesting that increasing the weight of estimation error Q is nearly equivalent to decreasing either the weight of control cost M or the level of intrinsic noise F in terms of phase transitions.

These transitions cannot be observed in the conventional Bayesian filtering theory, which always uses memory to enhance estimation performance [38–40]. This aligns with our results because the setup of Bayesian theory corresponds to the limit of no intrinsic noise, $F \rightarrow 0$, with no memory control cost $M \rightarrow 0$ (equivalently $Q \rightarrow \infty$) [53]. Therefore, the conventional Bayesian filtering theory addresses only limited and ideal situations of biological information processing, overlooking the qualitative impacts of resource limitations.

Extension to include control. We further extend our analysis to a biological decision-making problem in which an agent controls its own behavior to chase a target based on stochastic observation [Fig. 4(a)]. The target tracking problem is prevalent in many biological phenomena, such as cellular chemotaxis [10,49,61], insect olfactory search [37,52,62], and animal foraging behaviors [63–65]. While the conventional Bayesian estimation and optimal control theories are typically

treated separately [40–42], our framework can seamlessly integrate both estimation and control processes [53,66–68]. We show that the discontinuous phase transitions also emerge in this target tracking problem.

Let $x_t^{\text{target}} \in \mathbb{R}$ and $x_t^{\text{agent}} \in \mathbb{R}$ denote the positions of the target and the agent, respectively, which evolve by

$$dx_t^{\text{target}} = \sqrt{D}d\omega_t, \quad dx_t^{\text{agent}} = -u_t dt, \quad (8)$$

where $\omega_t \in \mathbb{R}$ is a standard Wiener process, $D \geq 0$ is the diffusion constant, and $u_t \in \mathbb{R}$ is the state control of the agent. From the translation invariance, the target tracking problem concerns only with the difference $x_t := x_t^{\text{target}} - x_t^{\text{agent}}$, which evolves by the following SDE:

$$dx_t = u_t dt + \sqrt{D}d\omega_t. \quad (9)$$

The agent receives a noisy observation $y_t \in \mathbb{R}$, which is generated from a Gaussian distribution with mean x_t : $y_t \sim \mathcal{N}(y_t|x_t, E)$, where $E \geq 0$ is the intensity of the observation noise. We model the intrinsic dynamics of the agent memory $z_t \in \mathbb{R}$ by the following SDE: $dz_t = v_t dt + \sqrt{F}d\xi_t$, where $v_t \in \mathbb{R}$ is the memory control of the agent, $\xi_t \in \mathbb{R}$ is a standard Wiener process, and $F \geq 0$ is the intrinsic noise intensity of the memory dynamics. The objective function to be minimized is

$$J[u, v] := \lim_{T \rightarrow \infty} \frac{1}{T} \mathbb{E} \left[\int_0^T (Qx_t^2 + Ru_t^2 + Mv_t^2) dt \right],$$

where the three terms are the distance between the target and the agent, the state control cost, and the memory control cost, respectively. $Q > 0$, $R > 0$, and $M > 0$ are weighting parameters.

The optimal state control u^* and memory control v^* are obtained via the optimization problem $u^*, v^* := \arg \min_{u, v} J[u, v]$, which results in

$$u^*(y, z) = -R^{-1} \Pi_{xx} \hat{x}^*(y, z) - R^{-1} \Pi_{xz} z, \quad (10)$$

$$v^*(y, z) = -M^{-1} \Pi_{zx} \hat{x}^*(y, z) - M^{-1} \Pi_{zz} z, \quad (11)$$

where $\hat{x}^*(y, z)$ is the optimal state estimator [Eq. (7)]. The control gains, Π_{xx} , Π_{xz} , Π_{zx} , and Π_{zz} , are obtained from the HJB-FP equations [53].

Figure 4(b) demonstrates that the agent tracks the target accurately despite the high observation noise. Similar to the estimation problem, we observe the discontinuous phase transitions from $\Pi_{zx} = 0$ to $\Pi_{zx} \neq 0$ as observation noise E increases [Figs. 4(d) and 4(e)] or memory noise F decreases [53]. This means that there exists a transition from the responsive control, where only instantaneous observation y_t is used for state control, to the memory-dependent control, where internal memory z_t is additionally utilized.

Finally, we compute the phase diagram for observation noise E and intrinsic noise F , in which no reverse transition is observed even when E is increased [Fig. 4(c)]. This means that using memory for state control is still advantageous even when observations become extremely noisy. This difference could be attributed to the unbounded state variance in the target tracking problem: Even a small amount of information about x_t could benefit for suppressing the divergence of the

state variance to $\pm\infty$ [53]. We also find that the scaling relationship Q/MF does not hold in the target tracking problem [53]. These results suggest that the discontinuity may be a more fundamental characteristic under resource limitations than the nonmonotonicity or the scaling relationship. Overall, our analysis spotlights the potential diversity and complexity in optimal estimation and control strategies under resource limitations.

Discussion. In this work, we identified discontinuous and nonmonotonic phase transitions in optimal memory strategies as functions of available resources. Since memory use is fundamental to many forms of intelligent information processing, these results may provide theoretical insights into how such processing systems develop and evolve under resource constraints.

While several studies have investigated the relationship between biological information processing and resource limitations from the perspectives of thermodynamics and information theory [20–34], our study addresses this issue from the viewpoint of optimal control theory. This framework enables the seamless integration of biological information processing and decision-making under resource limitations, as exemplified by the target tracking problem. Furthermore, by explicitly computing optimal strategies, we reveal that resource limitations can induce discontinuous and nonmonotonic phase transitions. While a few previous studies have reported discontinuous [32–34] or nonmonotonic [35,36] phase transitions, most others have found only gradual and monotonic changes in response to varying resource availability [20–29].

It remains an open and important question which classes of problems give rise to such nontrivial transitions, and identifying these classes may clarify which biological systems are expected to exhibit discontinuous or nonmonotonic shifts in their information processing strategies depending on resource availability.

While this Letter investigated the simplest linear environmental dynamics with the quadratic objective function, our general framework can accommodate nonlinear environmental dynamics and nonquadratic objective functions [53]. In principle, it allows us to investigate optimal information processing for more complex environmental dynamics such as oscillations under more thermodynamically realistic cost functions [20–31]. Furthermore, by considering imbalanced dimensions between environmental and memory states, we may approach the dynamical information compressions observed in biological systems [69–72]. To fully realize these applications, more efficient and versatile methods are required for solving the joint optimization problem [Eq. (5)], and this could be facilitated by leveraging recent advances in optimal control theory [73–75].

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Data availability. The sample code is available at [76].

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