

Theoretical Analysis of Resource-Induced Phase Transitions in Estimation Strategies

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Organisms adapt to volatile environments by integrating sensory information with internal memory, yet their information processing is constrained by resource limitations. Such limitations can fundamentally alter optimal estimation strategies in biological systems. For example, recent experiments suggest that organisms exhibit phase transitions between memoryless and memory-based estimation strategies depending on energy availability and sensory reliability. However, a theoretical understanding of how resource limitations induce these transitions is still missing. This Letter presents an analytical characterization of the resource-induced phase transitions in optimal estimation strategies. Our results identify the conditions under which resource limitations alter estimation strategies and analytically reveal the mechanism underlying the emergence of discontinuous, nonmonotonic, and scaling behaviors. These results provide a theoretical foundation for understanding how limited resources shape information processing in biological systems.

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Introduction—Organisms adapt to changing environments by integrating sensory information with internal memory [1–10]. However, the resources they can devote to information processing are intrinsically limited [11–26], which in turn shapes their optimal estimation strategies. For example, when energy resources are sufficient, organisms can engage in deliberative decision-making, whereas under severe resource limitations their behaviors tend to be more reactive [27–29]. Moreover, recent experiments suggest that although organisms exploit their internal memory when sensory information is moderately uncertain, they abandon it when sensory uncertainty is either too low or too high [30]. Despite these experimental observations, a theoretical framework that explains when and how resource limitations induce transitions in optimal estimation strategies remains missing.

We address this gap by employing an optimal control framework. Based on optimal control theory, we have recently developed an optimal estimation framework under resource limitations [31–35]. In this Letter, we apply this framework to a minimal model of biological information processing, showing that resource limitations induce

transitions between memoryless and memory-based estimation strategies (Fig. 1). These transitions also exhibit nontrivial features, such as discontinuity, nonmonotonicity, and a scaling relation (Fig. 2), and qualitatively agree with recent human behavioral experiments [30]. By developing a more analytical approach to these resource-induced transitions, we unveil the mechanism underlying the emergence of the discontinuous, nonmonotonic, and scaling behaviors. These results provide a theoretical foundation for understanding when and how resource limitations induce transitions in optimal estimation strategies.

Model—We formulate a minimal model of biological information processing, in which an organism estimates an environmental state $x_t \in \mathbb{R}$ by integrating a noisy observation $y_t \in \mathbb{R}$ and an internal memory $z_t \in \mathbb{R}$ [34,35]. In cellular information processing, x_t , y_t , and z_t represent ligand concentrations, receptor activities, and downstream signals, respectively [1–4,16,17,34,35], whereas in human information processing they correspond to target positions, sensory information, and brain activity, respectively [8,30,36–38]. By adopting a minimal setting, this Letter aims to reveal essential features independent of detailed modeling.

The environmental state $x_t \in \mathbb{R}$ evolves according to an Ornstein-Uhlenbeck process [Fig. 1(a)] [2,3,16,17],

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

where $\omega_t \in \mathbb{R}$ is a standard Wiener process and $D > 0$ denotes the intensity of state fluctuations. The organism receives a noisy observation $y_t \in \mathbb{R}$, which is given by

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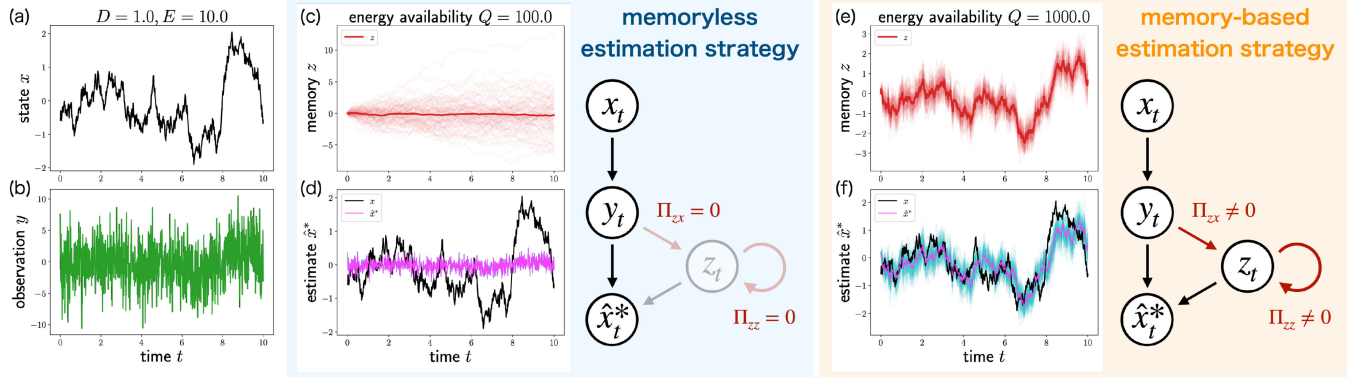


FIG. 1. (a) Environmental state x_t . (b) Noisy observation y_t . (c),(e) Internal memory z_t . (d),(f) Optimal estimate $\hat{x}_t^*$. Thin red and cyan curves are 100 sample trajectories, whereas thick red and magenta curves are their means. While memoryless estimation strategy ($\Pi_{zx}, \Pi_{zz} = 0$) is optimal at $Q = 100$ [(c), (d)], memory-based one ($\Pi_{zx}, \Pi_{zz} \neq 0$) is optimal at $Q = 1000$ [(e), (f)]. The rest of the parameters are set to $F = 1$ and $M = 1$. D, E , and F denote the intensities of state, observation, and memory noise, respectively, whereas Q and M represent energy availability and its limitation.

$$y_t = x_t + \sqrt{E}\nu_t, \quad (2)$$

where $\nu_t \in \mathbb{R}$ follows a standard Gaussian distribution and $E > 0$ denotes the intensity of observation noise [Fig. 1(b)]. To utilize the information about past observations, the organism maintains an internal memory $z_t \in \mathbb{R}$, which is updated as

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

where $\xi_t \in \mathbb{R}$ is a standard Wiener process and $F > 0$ denotes the intensity of intrinsic noise [Figs. 1(c) and 1(e)]. The control function $v_t = v(y_t, z_t)$ determines how the organism encodes past observations into internal memory. The organism estimates the environmental state x_t by integrating the current observation y_t with the internal memory z_t as $\hat{x}_t = \hat{x}(y_t, z_t)$ [Figs. 1(d) and 1(f)].

The optimal state estimate $\hat{x}^*$ and memory control v^* are defined as the minimizers of the following objective:

$$\hat{x}^*, v^* := \arg \min_{\hat{x}, v} J[\hat{x}, v], \quad (4)$$

$$J[\hat{x}, v] := \lim_{T \rightarrow \infty} \frac{1}{T} \mathbb{E} \left[\int_0^T (Q(x_t - \hat{x}_t)^2 + Mv_t^2) dt \right]. \quad (5)$$

The first and second terms in Eq. (5) represent the state estimation error and the memory control cost, respectively. The parameters $Q > 0$ and $M > 0$ quantify energy availability and limitation, respectively. Increasing Q or decreasing M allows the organism to invest more energy in estimation. Stronger memory control v_t reduces the relative effect of memory noise in Eq. (3), thereby achieving more accurate state estimation at the expense of a higher memory control cost.

We note that the expected cumulative cost $\mathbb{E}[\int_0^T (\cdot) dt]$ is a standard objective in optimal control theory, which

captures the trade-off between current and future costs [39–46]. This trade-off is essential here because the memory control incurs a current cost but improves future state estimation. In the infinite-horizon time-averaging setting as $\lim_{T \rightarrow \infty} (1/T) \mathbb{E}[\int_0^T (\cdot) dt]$, the optimal solution becomes stationary and independent of the terminal time T , which is more biologically plausible.

Optimal solution—By applying our optimal control framework [35] to this model, we derive the solutions satisfying the stationary condition of $J[\hat{x}, v]$, i.e., $\delta J[\hat{x}, v]/\delta \hat{x} = 0$ and $\delta J[\hat{x}, v]/\delta v = 0$,

$$\hat{x}^*(y, z) = \mathbb{E}_{p(x|y,z)}[x], \quad (6)$$

$$v^*(y, z) = -M^{-1}\Pi_{zx}\hat{x}^*(y, z) - M^{-1}\Pi_{zz}z. \quad (7)$$

The optimal state estimate $\hat{x}^*(y, z)$ is given by the conditional expectation of state x given observation y and memory z . The optimal memory control $v^*(y, z)$ is the linear function of optimal state estimate $\hat{x}^*(y, z)$ and memory z . Π_{zx} and Π_{zz} are the optimal memory control gains obtained by solving the observation-based Riccati equation, which is a new equation in our optimal control framework [35] [see Sec. I in Ref. [47]]. This equation is multivariable and nonlinear, making analytical treatment intractable. To manage this difficulty, we first investigate the optimal solutions numerically, and then develop an analytical characterization of these behaviors.

Numerical analysis—We investigate the optimal estimation strategy by solving the observation-based Riccati equation numerically [see Sec. I in Ref. [47]]. At low energy availability ($Q = 100$), the optimal memory control gains Π_{zx} and Π_{zz} are zero, indicating that no observational information is encoded into the memory z_t [Figs. 1(c) and 1(d)]. As a result, the organism estimates the environmental state x_t solely based on the current observation y_t , corresponding to a

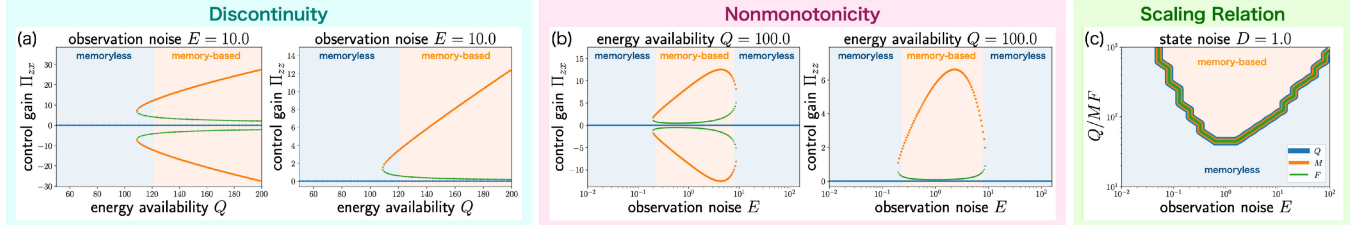


FIG. 2. (a),(b) Π_{zx} and Π_{zz} as functions of Q and E . Blue, green, and orange dots are the numerical solutions of the observation-based Riccati equation, and correspond to zero, intermediate, and high memory control gains, respectively. The blue and orange dots are local minima, whereas the green dots are local maxima. The blue and orange dots are optimal in the blue and orange regions, respectively, whereas the green dots never become optimal. (c) Phase boundaries with respect to E and Q/MF . Blue, green, and orange curves vary Q , M , and F , respectively. The rest of the parameters are set to 1.

memoryless estimation strategy. In contrast, when more energy is available ($Q = 1000$), Π_{zx} and Π_{zz} take nonzero values, and a memory-based estimation strategy becomes optimal [Figs. 1(e) and 1(f)].

This phase transition is discontinuous even though the model is linear and Gaussian [Fig. 2(a)]. At low Q , only $\Pi_{zx} = \Pi_{zz} = 0$ appears as a solution and it is optimal. As Q increases, $\Pi_{zx}, \Pi_{zz} \neq 0$ emerge discontinuously, although $\Pi_{zx} = \Pi_{zz} = 0$ remains optimal. After further increase of Q , the optimal solution discontinuously switches from $\Pi_{zx} = \Pi_{zz} = 0$ to $\Pi_{zx}, \Pi_{zz} \neq 0$. This result indicates that the optimal estimation strategy changes qualitatively with energy availability.

While increasing Q induces a monotonic transition from memoryless to memory-based estimation [Fig. 2(a)], increasing the observation noise E leads to a nonmonotonic transition [Fig. 2(b)]. At low E , memoryless estimation is optimal since the current observation contains sufficient information. As E increases, the current observation becomes less reliable, and memory-based estimation becomes favorable. However, when E becomes too high, memory control becomes ineffective, and memoryless estimation becomes optimal again. This nonmonotonic transition is also observed in recent human behavioral experiments [30], which suggests that human decision-making strategies may be shaped by resource limitations. We note that the state noise D also induces a similar nonmonotonic transition [34,35].

Similar to the transition with respect to Q , those with respect to M and F also occur monotonically but in the opposite direction: increasing M or F induces a transition from memory-based to memoryless estimation [34,35]. Moreover, the phase boundaries with respect to Q , M , and F collapse onto a single curve when plotted against Q/MF [Fig. 2(c)], indicating a scaling relation among these parameters. While the scaling relation Q/M can be understood directly from Eq. (5), the scaling relation Q/MF is nontrivial because Q/M represents energy availability and F characterizes intrinsic noise. This result indicates that increasing energy availability has a similar effect to decreasing intrinsic noise. The scaling relation is

also helpful for understanding the essential factors in these phenomena.

Theoretical analysis—From the numerical analysis, we found that resource limitations induce phase transitions in optimal estimation strategies and exhibit discontinuous, nonmonotonic, and scaling behaviors. While these numerical results were also implied in our preliminary work [34,35], their mechanism and generality are still elusive due to the lack of an analytical understanding. Here, we analytically clarify the mechanism of these numerically observed phenomena.

The main obstacle hindering analytical treatment is the complexity of the observation-based Riccati equation, which must be solved to obtain the optimal memory control gains Π_{zx} and Π_{zz} [Eq. (7)]. To avoid this difficulty without losing generality, we reformulate the memory control function as a linear function of the observation y and memory z ,

$$v_{\Phi}(y, z) := -\Phi_{zy}y - \Phi_{zz}z, \quad (8)$$

where $\Phi_{zy} \in \mathbb{R}$ and $\Phi_{zz} \geq 0$ denote new memory control gains. The first term encodes observational information into internal memory, whereas the second term suppresses memory noise through negative feedback. This reformulation does not compromise optimality because $v^*(y, z)$ is linear with respect to y and z (see Sec. II in Ref. [47]). Moreover, it enables us to derive an analytical expression of the objective function J (see Sec. II in Ref. [47]), leading to a theoretical analysis of the stationary conditions $\partial J / \partial \Phi_{zy} = 0$ and $\partial J / \partial \Phi_{zz} = 0$.

First, we fix Φ_{zz} and optimize only Φ_{zy} . From the stationarity condition $\partial J / \partial \Phi_{zy} = 0$, we obtain the following optimal control gain (see Sec. III in Ref. [47]):

$$\Phi_{zy}^* = 0, \pm \sqrt{\frac{(\Phi_{zz} + 1)^2(D + 2E)F}{\{D + 2(\Phi_{zz} + 1)E\}D}}(\sqrt{\Theta} - 1), \quad (9)$$

$$\Theta := \frac{4\Phi_{zz}D^2E^2(Q/MF)}{(\Phi_{zz} + 1)\{D + 2(\Phi_{zz} + 1)E\}(D + 2E)^2}. \quad (10)$$

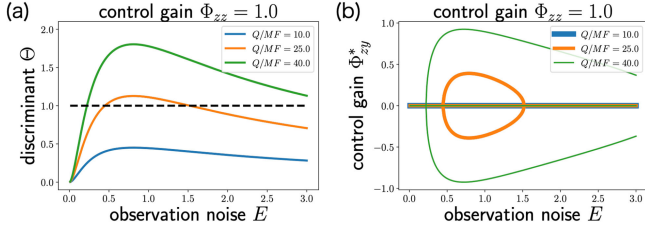


FIG. 3. (a) Discriminant Θ [Eq. (10)] and (b) optimal memory control gain Φ_{zy}^* [Eq. (9)] at $\Phi_{zz} = 1$. D is set to 1.

When $\Theta \leq 1$, the only real solution is $\Phi_{zy}^* = 0$, meaning that no observational information is encoded into memory. Thus, the memoryless estimation strategy is optimal. On the other hand, when $\Theta > 1$, nonzero real solutions $\Phi_{zy}^* \neq 0$ emerge, indicating that memory-based estimation can be optimal. Therefore, Θ serves as a discriminant identifying the phase boundary between memoryless and memory-based estimation.

Θ captures the scaling relation Q/MF because it depends on Q , M , and F only through this form. Moreover, while Θ increases monotonically as Q/MF increases, it varies non-monotonically with E and D [Fig. 3(a)]: When $E \ll D$, $\Theta \approx 4(Q/MF)(\Phi_{zz} + 1)^{-1}\Phi_{zz}D^{-1}E^2$, which increases with increasing E or decreasing D . Conversely, when $E \gg D$, $\Theta \approx (Q/MF)(\Phi_{zz} + 1)^{-2}\Phi_{zz}D^2E^{-1}$, which decreases with increasing E or decreasing D . Therefore, Θ also accounts for the nonmonotonic transitions with respect to E and D .

However, Eqs. (9) and (10) do not capture the discontinuous transitions, since Φ_{zy}^* varies continuously from zero to nonzero values [Fig. 3(b)]. In fact, the intersections between $\partial J/\partial\Phi_{zy} = 0$ [Figs. 4(a)–4(c), red] and $\Phi_{zz} = \text{constant}$ [Figs. 4(a)–4(c), cyan] change continuously from zero to nonzero values as Q increases [Fig. 4(d), cyan]. By contrast, the intersections between $\partial J/\partial\Phi_{zy} = 0$ [Figs. 4(a)–4(c), red] and $\partial J/\partial\Phi_{zz} = 0$ [Figs. 4(a)–4(c), magenta] emerge discontinuously at nonzero values [Fig. 4(d), magenta]. These results indicate that the simultaneous optimization of two distinct memory control gains Φ_{zy} and Φ_{zz} is essential for producing the discontinuous transitions.

We next investigate the simultaneous optimization of Φ_{zy} and Φ_{zz} more analytically. While $\partial J/\partial\Phi_{zy} = 0$ can be solved analytically, $\partial J/\partial\Phi_{zz} = 0$ is analytically intractable. To address this issue, we decompose the objective function J into the state estimation error J_Q and the memory control cost J_M as follows:

$$J = J_Q + J_M, \quad (11)$$

$$J_Q := \lim_{T \rightarrow \infty} \frac{1}{T} \mathbb{E} \left[\int_0^T Q(x_t - \hat{x}_t)^2 dt \right], \quad (12)$$

$$J_M := \lim_{T \rightarrow \infty} \frac{1}{T} \mathbb{E} \left[\int_0^T M v_t^2 dt \right]. \quad (13)$$

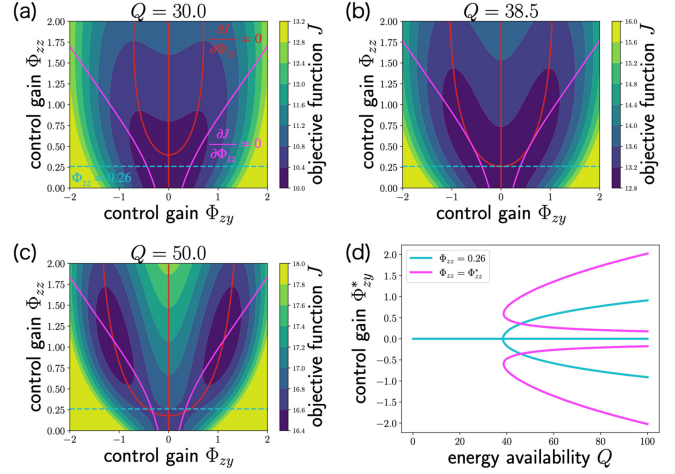


FIG. 4. (a)–(c) J as functions of Φ_{zy} and Φ_{zz} . Red and magenta curves represent $\partial J/\partial\Phi_{zy} = 0$ and $\partial J/\partial\Phi_{zz} = 0$, respectively, while cyan lines indicate $\Phi_{zz} = 0.26$. (d) Φ_{zy}^* as a function of Q . Cyan curves are the intersections between $\partial J/\partial\Phi_{zy} = 0$ and $\Phi_{zz} = 0.26$, whereas magenta curves correspond to the intersections between $\partial J/\partial\Phi_{zy} = 0$ and $\partial J/\partial\Phi_{zz} = 0$. The rest of the parameters are set to 1.

Although $\partial J/\partial\Phi_{zz} = 0$ is intractable, its components $\partial J_Q/\partial\Phi_{zz} = 0$ and $\partial J_M/\partial\Phi_{zz} = 0$ are more tractable because this decomposition allows us to ignore the denominators of $\partial J_Q/\partial\Phi_{zz}$ and $\partial J_M/\partial\Phi_{zz}$ (see Sec. IV B in Ref. [47]). Moreover, the values of Φ_{zz} that satisfy $\partial J_Q/\partial\Phi_{zz} = 0$ [Figs. 5(a)–5(c), green] and $\partial J_M/\partial\Phi_{zz} = 0$ [Figs. 5(a)–5(c), orange] serve as the upper and lower bounds, respectively, for the value of Φ_{zz} that satisfies $\partial J/\partial\Phi_{zz} = 0$ [Figs. 5(a)–5(c), magenta] (see Sec. IV B in Ref. [47]). Thus, analyzing $\partial J_Q/\partial\Phi_{zz} = 0$ and $\partial J_M/\partial\Phi_{zz} = 0$ provides necessary and sufficient conditions, respectively, for the intersection between $\partial J/\partial\Phi_{zy} = 0$ and $\partial J/\partial\Phi_{zz} = 0$: if $\partial J_Q/\partial\Phi_{zz} = 0$ (green) does not intersect $\partial J/\partial\Phi_{zy} = 0$ (red) at nonzero Φ_{zy} , then $\partial J/\partial\Phi_{zz} = 0$ (magenta) does not intersect $\partial J/\partial\Phi_{zy} = 0$ (red), and nonzero memory control gains do not emerge [Fig. 5(a)]. In contrast, if $\partial J_M/\partial\Phi_{zz} = 0$ (orange) intersects $\partial J/\partial\Phi_{zy} = 0$ (red), then $\partial J/\partial\Phi_{zz} = 0$ (magenta) also intersects $\partial J/\partial\Phi_{zy} = 0$ (red), and nonzero memory control gains emerge [Fig. 5(c)].

To clarify this fact more analytically, we define the conditions under which $\partial J/\partial\Phi_{zz} = 0$, $\partial J_Q/\partial\Phi_{zz} = 0$, and $\partial J_M/\partial\Phi_{zz} = 0$ intersect $\partial J/\partial\Phi_{zy} = 0$ by $\Theta_T \geq 1$, $\Theta_Q \geq 1$, and $\Theta_M \geq 1$, respectively. $\Theta_i = 1$ indicates the tangency condition ($i \in \{T, Q, M\}$). Although Θ_T is analytically intractable, Θ_Q and Θ_M are given by

$$\Theta_Q = \frac{2\beta^2\delta}{(1+2\beta)^2(1+4\beta)}, \quad (14)$$

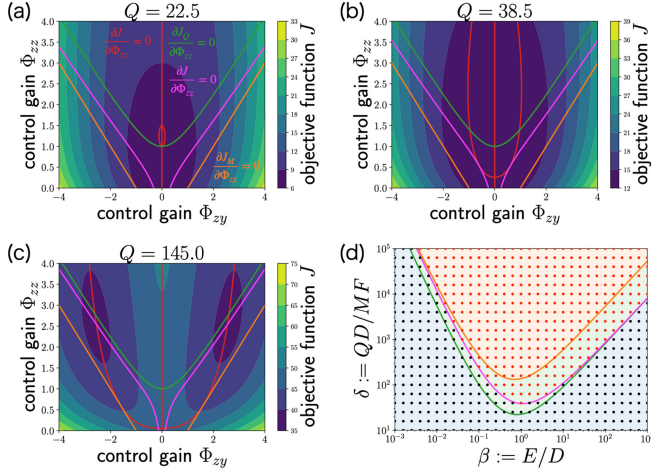


FIG. 5. (a)–(c) Red, magenta, green, and orange curves indicate $\partial J / \partial \Phi_{zy} = 0$, $\partial J / \partial \Phi_{zz} = 0$, $\partial J_Q / \partial \Phi_{zz} = 0$, and $\partial J_M / \partial \Phi_{zz} = 0$, respectively. The parameters except for Q are set to 1. (d) Magenta, green, and orange curves are the parameter values at which $\partial J / \partial \Phi_{zy} = 0$, $\partial J_Q / \partial \Phi_{zz} = 0$, and $\partial J_M / \partial \Phi_{zz} = 0$ are tangent to $\partial J / \partial \Phi_{zy} = 0$, respectively. The magenta curve ($\Theta_T = 1$) is obtained numerically, whereas the green curve ($\Theta_Q = 1$) and the orange curve ($\Theta_M = 1$) are obtained analytically from Eqs. (14) and (15), respectively. Blue, green, and orange regions correspond to $\Theta_Q < 1$, $1 \leq \Theta_Q$ and $\Theta_M < 1$, and $1 \leq \Theta_M$, respectively. The memory control gains Π_{zx} and Π_{zz} obtained numerically from the observation-based Riccati equation are zero at black dots and take nonzero values at red dots.

$$\Theta_M \approx \frac{\beta^2 \delta}{(1 + 2\beta)^2 \left\{ (1 + 6\beta) + \sqrt{4\beta(4 + 13\beta)} \right\}}, \quad (15)$$

where $\beta := E/D$ and $\delta := QD/MF$ represent sensory uncertainty and resource availability, respectively (see Secs. IV C and IV D in Ref. [47]). Equations (14) and (15) capture the nonmonotonic transition with respect to β and the scaling relation Q/MF through δ .

The phase boundary for the emergence of nonzero memory control gains ($\Theta_T = 1$) [Fig. 5(d), magenta curve] lies between $\Theta_Q = 1$ and $\Theta_M = 1$ (i.e., $1 \leq \Theta_Q$ and $\Theta_M < 1$) [Fig. 5(d), green region] because $\partial J / \partial \Phi_{zz} = 0$ is bounded by $\partial J_Q / \partial \Phi_{zz} = 0$ and $\partial J_M / \partial \Phi_{zz} = 0$. Thus, nonzero memory control gains do not emerge when $\Theta_Q < 1$ [Fig. 5(d), blue region], whereas they do when $\Theta_M \geq 1$ [Fig. 5(d), orange region]. Since this analytical classification [Fig. 5(d), blue, green, and orange regions] is consistent with the numerical results [Fig. 5(d), black and red dots], an analytical foundation for the resource-induced transitions in optimal estimation strategies is established.

Discussion—In this Letter, we provided a theoretical foundation for the resource-induced transitions in optimal estimation strategies and revealed the analytical mechanism underlying the discontinuous, nonmonotonic, and scaling

behaviors. Phase transitions in information-processing strategies have also been reported within the information bottleneck [61–66]. While the information bottleneck formulates resource limitations in terms of mutual information, our optimal control framework expresses them through control cost [31–35]. Despite these differences, both frameworks exhibit phase transitions, suggesting that such transitions could be characteristic of resource-limited information processing. The connection between the information bottleneck and our optimal control framework is further discussed in Sec. VI of Ref. [47].

In addition, our Letter analytically revealed nonmonotonic transitions with respect to sensory uncertainty. Similar nonmonotonic transitions have been observed in recent human behavioral experiments [30]. These experiments have also reported that increasing environmental volatility induces a monotonic transition from memory-based to memoryless estimation strategies [30]. Our proposed framework reproduces this behavior as well (see Sec. V in Ref. [47]). These results suggest that human information-processing strategies may be characterized by computational resource limitations.

Memory plays an essential role in several biological phenomena, including molecular networks [67–74], bacterial chemotaxis [5,75–83], developmental patterning [43,84–91], and animal decision-making [9,92–99] (see Sec. VII in Ref. [47] for more discussion). Thus, our Letter would provide a deeper understanding of the optimality of these biological phenomena.

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