Internal Feedback in Biological Control: Diversity, Delays, and Standard Theory

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Abstract—Neural architectures in organisms support efficient and robust control that is beyond the capability of engineered architectures. Unraveling the function of such architectures is challenging; their components are highly diverse and heterogeneous in their morphology, physiology, and biochemistry, and often obey severe speed-accuracy tradeoffs; they also contain many cryptic internal feedback pathways (IFPs). We claim that IFPs are crucial architectural features that strategically combine highly diverse components to give rise to optimal performance. We demonstrate this in a case study, and additionally describe how sensing and actuation delays in standard control (state feedback, full control, output feedback) give rise to independent and separable sources of IFPs. Our case study is an LQR problem with two types of sensors, one fast but sparse and one dense but slow. Controllers using only one type of sensor perform poorly, often failing even to stabilize; controllers using both types of sensors perform extremely well, demonstrating a strong diversity-enabled sweet spot (DESS). We demonstrate that IFPs are key in enabling this DESS, and additionally that with IFPs removed, controllers with delayed sensing perform poorly. The existence of strong DESS and IFP in this simple example suggest that these are fundamental architectural features in any complex system with diverse components, such as organisms and cyberphysical systems.

I. INTRODUCTION

Neural architectures have evolved to support exceptionally efficient and robust sensorimotor control, despite the fact that biological components communicate and compute more slowly and more noisily than engineered components. These differences and known neuroanatomy suggest that neural control architectures are unlike those currently found in engineering theory. Better understanding of neural architectures is beneficial for both neuroscientists and engineers, who wish to build systems that are as scalable, efficient, and robust as organisms, and with similarly constrained hardware.

A prominent feature of neural architectures that has eluded understanding is the presence of many internal feedback pathways (IFPs), whose role in biological control remains ambiguous. IFPs are prevalent in neuronal systems [3], [5]–[7] and can also be found in the immune system [8]–[10] and many others; for a more detailed survey of IFPs in biology, refer to our companion paper [1]. Survival-critical behaviors, such as reflexive escape and object-tracking, are thought to be generated by fast forward pathways, shown in black in the top panel of Fig. 1 for primate visual cortex. However, physiological evidence tells us that the IFPs are more complex and diverse in speed and composition than forward paths, far more so than can be shown in a single figure. Such massive and diverse IFPs are a mystery since they have no obvious function for fast reflexes. Nonetheless, massive and diverse IFPs are found in almost all nervous systems across species and life stages. We require new theory that explains the presence, complexity, and function of IFPs.

Another feature of neural architectures that remains somewhat mysterious is the vast diversity in morphology, physiology, and biochemistry of the underlying components. Due to energy constraints, these components often face speed-accuracy tradeoffs (SATs); they are either fast and inaccurate or slow and accurate but not both [4]. Recent work suggests that diverse hardware-level components (which obey SATs) and layered architectures enable performance that overcomes....

Fig. 1. Forward pathways (in black) carry information from sensing toward actuation (left to right). Internal feedback pathways (IFPs, in red) travel in the reverse direction. (Top) Primate visual cortex contains large amounts of IFPs [3]. Not shown are the diverse compositions of IFPs; each IFP arrow represents axon bundles with a range of sizes, receptors, and neurotransmitters corresponding to diverse speeds and accuracies. (Bottom) Controller with sensor delays and lots of IFPs, described in Sections III and IV. Delayed signaling is a central feature of the brain [4], and the presence of delays in this controller motivates the presence of IFPs.

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This paper is one of three in a series on internal feedback in biological control architectures. These papers may be read in any order, though a suggested order is [1], then this, then [2].
We now present the setup of a system with diverse sensing, where we will analyze DESS (Section III) and IFP (Section IV). The goal of this analysis is not to model any biological system in detail, but to study simple examples that give rise to fundamental theory on the existence and characteristics of DESS and IFP using standard control theory.

We consider a system of $n$ nodes in a ring formation. State dynamics in this ring can be described by the difference equation $x_r(t+1) = A_r x_r(t)$, where $x_r \in \mathbb{R}^n$ represents ring states and $A_r \in \mathbb{R}^{n \times n}$ is:

$$A_r = \frac{\alpha}{3} \begin{bmatrix} 1 & 1 & 0 & \ldots & 1 \\ 1 & 1 & 0 & \ldots & 1 \\ 0 & \ddots & \ddots & \ddots & \vdots \\ \vdots & \ddots & \ddots & \ddots & 1 \\ 1 & 0 & \ldots & 1 & 1 \end{bmatrix}$$

Here $\alpha$ determines the spectral radius of $A_r$; $\alpha = 1$ leads to a neutrally stable system, and $\alpha > 1$ to an unstable system.

We consider two types of sensors: fast and sparse, and slow and dense. This is reminiscent of biological components which obey speed-accuracy tradeoffs (e.g. proprioception vs. vision, retinal fovea vs. surround). These sensors lie on opposite ends of the speed-accuracy spectrum. We focus on the case of perfect actuation and diverse sensing, i.e. full control (FC), and assume zero sensor noise for simplicity. All analysis and findings naturally apply to the dual case of perfect sensing and diverse actuation, i.e. state feedback (SF).

We will also briefly discuss the case of imperfect actuation and sensing in output feedback (OF) at the end of Section IV, and a simple extension to standard separation theory.

Consider the discrete-time linear time-invariant system:

$$x(t+1) = A x(t) + B_2 u(t) + B_1 w(t)$$
$$y(t) = C x(t)$$

where $x$, $u$, $w$, and $y$ are the state, control action, disturbance, and output, respectively.

To model internal sensing delays, we add delay states to the model. Assume we sense each state, but with a delay of $d$ timesteps; then, we introduce $d$ copies of each ring state to represent information internal to the delayed sensors. The resulting state vector is $x = \begin{bmatrix} x_r^T & x_s^T \end{bmatrix}^T \in \mathbb{R}^{n(d+1)}$. $x_r$ corresponds to the original ring states; $x_s$ represent delayed sensor states. Note: we define $x_s$ as being internal to the agent; these correspond to the arrows exiting the delay blocks in Fig. 1. We can think of $x_s$ as information sensed by the eye that is being passed along a delayed visual pathway to LGN, then V1, and so on. The motor areas of the brain can only access the most delayed information, i.e. the values of $x_s$ corresponding to a delay of $d$; these will be picked out by the ‘sensing’ matrix $C$.

For full control, we define the input vector $u = \begin{bmatrix} u_r^T & u_s^T \end{bmatrix}^T \in \mathbb{R}^{n(d+1)}$; this has dimension equal to $x$. $u_r$ represents physical actuation upon the ring states, and $u_s$ denotes internal wires to internal delayed states; this

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1 We assume zero sensor noise purely for pedagogical purposes; our findings on DESS and IFP are replicable with sensor noise, although the associated plots are slightly less clearly interpretable.
corresponds to the red IFP arrows exiting the L blocks in Fig. 1. Although both \( u_r \) and \( u_s \) are control signals in the standard sense, they have vastly different interpretation and engineering cost; \( u_r \) represents physical actuation, which for an organism requires high-cost muscle cells, etc, while \( u_s \) represents low-cost internal communication, i.e. neurons.

The state matrix \( A \) for the vector \( x \) including delay states has dimension \( n(d+1) \times n(d+1) \), and can be written as

\[
A = \begin{bmatrix}
\hat{A}_r & 0_{n \times n} \\
I_{nd \times nd} & 0_{nd \times nd}
\end{bmatrix}
\]

(3)

where \( \hat{A}_r = [A_r \ 0_{n \times n(d-1)}] \) has dimension \( n \times nd \), and \( I \) and 0 are identity and zero matrices. \( A \) has equal spectral radius as \( A_r \); its stability is also determined by \( a \). For full control (FC), we have full actuation, i.e. \( B_2 = I_{n(d+1) \times n(d+1)} \). Additionally, we only consider disturbances that affect the ring states, i.e. \( B_1 = [I_{n \times n} \ 0_{n \times nd}]^\top \).

For fast and sparse sensing, instead of sensing each state, we choose to sense along eigenvectors of the ring state matrix \( A_r \). We will choose some \( q \) eigenvectors, typically corresponding to the \( q \) highest-magnitude eigenvalues of \( A_r \). \( C_f \) has dimension \( q \times n(d+1) \), and is written as \( C_f = [E \ 0_{q \times nd}] \), where the rows of \( E \in \mathbb{R}^{q \times n} \) are the \( q \) selected eigenvectors of \( A_r \). \( C_f \) represents instant sensing which senses along the \( q \) “worst directions” of impulse propagation. For slow and dense sensing, we sense each state with a delay of \( d \) timesteps. \( C_s \) is of size \( n \times n(d+1) \), and can be written as \( C_s = [0_{n \times nd} \ I_{n \times n}] \). We will study the system with fast-only, slow-only, and diverse (both fast and slow) sensors, corresponding to \( C = C_f \), \( C = C_f \), and \( C = [C_f^\top \ C_s^\top]^\top \), respectively.

We consider a standard LQR cost with state penalty \( Q = B_1^\top B_1 \). Note that we only penalize the \( n \) ring states, not the delayed sensing states. The optimal controller is \( u(t) = -Lq(t) \), where \( L = A_f^\top S C_f (C_f^\top S C_f)^{-1} \) for matrix \( S \) that solves the DARE. Assuming no sensor noise, the LQR cost can be calculated via \( \text{Tr}(B_1^\top S B_1) \). We now use this system to demonstrate substantial presence of both DESS and IFPs.

III. DIVERSITY-ENABLED SWEET SPOT (DESS)

As described above, we consider two sensor types: fast and sparse, and slow and dense. We first study system performance with uniform sensors; this gives terrible performance and incurs extreme costs. We then use diverse sensors, which give a dramatic performance improvement and demonstrate the existence of a DESS. For the remainder of this paper, unless otherwise specified, we use parameters \( n = 5 \), \( a = 1.856 \) (to be explained), \( q = 1 \), and \( d = 3 \).

A. Fast-and-sparse sensing

For a controller with only fast-and-sparse sensing, we show the relationship between the cost and the stability value \( a \) in the left panel of Fig. 3. For each line, there is clearly a breaking point at which fast-only sensing results in instability and infinite cost. These breaking points occur when we reach a value of \( a \) that gives more than \( q = 1 \) unstable eigenvalues in \( A_r \); in this case, fast-only sensing is no longer sufficient for the controller to reject all directions of unstable impulse propagation. Thus, certain states never converge to zero, yielding infinite cost.

The right panel of Fig. 3 shows the breaking point values of \( a \) for which fast-only sensing results in infinite costs (i.e. fails to stabilize). As the system size \( n \) increases, the controller is less able to stabilize unstable open-loop systems. For large system sizes, the controller can only handle marginally unstable systems (i.e. \( a \) very close to 1).

For \( n = 5 \), the minimum value of \( a \) that causes instability and incurs infinite cost is \( a = 1.856 \). The corresponding impulse response is shown on the left in Fig. 4 which does not get attenuated to zero, as expected.

B. Slow-and-dense sensing

Consider a controller with only slow-and-dense sensing; the impulse response is shown in the middle panel of Fig. 4. In the first three timesteps, the system behaves as if it were open-loop; no action is taken because due to delayed sensing,
the controller does not yet know about the disturbance. Once the delayed information reaches the controller, the impulse propagation is immediately killed off, thanks to the dense information provided by the slow sensor.

C. Diverse sensing

Consider a controller with diverse sensors, i.e. both the fast-and-sparse and slow-and-dense sensors. The impulse response is shown in the right panel of Fig. 4. The diverse controller displays a mix of behaviors from the fast-only and slow-only setups. In the first three time steps, the behavior is identical to the fast-only system; when information from the slow sensor reaches the controller, all impulse propagation is completed attenuated and the state values go to zero. This controller also has much-improved cost; it incurs a performance cost that is nearly six times smaller than the best non-diverse setup. This displays a dramatic DESS.

We vary the delay parameter and show that this DESS only becomes more dramatic for increased values of delay; this is shown in Fig. 5. Clearly, the diversity in sensors achieves a sweet-spot; while fast-only sensing incurs effectively infinite costs and slow-only sensing incurs dramatic exponentially increasing costs, diverse sensing allows us to keep the cost below $10^3$. Thus, delayed sensing is acceptable if paired with a fast-but-sparse sensor; similarly, sparse sensing is acceptable if paired with a dense-but-slow sensor. This sweet spot is consistent with what we expect from the sensorimotor system and neural systems in general; neurons and cells typically obey SATs, but a combination of diverse neurons (i.e. both fast and slow) allows the system to achieve a DESS.

Overall, this simple but striking example suggests that DESS is a fundamental feature in the presence of diverse components. Even with only two types of sensors, we observe a strong DESS. We expect that in systems with more diversity between components (i.e. biological and neural systems), even more extreme DESS may be found.

We remark that for systems with larger values of $n$ and $\alpha$, even more pronounced DESS is observed. This is because fast-only sensing becomes more sensitive to instability as $n$ increases, as suggested in Fig. 3. On the other hand, increasing $q$ improves the performance of the fast-only system. As long as $q$ is less than the number of unstable eigenvalues in $A_r$, we observe dramatic DESS. When $q$ is greater or equal to the number of unstable eigenvalues in $A_r$, we still observe a DESS, albeit less drastic one. Also, all analysis and results in this section apply to the dual case of diverse actuation, in which dramatic DESS is also observed.

Considering the terrible performance of the non-diverse setups, we conclude that the diverse setup of sensors performs far better than the sum of its individual parts. This illustrates a basic principle at work: by cleverly using architecture, we can combine individual components that together perform better than the sum of their parts (i.e. achieve a DESS). We now study a fundamental architectural feature that enables this DESS – internal feedback pathways (IFPs).

IV. INTERNAL FEEDBACK PATHWAYS (IFPs)

We now observe the structure of the controller that gives the dramatic DESS found above. We show that IFPs are an essential architectural feature that enable DESS and that removing IFPs destroys system performance.

The IFPs in controllers are defined as information from the actuation output to the sensor input. We show the presence of IFPs in our FC controller with delayed sensing and its dual (SF controller with delayed actuation) in Fig. 6. Our definition of the delay states as internal, sensor states means that all control action to them (i.e. the orange arrow exiting from $L_2$ in Fig. 6) constitute IFPs. This corresponds to internal wires in the controller rather than actuation upon the external environment. Conversely, in a system with no internal states, a static gain controller $u = Kx$ or $u = Ly$ would contain only forward paths from sensor input ($x$ for SF and $y$ for FC) to actuation output $u$, with no IFPs.

In our model, IFPs only appear in the model when the slow sensor (i.e. delayed internal states) is present, whether on its own or in a diverse-sensor setup. For the optimal FC controller $L = \begin{bmatrix} L_1^T & L_2^T \end{bmatrix}^\top$ where $L_1 \in \mathbb{R}^{n \times n}$, entries in $L_2$ corresponds to IFP. We show our slow-only and diverse controllers from the previous section in Fig. 7. For the
slow-only controller, the shape of the $A_r$ matrix is clearly visible within both the forward and IFP blocks. This is not a coincidence, since both forward and feedback (i.e. IFP) paths utilize $A_r$ to predict and counteract the behavior of the ring states. For the controller with both fast and slow sensors, the shape of the blocks are still similar, although including the fast sensor changes the magnitudes of the entries in the controller corresponding to the slow and dense sensor.

In both controllers, the system uses IFPs to produce systems with optimal performance – in the case of the diverse controller, IFPs are required to give the DESS discussed in the previous section. To further study the impact of IFPs, we remove the IFPs in setups with slow and diverse sensing and observe the resulting performance. This is done by setting $L_2$ to be zero in the optimal controller. We remark that this directly corresponds to experimental conditions in which an organism’s IFPs are knocked out via surgery or medication.

A. System performance without IFPs

The removal of IFPs severely degrades performance, as shown in Fig. 8. With IFPs, both the slow-only and diverse controller delivered stable performance. After removing IFPs, both controllers become unstable.

Removal of IFPs causes a gap in system information about previously implemented actions and current state. The resulting system acts based on what has been sensed $d$ timesteps ago without taking previous, more recent actions into account. This is apparent in the impulse response of the slow-only setup on the left in Fig. 8. The impulse is attenuated perfectly after $d + 1$ time steps. However, immediately in the next timestep, more attenuating control action is received, causing the states to become negative (due to the positive sensed state $d$ timesteps ago). The system will fluctuate between positive and negative states, each time growing in magnitude. Overall, the removal of IFPs causes the system with slow-only sensing to become unstable.

Removing IFPs in the diverse sensing case yields similarly bad results; the impulse response again fluctuates such that the amplitude increases to infinity. Compared to the slow-only setup, the initial state magnitudes are smaller; however, states eventually diverge due to instability.

An interesting observation: if we reduce the instability value $a$ of the system, then a setup with fast-only sensing is sufficient to stabilize the system. If we add slow sensing to this to create a diverse sensing setup, then remove IFPs, the resulting system still fluctuates but eventually decays to zero instead of blowing up. In this case, the diverse setup is worse than the fast-only setup. This again emphasizes the importance of IFPs, not only for performance but also to facilitate DESS in systems where delays are present.

B. IFPs in Standard Controllers

In the above sections, we used standard full control (FC) models to describe a simplified model with sensing delays. These results also apply to the dual state feedback (SF) case with actuation delays; both produce IFP connections, as shown in Fig. 6. An additional model to consider is output feedback (OF) where we consider a system described by

$$x(t + 1) = A_rx_r(t) + B_2r_u_r(t) + B_1w(t)$$
$$y_r(t) = C_rx_r(t)$$

(4)

where $x_r \in \mathbb{R}^n, u_r \in \mathbb{R}^m$, and $y_r \in \mathbb{R}^p$ correspond to states, control action, and sensed outputs, respectively. The OF controller for this system inherently contains IFPs irrespective of delays being present; these are represented by ‘IFP-Sense-2”, “IFP-State”, and “IFP-Act-2” in Fig. 2. We shall refer to these as OF-IFPs. IFP-State estimates state evolution in the absence of noise and actuation, IFP-Act-2 accounts for controller action, and IFP-Sense-2 predicts incoming sensory information based on the internal estimated state. We remark that in principle, if only Bayesian estimation of the initial condition is required, no IFPs are required. However, if timely state estimations are required for action (e.g. in the Kalman filter), then OF-style IFP is necessary; thus, IFPs in OF are somewhat Bayesian in nature, they represent more than just pure Bayesian estimation. Additionally, in the adversarial $H_{\infty}$ setting, an additional IFP path is necessary to anticipate the worst-case adversarial disturbance.

As with the FC and SF cases, we can introduce internal delay states. Let the augmented state be $x = [x_r^T \ x_a^T \ x_s^T]^T$. 

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where $x_a$ represents delayed actuation states and $x_s$ represents delayed sensing states. Then, $x_a$ has length $d_a m$ where $d_a$ is the number of actuation delay steps; the last $m$ elements of $x_a$ represent delayed physical actuation upon the real physical state $x_r$. Similarly, $x_s$ has length $d_s p$ where $d_s$ is the number of sensing delay steps; the last $p$ elements of $x_s$ represent delayed information from the sensor. For ease of notation, we assume that $d_a = d_s = d$; our setup trivially extends to the case that they are unequal.

We also augment the input, i.e. $u = [u_r^T, u_s^T]^T$. Now, $u_r$ represents control input which is will be delayed before reaching the physical states; $u_s \in \mathbb{R}^{p d}$ represent the internal wires to internal delay states $x_s$ (as in the FC case).

Let $Z_{x,y} \in \mathbb{R}^{y \times x}$ be the block-downshift matrix, with identity matrices of size $y$ along its first block sub-diagonal and zeros elsewhere. The system matrices for the augmented system are written in block matrix form:

$$A = \begin{bmatrix} A_r & B_{2r} & 0 \\ 0 & Z_{d,m} & 0 \\ C_r & 0 & Z_{d,p} \end{bmatrix}, \quad B_2 = \begin{bmatrix} 0 \\ 0 \\ I \end{bmatrix}, \quad B_1 = \begin{bmatrix} B_{1r} \\ 0 \\ 0 \end{bmatrix},$$

$$C = \begin{bmatrix} 0 & 0 & I_C \end{bmatrix},$$

$$\hat{B}_{2r} = \begin{bmatrix} 0_{n \times m(d-1)} & B_{2r} \end{bmatrix}, \quad \hat{C}_r = \begin{bmatrix} C_r^T & 0_{n \times p(d-1)} \end{bmatrix}^T,$$

$$\hat{I}_C = \begin{bmatrix} 0_{p \times p(d-1)} & I_{p \times p} \end{bmatrix}, \quad \hat{I}_B = \begin{bmatrix} I_{m \times m} & 0_{m \times m(d-1)} \end{bmatrix}^T.$$

We solve DAREs to obtain the optimal estimator gain $L = [L_1^T, L_2^T, L_3^T]$ and optimal controller gain $K = [K_1, K_2, K_3]$. By virtue of the block-matrix structure of our system matrices, $L_2$ and $K_3$ are generally zero. This allows us to simplify the resulting OF estimator and controller into the one shown in Fig. 2. For illustrative purposes, we write the simplified equations for $d = 1$ below, though our observations extend to larger values of $d$:

$$\delta(t+1) = C_r x_r(t) - C_r \hat{x}_r(t) - L_3 \delta(t),$$

$$\hat{x}_r(t+1) = A_r \hat{x}_r(t) + B_{2r} x_a(t) + L_1 \delta(t),$$

$$u_a(t) = K_1 \hat{x}_r(t) + K_2 x_a(t).$$

Here, $\delta$ is the delayed difference between the estimated sensor output and true sensor output, discounted by the observer term $L_3 \delta(t)$. The resulting controller, shown in Fig. 2, contains two sources of IFPs due to delay: “IFP-Sense-1” and “IFP-Act-1”. These resemble the IFPs from our FC- and SF-only delay models from Fig. 6, respectively. The remaining IFPs are intrinsic to the Kalman filter in the standard OF controller. Thus, a kind of separation principle is at play: the total controller is nearly exactly the sum of its parts (FC-delayed, SF-delayed, and OF without delay).

We also note that the delay-motivated IFPs are much bigger in dimension than the OF-IFPs; both delay-motivated IFPs have dimension of $nd$. Of the three OF-IFPs, IFP-State and IFP-Sense-2 have dimension $n$, while IFP-Act-1 has dimension $m$. Together, these five IFPs comprise the main sources of IFP that can be modelled using standard control; all are smaller in dimension and less complex than the SLS-based IFP described in our companion paper [2].

V. DISCUSSION

The results of this paper show that dramatic DESS in systems with diverse sensing and actuation can exist, where two poorly performing components separately create a well-functioning system when combined. The results also show the importance of IFPs within delayed components, where the system performance becomes unstable without the correct feedback information. These theoretical considerations can be applied to biological control and to other complex structures that carry out large computations. The natural next steps are to extend the IFP analysis further using SLS (as is done [2]), and to apply this analysis toward real biological architectures via experimentation (as proposed in [1]).

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