Why internal feedback is necessary in the perception-action loop

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Animals can move reliably in unpredictable environments. The study of sensorimotor control has assumed that sensory information from the environment leads to actions, which then act back on the environment, creating a single, unidirectional perception-action loop. This loop contains internal delays in sensory and motor pathways, which can lead to unstable control. We show here that these delays can be compensated by internal feedback signals that flow backwards, which are ubiquitous in neural sensorimotor systems. Recent advances in control theory show that internal feedback plays a key role in compensating internal delays. Based on these theoretical advances, we use a basic, mathematically tractable control model to show that internal feedback has an indispensable role in state estimation, can explain localization of function – why different parts of cortex control different parts of the body – and how attention can improve motor performance, all of which are crucial for effective sensorimotor control. Control theory can explain anatomical, physiological and behavioral observations, including motor signals in visual cortex, heterogeneous kinetics of sensory receptors and the presence of giant Betz cells in motor cortex.

Feedback control is an essential strategy for both engineered and biological systems to achieve reliable movements in unpredictable environments (1). Optimal and robust control theory, which provide a general mathematical foundation to study feedback systems, have been used successfully to explain behavioral observations by modeling the sensorimotor system as a single control loop called the perception-action cycle (2–4). In these models, the sensorimotor system senses the environment, communicates signals from sensors to the brain, computes actions, and then acts on the environment, feeding back to the sensors and forming a single unidirectional loop as shown in Fig. 1.

Consider the canonical model of localized function in the primate visuomotor cortical pathway, depicted in Fig. 2: A visual signal is encoded on the retina, then travels to the lateral geniculate nucleus (LGN) in the thalamus, and on to the primary visual cortex (V1), progressing through successive transformations until it reaches the primary motor cortex (M1), the spinal cord, and ultimately the muscles. The single-loop feedback model also makes implicit assumptions about the interpretation of responses from sensory and motor populations of neurons, which represent sensory signals and action signals, respectively. While intuitive, this model neglects a well-known and ubiquitous feature of sensorimotor processing: internal feedback, which is the main focus of this paper.

The perception-action control model does not have a direct role for internal feedback connections. Internal feedback in-
includes all signals that do not flow from sensing towards action. We can divide internal feedback into two broad categories: counterdirectional between brain areas and lateral interactions within areas. Counterdirectional internal feedback is in the opposite direction of the single-loop model; these signals flow from action toward sensing. Lateral internal feedback consists of recurrent connections within areas that are used for local processing. This distinction emphasizes the importance of where control signals are spatially located.

One reason that the single-loop model has endured is that it offers a set of tools from control theory and a conceptual framework that allows subsystems to be treated in isolation. However, these subsystems are not isolated, and with internal feedback each subsystem has access to both bottom up and top down information. The eye is itself a site of computation and control: As the eye moves and senses different parts of the visual scene, lateral interactions within the retina control spatial and temporal filter properties that can adapt and identify important features under a wide range of illumination and scene dynamics (5, 6). Retinal ganglion cells project to relay neurons in the LGN, which then project to primary visual cortex, V1, but a much greater number of feedback neurons project back from V1 to LGN (7–9).

Projections from motor areas in cortex to visual areas have substantial diversity in morphology, myelination, and synapse kinetics (7, 10, 11). Given the position of M1 in the final common pathway, one might expect activity in M1 to be driven by current visual stimuli or current movements, but the neuronal responses are better explained by preparatory activity and internal rotational dynamics, suggesting that M1 is semi-autonomous (12). Furthermore, signals related to movements of the whole body are found in areas typically associated with particular parts of the body, such as the hand area, as well as sensory areas such as primary visual cortex (13–16). Although not typically studied together, all of these sensory and motor signals are generated by internal feedback and are the focus of this study.

Internal feedback has been studied in the context of predictive coding (17, 18) and other models (19–22). However, these models neglect key constraints on neural communication in both space and time. Achieving fast, accurate computation and communication over large distances is difficult and often impossible because communication may be slow, limited in bandwidth and constrained to localized populations.

Here, we build on the foundations of recent work in distributed control theory (23–27) and show that internal feedback is a solution to achieving rapid and accurate control given the spatial and temporal constraints on brain components and systems. We present an idealized model and prove mathematically that internal feedback is both plausible and necessary for achieving optimal performance. Internal feedback serves at least three functions in our model: estimation, localization of function and attention, all of which are crucial for effective sensorimotor control and survival. This theory explains why there are differences in population responses between M1 and V1, differences in kinetics between AMPA and NMDA receptors, roles of giant pyramidal cells in visuomotor control and localization of function in cortex. There is a general principle behind all of these differences.

**Task model and performance.** We analyze expected values and theoretical bounds on task performance for models of a simple, well-studied and ethologically relevant tracking task, consisting of reaching for and grasping a moving object. We define task success as continuous pursuit, as opposed to one-time contact between limb and object.

The complete tracking task requires identification of the object amidst a visual scene, prediction of the object’s movement, and generation and execution of bimanual limb movement. We consider different aspects of the tracking task and make simplifying assumptions. These assumptions are not essential to our conclusions, but they allow us to study internal feedback in an accessible way using familiar linear dynamical systems.

**Single-loop feedback control.** In the simplest case of the tracking problem, we consider tracking the endpoint of a limb on a plane. The variable to be controlled is the **tracking error** – the distance between the hand and the object. We start by assuming that the system controlling the limb can perfectly sense the position of limb and object at every instant, which will be relaxed in later models. The **cost** is defined as the Euclidean norm of the tracking error over time, with smaller cost indicating better tracking.

Let $x$, $u$, and $w$ represent the tracking error, the control action on the limb, and the action of the object, respectively. We also refer to $x$ as the **state** of the system. Let $A$ be a matrix that represents the intrinsic dynamics of $x$ – including the mechanical coupling between two dimensions of limb movement. The time-evolving dynamics of the tracking error follows from:

$$x(t + 1) = Ax(t) + u(t) + w(t)$$  \[1\]

Let $\alpha$ denote the magnitude of the maximum eigenvalue of $A$, as a proxy for task difficulty. Note that $\alpha < 1$ corresponds to a task in which tracking error $x$ will decrease with no limb action – this is an easy task.

The actions $u$ provide feedback control on the tracking error, computed by an arbitrary function $K$ that has access to all past and present tracking errors $x(1 : t)$, as follows:

$$u(t) = K(x(1 : t))$$  \[2\]
The optimal solution to this problem is the linear quadratic regulator (LQR) and the optimal controller is $K(x(1:t)) = -Ax(t)$. This controller fits into the single-loop model of sensorimotor control, but there is no internal feedback, nor does the addition of internal feedback provide any performance advantage.

Controllers without internal feedback are optimal for a large but special class of problems, including classical state feedback and full control problems from control theory. Though mathematically elegant, they can be impractical when applied to biological systems. In subsequent sections, we relax some of the assumptions implicit in this single-loop model and show that small deviations from assumptions relevant to biological systems give rise to the necessity of internal feedback and advantages that accrue.

Any of the controllers in subsequent sections can be implemented in a variety of ways, though whether or not a particular controller needs internal feedback is generic across all implementations. In order to study internal feedback, we choose particular non-unique controller implementations which, when optimized, attain the optimal performance over the relevant class of controllers. We choose implementations for which the optimal solution is relatively transparent and easy to interpret.

**Estimation requires counterdirectional internal feedback.**

**Internal feedback facilitates implicit estimation in the presence of sensor delays.** Simple modifications to the control problem described above lead to an optimal controller $K$ whose implementation requires internal feedback. One such modification is the introduction of sensor delays which are ubiquitous in nervous systems. Sensor delays can be modeled by introducing a virtual internal state $x_s$, which represents the adjusted tracking error from the previous time step (26). This formulation allows us to pose the delayed-sensor tracking problem as a standard control problem which can be optimally solved by LQR:

$$
\dot{x} = \begin{bmatrix} A & 0 \\ I & 0 \end{bmatrix} x + \begin{bmatrix} 0 & I \end{bmatrix} u(t), \quad x(0) = x_0
$$

$$
u(t) = K \begin{bmatrix} x(t) \\ x_s(t) \end{bmatrix}
$$

where the virtual internal state $x_s$ contains delayed information about the tracking error. Controller $K$ can be partitioned into two block-matrices, $(K = \begin{bmatrix} K_1^T & K_2^T \end{bmatrix})$. The resulting system is shown in Fig. 3. Here, the controller does not directly “perceive” the tracking error $x$ and only has access to the virtual internal state $x_s$. However, the controller can freely take actions that affect both the tracking error and the virtual state. The action on the virtual state, as shown in Fig. 3, is an example of counterdirectional internal feedback, and is determined by gain $K_2$.

For the delayed sensing problem, the optimal controller has a simple analytical form: $K_1 = -A^2$ and $K_2 = -A$. The nonzero value of $K_2$ indicates presence of internal feedback. If no internal feedback is allowed (i.e. we enforce $K_2 = 0$), then the optimal controller is $K_1 = -A^2/4$. We compare the performance of these two controllers in Fig. 4, and see that the controller with internal feedback far outperforms the controller without internal feedback. We also note that the task becomes more difficult, the controller without internal feedback is unable to stabilize the closed-loop system and tracking is no longer possible.

For a controller with sensory delays, internal feedback is required for optimal performance. This also applies to controllers with actuator delays (26). In both cases, internal feedback adjusts delayed signals to compensate for actions taken and information received during the delay; in other words, internal feedback implicitly compensates for the delays.

**Intrinsic internal feedback in the Kalman filter.** We now consider the case in which sensing is instantaneous, but imperfect. Consider the following system:

$$
x(t + 1) = Ax(t) + Bu(t) + w(t)
$$

$$
y(t) = Cx(t)
$$

where $y$ is the sensor input. Matrix $B$ represents the effect of action $u$ on tracking error $x$, and matrix $C$ represents how sensor input $y$ is related to tracking error $x$. This is a standard
where \( \hat{x} \) is an internal estimate of tracking error \( x \). This optimal controller uses the Kalman filter, which inherently contains three counterdirectional internal feedback pathways irrespective of delays being present. These pathways are represented by the blue arrows through in Fig. 5, and play a central role in state estimation. The pathway through \( A \) estimates state evolution in the absence of noise and actuation; the pathway through \( B \) accounts for controller action, and the pathway through \( C \) predicts incoming sensory signals based on the internal estimated state.

Sources of internal feedback are preserved in a Kalman filter with delays. We now create a model that combines features from previous sections: sensor delays, actuator delays, and imperfect sensing. The problem can be written using virtual states as follows:

\[
\begin{bmatrix}
    x(t+1) \\
    x_a(t+1) \\
    x_s(t+1)
\end{bmatrix} =
\begin{bmatrix}
    A & B & 0 \\
    0 & 0 & 0 \\
    C & 0 & 0
\end{bmatrix}
\begin{bmatrix}
    x(t) \\
    x_a(t) \\
    x_s(t)
\end{bmatrix} +
\begin{bmatrix}
    0 & 0 & 0 \\
    I & 0 & 0 \\
    0 & I & 0
\end{bmatrix}
\begin{bmatrix}
    u(t) \\
    u_s(t) + \delta(t) \\
    u_a(t)
\end{bmatrix}
\]

\[ y(t) = x_a(t) \]

where \( x_a \) and \( x_s \) are virtual internal states corresponding to delayed actuator commands and delayed sensor signals, respectively, and \( u_s \) represents compensation on virtual internal states. We can use standard control theory to obtain the optimal controller gain \( K \) and optimal estimator gain \( L \). Due to the block-matrix structure of the system matrices, the optimal gains have the following structure: \( K = \begin{bmatrix} K_1 & K_2 & 0 \end{bmatrix} \) and \( L = \begin{bmatrix} L_1^+ & 0 & L_2^+ \end{bmatrix} \). The controller can be implemented as follows:

\[
\begin{align*}
\delta(t+1) &= Cx(t) - C\hat{x}(t) - L_2\delta(t) \\
\hat{x}(t+1) &= Ax(t) + Bx_a(t) + L_1\delta(t) \\
u(t) &= K_1\hat{x}(t) + K_2x_a(t)
\end{align*}
\]

Here, \( \delta \) is the delayed difference between the estimated sensor input and true sensor input, discounted by the observer term \( L_2\delta(t) \). The resulting controller, shown in Fig. 6, contains two internal feedback pathways related to delay; one pathway compensates for sensor delays, and the other compensates for actuator delays. The remaining internal feedback is inherent to the Kalman Filter, as described in the previous section and shown in Fig. 5. Overall, the inclusion of sensor delays, actuator delays, and imperfect sensing result in an optimal controller with several internal feedback pathways, each of which serves a specific, interpretable purpose.

Localization of function requires lateral internal feedback. Neuron-to-neuron computation and communication are typically spatially and temporally constrained for signals between regions, compared with signals within a local region. Although signals within each region may conform to the single-loop model, signals between regions are an example of lateral internal feedback. These signals play a crucial role in enabling good performance.

Localization of communication naturally leads to the localization of function in cortex; sensory and motor areas are spatially localized (with some cross-talk), as are different motor areas. Here, we focus on the latter. We start with the problem formulation described by Eq. Eq. (1), and partition tracking errors into two sets \( x_1 \) and \( x_2 \), representing two distinct but possibly coupled subsystems (e.g., two distinct limbs that are mechanically coupled). The overall tracking error is \( x = \begin{bmatrix} x_1^T & x_2^T \end{bmatrix}^T \). Correspondingly, we partition actuators into two sets \( u_1 \) and \( u_2 \) that act on their respective subsystems, via local controllers; \( u = \begin{bmatrix} u_1^T & u_2^T \end{bmatrix}^T \).

Each local controller senses and controls one subsystem; i.e., local controller 1 senses \( x_1 \) and computes \( u_1 \), and local controller 2 senses \( x_2 \) and computes \( u_2 \). Local controllers may communicate to one another; however, due to localization constraints, cross-communication is subject to some delay.
Thus, local controller 1 cannot directly access $x_2$ without some delay, and similarly for local controller 2.

We first remark that without the constraint of localized communication, the optimal controller for Eq. Eq. (1) is $u = -Ax$. If $A$ is block-diagonal (i.e. $x_1$ and $x_2$ are uncoupled), then this controller obeys localized communication constraints; in fact, no cross-communication (i.e. internal feedback) is required between the two local controllers. However, if the two subsystems are coupled, then this controller requires rapid, global communication, which violate localized communication constraints. To enforce localized communication, we reformulate the problem by introducing virtual states $x'_1$ and $x'_2$, which represent delayed cross-communication between the two local controllers. $x'_i$ is information sent from local controller 1 to local controller 2, with delay; and similarly for $x'_2$. We also define $u'_1$ and $u'_2$, which model interconnections between virtual states and real tracking errors. For simplicity, we assume unit delay. The reformulated problem is as follows:

$$
\dot{x}' = \begin{bmatrix}
    x'_1 \\
    x'_2 \\
end{bmatrix},
\quad
\dot{u}' = \begin{bmatrix}
    u'_1 \\
    u'_2 \\
end{bmatrix},
\quad
\dot{w}' = \begin{bmatrix}
    w'_1 \\
    w'_2 \\
end{bmatrix},
\quad
A = \begin{bmatrix}
    A_{11} & 0 & A_{12} \\
    0 & 0 & 0 \\
    A_{21} & 0 & A_{22} \\
end{bmatrix},
\quad
K = \begin{bmatrix}
    * & \triangle & * & 0 \\
    \triangle & * & \triangle & * \\
    0 & \triangle & * \triangle & * \\
end{bmatrix} \quad [8]
$$

The zeros in the top right and bottom left corners of the $K$ matrix preserve localized communication; they ensure that the two local controllers cannot communicate instantaneously to one another. Asterisks and triangles indicate free values; triangles represent sites of potential cross communication, or lateral internal feedback. We optimize over these free values to determine the $K$ matrix that achieves optimal performance with localized communication:

$$
K = \begin{bmatrix}
    -A_{11} & 0 & -A_{12} & 0 \\
    0 & 0 & -A_{12} & A_{12} \\
    A_{21} & -A_{21} & 0 & 0 \\
    0 & -A_{21} & 0 & -A_{22} \\
end{bmatrix} \quad [9]
$$

The resulting local controllers are shown in Fig. 7. Note that the $-A_{12}$ term in the second row and the $-A_{21}$ term in the fourth row of $K$ correspond to lateral internal feedback. Here, these internal feedback signals carry predicted values of the unsensed tracking errors for each controller, after taking control action into account; for instance, internal feedback from local controller 2 to local controller 1 conveys the predicted value of $x_2$, after taking control action from controller 2 into account. We can develop intuition for this implementation by following an impulse $w$ through time:

$$
\dot{x}'(1) = \begin{bmatrix}
    w'_1 \\
    0 \\
    w'_2 \\
end{bmatrix} \rightarrow \dot{x}'(2) = \begin{bmatrix}
    A_{12}w'_2 \\
    A_{12}w'_2 \\
    A_{21}w'_1 \\
    A_{21}w'_1 \\
end{bmatrix} \rightarrow \dot{x}'(3) = 0 \quad [10]
$$

We compare the performance of this controller to the controller without internal feedback in Fig. 8. For the controller without internal feedback, we choose the best possible linear controller; however, the lack of internal feedback results in severe performance degradation. As task difficulty increases, this controller is unable to stabilize the closed-loop system and tracking becomes infeasible. With internal feedback, task performance stays near the centralized optimal (i.e. the case where local controllers can communicate freely without delay). The foregoing analysis shows that localization of motor function (i.e. specialization of parts of motor cortex to particular parts of the body) in fact requires cross-communication, or internal feedback, between local controllers. This is supported by the presence of signals relating to the whole body in parts of the motor cortex specialized to particular parts of the body. In this case, internal feedback enables localization of function when subsystems are coupled; in reality, all body movements are mechanically coupled, something which the motor system can conceal through effective localization.

**Speed-accuracy tradeoffs necessitate the use of layering and internal feedback for attention.** We have shown that estimation and localization of functions require internal feedback to correct for self-generated or predictable movements. We now consider the role of internal feedback in **attention**.

Up to this point, we have assumed that the controller can directly sense the position of the object (perhaps with some delay). In a real world a scene can have many objects, which makes it more difficult for a sensorimotor system to determine the position of an object in the scene. However, a moving object, once identified, can be discriminated from a static visual scene. This illustrates the distinction between scene-related tasks (i.e. object identification) and error-related tasks (i.e. object tracking), which in the visual cortex is accomplished by the ventral and dorsal streams, respectively.

This distinction also mirrors the separation between bumps and trails in the mountain-biking task studied in [24], allowing...
us to build on the control architecture in that task. The main difference is that instead of separating into two control loops, we use layering and internal feedback to supplement the control actions of the main control loop.

For simplicity of presentation, we consider a one-dimensional problem (tracking on a line), and use as the metric $||x||_\infty$ rather than $||x||_2$. We assume that the object we want to track is located in some interval $[-\gamma, \gamma]$, and the change in position of the object per time step, $w_{obj}(t)$, is small, i.e. $|w_{obj}(t)| \leq \epsilon_{obj}$ for all $t$, $\epsilon_{obj} \ll \gamma$. We also assume the initial position of the object is known.

Consider a sensor that senses some interval of size $2\beta$ on the continuous line. Information from the sensor must be communicated to the controller (via axons), but this communication is subject to speed-accuracy tradeoffs. Let $R$ be the signaling rate (bits per unit time), let $T$ be the signaling delay, and let $\lambda$ be the resource cost to build and maintain axons. The speed-accuracy tradeoff can be formalized as $R = \lambda T$ (28). The signaling rate $R$ is related to the resolution of information sent about the sensed interval.

We implement this speed-accuracy tradeoff using a static, memoryless quantizer $Q$ with uniform partition, followed by a communication delay, as shown on the top in Fig. 9. This choice of quantizer does not add to the cost, since it recovers the optimal cost over all possible quantizers (29). The controller can move the sensor around; the interval sensed by the controller is $[\epsilon f(t)+1, \epsilon f(t)+1]$. To further facilitate speed in the fast path, we allow the controller to send only a subset of information from the sensor (i.e. only send information about a small part of the sensed scene). Mathematically, let the fast path send information about an interval of size $2\beta_f$, with $\beta_f < \beta$, and let this smaller interval be contained within the sensor interval. This smaller interval is an implementation of attention. The fast path is the main actuation path, while the slower path provides compensatory signals via internal feedback; this is shown on the bottom in Fig. 9. In this case, the best possible cost is

$$\epsilon T_f + \frac{\beta_f + \epsilon T_s + \frac{\beta}{2^{\lambda T_f - 1}}}{\epsilon_f T_f}$$

This is achieved by the controller depicted on the bottom in Fig. 9. The cost, as a function of $T_s$, is plotted in 10 with the label ‘No Internal Feedback’ ($T = T_s$). Here, the speed-accuracy tradeoff is implicit. Very low values of $T$ correspond to very low signaling rates – the controller does not receive enough information to act accurately, so performance is poor. The opposite problem occurs at very high values of $T$: though the information is high-resolution, the time elapsed between information and action is too long, leading to poor performance. The best performance occurs between these two extremes.

We can improve this performance by nearly an order of magnitude by adding an additional communication pathway and the requisite internal feedback. We now have two communication paths from the sensor, each with its own quantizer and delay block. The slower communication path uses quantizer $Q_s$ with delay $T_s$, while the faster path uses $Q_f$ with delay $T_f$. To further facilitate speed in the fast path, we allow it to send only a subset of information from the sensor (i.e. only send information about a small part of the sensed scene). Mathematically, let the fast path send information about an interval of size $2\beta_f$, with $\beta_f < \beta$, and let this smaller interval be contained within the sensor interval. This smaller interval is an implementation of attention. The fast path is the main actuation path, while the slower path provides compensatory signals via internal feedback; this is shown on the bottom in Fig. 9. In this case, the best possible cost is

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The delay of the fast layer is held constant. Unlike in the single-pathway case, no such performance boost occurs.

Functionally, the inclusion of a faster communication pathway allows action to be taken in a more timely manner than in the single-pathway case. Unlike in the single-pathway case, we are not encumbered by issues of low-resolution information; the slower communication pathway corrects the fast pathway through internal feedback. Here, as in previous examples, the internal feedback carries signals correcting for self-generated and slow, predictable changes. Overall, despite speed-accuracy tradeoffs in communication, the system achieves fast and accurate behavior with the help of internal feedback, under reasonable assumptions about the dynamics of the scene and environment.

Discussion

We have analyzed a group of simple models to isolate and illustrate how internal feedback in an action-perception loop can improve estimation, localization of function, and attention. This is a first step toward an end-to-end model of sensorimotor processing from which we extracted mathematical principles to explain previously cryptic features of biological sensorimotor control.

In this section, we will synthesize observations from animal visuomotor systems and interpret them in the context of our results. We will use evidence from primate, mouse, and feline visuomotor systems. Mice, as small prey animals, have quite different visual systems from primates in several respects, so we incorporate evidence from mice cautiously and only where necessary in the context of the larger explanatory framework.

Biophysical speed-accuracy tradeoffs necessitate internal feedback. Due to evolutionary and biophysical constraints, neurons generally obey speed-accuracy tradeoffs; they may rapidly convey a few bits of information, or slowly convey many bits of information, but they cannot rapidly convey many bits of information. Key mechanisms that underlie this speed-accuracy tradeoff include the tradeoff between smoothing and timeliness at a synapse, and the tradeoff between the number of neurons (i.e., bits of information) and axonal diameter (i.e., conduction speed) of each neuron in long-range projections (30). As a result, signaling delays and local communication – which were featured in our models – are key considerations for the analysis of sensorimotor systems.

Individual organisms contain a highly diverse population of neurons; for example, the range of neural conduction speeds in humans spans several orders of magnitude (30). In the sensorimotor system, these diverse neurons are multiplexed in a task-specific that approximates the performance of a single-loop system composed of ideal (e.g., fast and accurate) components. The fastest components are used in the single-loop, sending information from sensing (e.g., visual) areas toward motor areas. Internal feedback compensates for accuracy by filtering out slow-changing, predictable, or task-irrelevant stimuli, such that the fewest possible bits need to travel along the fastest possible neurons. From an evolutionary perspective, once a system can achieve fast responses, it becomes possible to add successive layers to achieve more accurate and flexible behavior.

We note that even though the fastest neurons are used in the single-loop, the speed of these neurons remains slow relative to the speed of electronics, which are typically used to implement control loops in an engineering setting. Thus, controls-based analyses of the forward loop should explicitly contain delays, as per Fig. 4.

Fast forward conduction is key to successful sensorimotor task performance. In cortex, the fastest, largest, and most striking neurons are the large pyramidal cells, also called Meynert Cells in visual cortex and Betz Cells in motor cortex. These neurons transmit rapid moving-object changes in visual scenes or rapid responses to perturbations in planned movements, respectively (31–33); this is consistent with our above claim that the fastest components convey information from visual areas toward motor areas.

The visual stream diverges into the dorsal and ventral streams, which are responsible for object motion and object identity, respectively. In natural scenes, object locations may change quickly, but object identities are relatively slow-changing; to a predator animal, a prey animal may move around rapidly, but its identity – a prey to be captured – does not change. Thus, speed is crucial for the dorsal stream, but not the ventral stream. This is captured in our minimal model of attention, and is also true physiologically; Meynert Cells project from V1 to MT (an object motion area in the dorsal stream), but no equivalently large cells project from MT to V1, nor from V1 to IT (an object identity area in the
ventral stream). Since reaching and tracking tasks are widely studied in motor neuroscience, our theory suggests additional experimental directions in reaching tasks that involve rapidly and unpredictably moving objects against predictable but not static backgrounds.

Internal feedback facilitates fast forward signals in visual cortex. In recent years, visual cortex has provided many examples of internal feedback that challenge the canonical single-loop view of sensorimotor control. In the canonical view (whose shortcomings are by now well-understood), visuomotor processing consists of a series of successive transformations from stimulus to response, with each cortical area along the way tuned to some aspect of stimulus space (34). However, although V1 does include static representations of stimuli, it also includes counterdirectional motor-based internal feedback and task/attention-related modulatory internal feedback (11, 15, 16). The neurons between V1 and V2 are a well-characterized case study; roughly the same number of neurons, of similar conduction speed, project from V1 to V2 as from V2 to V1 (7–9). However, these neurons are very different in morphological and molecular characteristics: V1-V2 neurons primarily use the AMPA receptor, while V2-V1 neurons primarily use the NMDA receptor (35). While AMPA and NMDA use the same neurotransmitter, glutamate, AMPA-mediated currents are cleared from the synapse in under 10ms, while NMDA-mediated currents can linger in the synapse for 100ms or longer (36). This distinction is believed to be relevant for learning, and is also relevant for top-down signaling to shape and direct perception during action.

In the context of our theory and minimal model of attention, V2-V1 internal feedback informs V1 of predictable elements of future stimuli. If we take the conventional view that V1 detects edges and V2 detects more involved elements of objects, such as contours, then V2 can facilitate edge detection by providing signals that inform V1 about where edges ought to be. Since the visual space cannot be sampled losslessly, these signals help target the resolution of V1. Accordingly, experiments that pharmacologically knock out NMDA show a loss of figure-ground discrimination, that is, a loss in capacity to contextually interpret the visual scene (35).

Internal feedback facilitates localization of function in motor cortex. Primary motor cortex (M1) has also provided many examples of internal feedback that challenge the standard view. M1 is dominated by its own past activity rather than static representations (12). In the context of the estimation problem we considered in Figure 6, motor cortex is dominated neither by motor representations nor by pattern generation, but by predictions of the consequences of self-action through local internal feedback, which need to be sent throughout the body. By the same principle, the localization of function within motor cortex that we considered in Figure 8 explains why the conventional view of homuncular organization becomes fuzzier, with, for instance, body-related signals found in putatively hand-related parts of motor cortex, as well as contralateral hand signals (13, 14, 37). As with motor signals in visual cortex, these signals do not overturn the preceding view that function is localized. These additional signals, in fact, are necessary for localization of function.

Existing frameworks for internal feedback facilitate fast forward signals in visual cortex. In recent years, visual cortex has provided many examples of internal feedback that challenge the canonical single-loop view of sensorimotor control. In the canonical view (whose shortcomings are by now well-understood), visuomotor processing consists of a series of successive transformations from stimulus to response, with each cortical area along the way tuned to some aspect of stimulus space (34). However, although V1 does include static representations of stimuli, it also includes counterdirectional motor-based internal feedback and task/attention-related modulatory internal feedback (11, 15, 16). The neurons between V1 and V2 are a well-characterized case study; roughly the same number of neurons, of similar conduction speed, project from V1 to V2 as from V2 to V1 (7–9). However, these neurons are very different in morphological and molecular characteristics: V1-V2 neurons primarily use the AMPA receptor, while V2-V1 neurons primarily use the NMDA receptor (35). While AMPA and NMDA use the same neurotransmitter, glutamate, AMPA-mediated currents are cleared from the synapse in under 10ms, while NMDA-mediated currents can linger in the synapse for 100ms or longer (36). This distinction is believed to be relevant for learning, and is also relevant for top-down signaling to shape and direct perception during action.

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Existing optimal control models neglect physiological limitations. Optimal control theory is a popular framework for sensorimotor modeling. Given a mathematical description of a system and some task specification, the optimal controller gives the best possible performance. Originally developed as a tool for engineers, control theory assumes that we have access to components that are very fast and accurate. Indeed, control circuits in engineering are implemented with fast and accurate electronics; a single sense-compute-actuate loop is generally sufficient, and achieves the desired behavior. Organisms, on the other hand, are not composed of fast, accurate components. Spiking neurons, though fast relative to other biological signaling mechanisms, are many orders of magnitude slower than electronics, and face more severe speed-accuracy tradeoffs – this results in communication constraints on how a control circuit can be implemented. However, by cleverly combining components and using internal feedback, organisms are able to perform survival-critical sensorimotor tasks (e.g. capturing prey) with speed and accuracy.

To use control theory to model physiological circuitry, a distinction between behavior and implementation must be made. The same behavior (i.e. optimal performance) may be achieved through a number of different implementations (i.e. underlying circuitry). Though traditional control theory excels as a model of sensorimotor behavior, it lacks the tools to incorporate the component-level constraints that are prevalent in organisms – thus, traditional control theory does not generate useful models of implementation. Recent advancements extend traditional control theory and incorporate component-level constraints (23, 24, 26, 27); we build on this
body of work to describe how constrained components affect the implementation of an optimal controller. In particular, we argue that internal feedback is a key part of any good controller whose components obey speed-accuracy tradeoffs; it filters out predictable changes so that fast, low-bandwidth components can be used to transmit unpredicted, actionable information toward the actuator.

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1. J Doyle, B Francis, A Tannenbaum, Feedback Control Theory. (Macmillan), (1992).
2. DM Wolpert, Z Ghahramani, MI Jordan, An internal model for sensorimotor integration. Science 259, 1880–1892 (1995).
3. E Todorov, Optimality principles in sensorimotor control. Nat. Neurosci 7, 907–915 (2004).
4. DW Franklin, DM Wolpert, Computational mechanisms of sensorimotor control. Neuron 72, 425–442 (2011).
5. L Zhang, Understanding Vision. (Oxford University Press), (2014).
6. T Gollisch, M Meister. Eye smarter than scientists believed: Neural computations in circuits of the retina. Neuron 65, 150–164 (2010).
7. EM Callaway, Feedbackward, feedback and inhibitory connections in primate visual cortex. Neuronal Networks 17, 625–632 (2004).
8. A Angelucci, J Bulter, Reaching beyond the classical receptive field of V1 neurons: Horizontal or feedback axons? J. Physiol. Paris 97, 141–154 (2003).
9. Y El-Shamy, AE, R Kumbhani, MT Drivv, JA Movshon, Visual response properties of v1 neurons projecting to v2 in macaque. J. Neurosci 33, 16594–16605 (2013).
10. DJ Felleman, DC Van Essen, Distributed hierarchical processing in the primate cortical cortex. Cereb. Cortex 1, 1–47 (1991).
11. L Muckli, LS Petro, Network interactions: non-geniculate input to V1. Curr. Opin. Neurobiol. 23, 195–201 (2013).
12. MM Churchill, et al., Neural population dynamics during reaching. Nature 487, 51–56 (2012).
13. FR Willett, et al., Hand knob area of premotor cortex represents the whole body in a compositional way (2020).
14. SD Stavisinsky, et al., Neural ensemble dynamics in dorsal motor cortex during speech in people with paralysis (2019).
15. C Stringer, et al., Spontaneous behaviors drive multidimensional, brain-wide activity. Science 364 (2019).
16. S Musall, MT Kaufman, AL Juavinett, S Gluf, AK Churchland, Single-trial neural dynamics are dominated by richly varied movements. Nat. Neurosci 22, 1677–1686 (2019).
17. RPN Rao, DH Ballard, Predictive coding in the visual cortex: a functional interpretation of some extra-classical receptive-field effects. Nat. Neurosci. 2, 79–87 (1999).
18. GB Keller, TD Mnsic-Flogel, Predictive processing: A canonical cortical computation (2018).
19. S Vyas, MD Golub, D Sussillo, KV Shenoy, Computation through neural population dynamics. Annu. Rev. Neurosci. 43, 249–275 (2020).
20. K Kar, J Kubilius, K Schmidt, EB Issa, JJ DiCarlo, Evidence that recurrent circuits are critical to the ventral stream’s execution of core object recognition behavior. Nat. Neurosci. 22, 974–983 (2019).
21. A Bastos, et al., Canonical microcircuits for predictive coding. Neuron 76, 695–711 (2012).
22. E Libby, TJ Perkins, PS Swain, Noisy information processing through transcriptional regulation. Proc. Natl. Acad. Sci. 104, 7151–7156 (2007).
23. J Anderson, JC Doyle, SH Low, N Matni, System level synthesis. Annu. Rev. Control. 47, 364–393 (2019).
24. Y Nakahira, Q Liu, TJ Sejnowski, JC Doyle, Diversity-enabled sweet spots in layered architectures and speed-accuracy trade-offs in sensorimotor control. Proc. Natl. Acad. Sci. United States Am. 118, 1–11 (2021).
25. AA Sarma, et al., Internal feedback in biological control: Architectures and examples in Proceedings of the IEEE American Control Conference. pp. 456–461 (2022).
26. J Stenberg, JS Li, AA Sarma, JC Doyle, Internal feedback in biological control: Diversity, delays, and standard theory in Proceedings of the IEEE American Control Conference. pp. 462–467 (2022).
27. JS Li, Internal feedback in biological control: Locality and system level synthesis in Proceedings of the IEEE American Control Conference. pp. 474–479 (2022).
28. Y Nakahira, N Matni, JC Doyle, Hard limits on robust control over delayed and quantized communication channels with applications to sensorimotor control in Proc. IEE CDC. pp. 7522–7525 (2015).
29. AA Sarma, JC Doyle, Flexibility and cost-sensitivity in a quantized control loop in Proceedings of the IEEE American Control Conference. (2019).
30. P Sterling, SB Laughlin, Principles of neural design. (MIT Press), (2015).
31. MS Livingstone, Mechanisms of direction selectivity in macaque v1. Neuron 20, 509–526 (1998).
32. V Chan-Palay, SL Palay, SM Billings-Gagliardi, Meynert cells in the primate visual cortex. J. Neurocytol 3, 631–658 (1974).
33. EE Fetz, Functional organization of motor and sensory cortex: symmetries and parallels in Dynamic Aspects Of Neocortical Function, ed. WC G.M. Edelman, W.E. Gall. (John Wiley), pp. 453–474 (1984).
34. DH Hubel, TN Wiesel, Receptive fields of single neurons in the cat’s striate cortex (1959).
35. MW Self, RN Kooijmans, H Supór, VA Lamme, PR Roelfsema, Different glutamate receptors convey feedforward and recurrent processing in macaque V1. Proc. Natl. Acad. Sci. United States Am. 109, 11031–11036 (2012).
36. D Altmann, A Gibb, Neuroenergetics and the kinetic design of excitatory synapses. Nat. Rev. Neurosci. 6, 841–849 (2005).
37. KC Ames, MM Churchland, Motor cortex signals for each arm are mixed across hemispheres and neurons yet partitioned within the population response. eLife 8 (2019).
38. M Leinweber, DR Ward, JM Sobczak, A Attinger, GB Keller, A sensorimotor circuit in mouse cortex for visual flow predictions (2017).