Phase transitions in when feedback is useful

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Abstract

Sensory observations about the world are invariably ambiguous. Inference about the world’s latent variables is thus an important computation for the brain. However, computational constraints limit the performance of these computations. These constraints include energetic costs for neural activity and noise on every channel. Efficient coding is one prominent theory that describes how such limited resources can best be used. In one incarnation, this leads to a theory of predictive coding, where predictions are subtracted from signals, reducing the cost of sending something that is already known. This theory does not, however, account for the costs or noise associated with those predictions. Here we offer a theory that accounts for both feedforward and feedback costs, and noise in all computations. We formulate this inference problem as message-passing on a graph whereby feedback serves as an internal control signal aiming to maximize how well an inference tracks a target state while minimizing the costs of computation. We apply this novel formulation of inference as control to the canonical problem of inferring the hidden scalar state of a linear dynamical system with Gaussian variability. Our theory predicts the gain of optimal predictive feedback and how it is incorporated into the inference computation. We show that there is a non-monotonic dependence of optimal feedback gain as a function of both the computational parameters and the world dynamics, and we reveal phase transitions in whether feedback provides any utility in optimal inference under computational costs.

1 Introduction

A critical computation for the brain is to infer the world’s latent variables from ambiguous observations. Computational constraints, including metabolic costs and noisy signals, limit the performance of these inferences. Efficient coding [1] is a prominent theory that describes how limited resources can be used best. In one incarnation, this leads to the theory of predictive coding [2], which posits that predictions are sent along feedback channels to be subtracted from signals at lower cortical areas; only the difference returns to the higher areas along feedforward channels, reducing the metabolic or informational cost of sending redundant signals already known to the higher areas. This theory does not, however, account for the additional costs or noise associated with the feedback. Depending on the costs for sending predictions and the reliability of signals encoding those predictions, we expect different optimal strategies to perform computationally constrained inferences. For example, if the feedback channel is too unreliable and expensive, we hypothesize that it is not worth sending any predictions at all. Here we offer a more general theory of inference that accounts for the costs and reliabilities of the feedback and feedforward channels, and the relative importance of good inferences about the latent world state. We formulate the inference problem as control via message-passing on a graph, maximizing how well an inference tracks a target state while minimizing the message costs. Messages become control actions with their own costs to reduce while improving how well an inference tracks a target state. We call this method inference as control, as it flips the interesting

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perspective of viewing optimal control as an inference problem [3]. We solve this problem under Linear-Quadratic-Gaussian (LQG) assumptions: Linear dynamics, Quadratic state and control costs, and Gaussian noise for the process, observations, and messages. Our theory enables us to determine the optimal predictions and how are they are integrated into computationally constrained inference. This analysis reveals phase transitions in when feedback is helpful, as we change the computation parameters or the world dynamics.

2 Related work

Our work brings together several related theories: Bayesian inference, efficient coding, and predictive coding. The idea that the brain performs Bayesian inference about latent variables amid uncertain sensory observation has been long studied in neuroscience [4–7]. Bayesian inference involves optimally combining prior information from the past or from surrounding context with the likelihood of current sensory observations [8–11]. The theory of efficient coding [1, 12–15] focuses on encoding the sensory observations themselves, capturing maximal information subject to limited biological resources. The theory of predictive coding [2] tackles such resource constraints by using top-down feedback predictions to suppress the part of sensory observations that is already known to the brain, and sending only the novel part of the observation back to the brain [16–21]. Understanding the utility of predictive feedback has also shown promise in gaining insights into deep learning algorithms and improving their performance, recently drawing wide interest in this topic [22–29].

Park et al. [30] brought together the ideas of a Bayesian brain and efficient coding, by identifying efficient neural codes as optimizing a posterior distribution while accounting for limited firing rates. Chalk et al. [18] unified theories of predictive coding, efficient coding, and sparse coding by showing how these regimes emerge in a three dimensional constraint space described by channel capacity, past information content about the world state, and the time point to which the estimate is targeted. Mlynarski et al. [31] investigated how sensory coding can adapt over time to account for the trade-off of an inference cost against a metabolic cost for high-fidelity encoding. Aitchison et al. [32] argued that Bayesian inference can be achieved using predictive coding, but is not necessary. While these works made important contributions towards unifying different encoding schemes that are optimal under different circumstances, they all assume that information is costly but computation is free. In particular, none of them have explicitly accounted for biological constraints along the feedback channel as well. In our work, we discuss how the optimal strategy changes when balancing inference performance against energetic costs, when there is noise in both feedforward and feedback pathways.

3 Defining the problem

We consider an inference task in which the brain tracks a latent world state $x^t$ based on its noisy sensory observations $o^t$ (Fig 1A). The trajectory of the world state follows a known stochastic linear dynamical system (Eq 1) with Gaussian process noise and Gaussian observations (Eq 2). At each time step, the brain sends a top-down prediction $p^t$ based on its best estimate $\hat{x}^{t-1}$ based on evidence up until the previous time step (Eq 3). The prediction is then sent through an additive white Gaussian noise feedback channel to the sensory level (Eq 4). The noisy prediction $\tilde{p}^t$ is then combined with the new observations $o^t$ to form a residual $\Delta^t$ (Eq 5). The residual is then sent through an additive...
white Gaussian noise feedforward channel to the brain (Eq[6]). Based on this noisy residual \( \hat{\Delta}^t \) and the prediction it had just sent, the brain updates its estimate \( \hat{x}^t \) (Eq[7]). A graphical representation of these dynamics is shown in Fig[1B].

Structurally, these dynamics are equivalent to a Kalman filter. The most common representation of this filter might even be viewed as predictive coding, as the update step uses the residual between the predicted and actual observation. However, the Kalman filter has no costs aside from the final inference, and no computational noise except the observation. Biological computation therefore may weigh fundamentally different tradeoffs in its inferences. Our goal is to find the parameters that minimize a weighted combination of inference loss, feedback energy cost, and feedforward energy cost (Eq[8]) given limitations caused by computational noise.

We optimize the following parameters: the gain \( L \) on the previous inference that is integrated into the new prediction; the prediction multiplier \( D \) and observation multiplier \( E \) that describe how the noisy prediction and the observation are weighted to form the residual; and the parameters \( F \), \( G \), and \( H \) that determine how the inference is updated in light of the new noisy residual. The optimization is done at steady state, assuming the observer must continually update its estimate in a stationary dynamic environment. For mathematical tractability, we assume that all messages are linear functions of their inputs, the three losses are quadratic, the weight on the inference loss is a scalar, and all noise is independent Gaussian white noise. The equations governing this problem are:

\[
\begin{align*}
x^{t} &= A x^{t-1} + \nu_{p}^{t} & \text{state dynamics} \\
o^{t} &= C x^{t} + \eta_{o}^{t} & \text{observation} \\
p^{t} &= L \hat{x}^{t-1} & \text{prediction} \\
\tilde{p}^{t} &= p^{t} + \eta_{f}^{t} & \text{noisy prediction, feedback} \\
\Delta^{t} &= D \tilde{p}^{t} + E o^{t} & \text{residual} \\
\tilde{\Delta}^{t} &= \Delta^{t} + \eta_{k}^{t} & \text{noisy residual, feedforward} \\
\hat{z}^{t} &= F \hat{x}^{t-1} + G \tilde{\Delta}^{t} + H p^{t} & \text{estimation}
\end{align*}
\]

\[
\text{Cost}_{\text{tot}} = \lim_{T \to \infty} \frac{1}{T} \sum_{t=1}^{T} \left( \frac{\|x^{t} - \hat{x}^{t}\|^{2}}{\text{Cost}_{\text{inf}}} + \tilde{p}^{T} W_{b} \tilde{p}^{t} + \tilde{\Delta}^{T} W_{t} \tilde{\Delta}^{t} \right) \tag{8}
\]

We consider how the optimal computational strategy varies with cost-weights \((W_{b}, W_{t})\) that determine the relative importance of feedback, feedforward, and inference costs \((\text{Cost}_{\text{inf}}, \text{Cost}_{\text{f}}, \text{Cost}_{\text{inf}})\). \(\eta_{p}, \eta_{o}, \eta_{f}, \text{and } \eta_{k}\) represent the process noise, observation noise, feedback noise, and feedforward noise with variances \(\sigma_{p}^{2}, \sigma_{o}^{2}, \sigma_{f}^{2}, \text{and } \sigma_{k}^{2}\) respectively. We will see below that certain combinations of parameters determine the system’s behavior at transition points.

### 4 Method: Inference as Control

We adopt a two-step approach to solve the optimization problem in Eq[8]. First we fix the parameters \( D \) and \( E \) that determine how the feedback is used to subtract predictions, and solve in closed form for the optimal feedback gain \((L)\) and optimal integration of residuals \((F, G, H)\) as a function of the fixed parameters. We then numerically optimize for \( D \) and \( E \), given the optimal feedback. Mathematically, we write

\[
\min_{D,E,L,F,G,H} \text{Cost}_{\text{tot}} = \min_{D,E} \left( \min_{L,F,G,H} \text{Cost}_{\text{tot}} \right) \tag{9}
\]

with an argmin determined analogously.

In order to find the closed form solution for fixed \( D \) and \( E \), we recast the minimization as an LQG control problem \([33]\) where the prediction is treated as an internal control. The LQG dynamical Eqs[10][11] are obtained by concisely writing Eqs[12] and [14] in terms of an augmented state \( z^{t} = [x^{t} \; \hat{\Delta}^{t}]^{\top} \) (see Appendix A.1). Augmented dynamics, control, and measurement matrices
$A_{aug}, B_{aug}, C_{aug},$ and the noise vector $\eta_{aug}$ are expressed in terms of $D$ and $E$. The feedforward and feedback energy costs are expressed as the LQG state and control costs respectively (Eq 12 derived in Appendix A.2), where $Q = \begin{bmatrix} 0 & 0 \\ 0 & W_f \end{bmatrix}$, and $R = W_b$.

\[
z^t = A_{aug} z^{t-1} + B_{aug} p^t + \eta_{aug}^{t-1}
\]

\[
\dot{z}^t = C_{aug} z^t
\]

\[
\min_p \lim_{T \to \infty} \frac{1}{T} \sum_{t=1}^{T} \left( \begin{array}{c} z^T Q z^t + p^T R p^t \\ \text{state cost} \\
\text{control cost} \end{array} \right)
\]

Note that in the above LQG objective function (Eq 12), the inference cost is not explicitly added. However, by invoking the separation principle [33], we show in Appendix A.3 that for a fixed $D$ and $E$ the LQG solution automatically minimizes the inference cost as well. The separation principle states that at each instant the observer needs to first make an optimal estimate of the world state, and then use this estimate to form the optimal control. Furthermore, we show in Appendix A.4–A.6 that the LQG solution also provides the optimal $F, G, H, L,$ and $\text{Cost}_\text{tot}$ in terms of $D$ and $E$. These are denoted as $F', G', H', L'$, and $\text{Cost}_{\text{tot}}'$, respectively. Finally, we numerically optimize $\text{Cost}_{\text{tot}}'$ with respect to $D$ and $E$ to solve the complete problem.

5 Results

In this paper we analyze our system for a one-dimensional world state to gain precise mathematical insight into the core computational problem. One useful perspective is that the feedback signal functions as a kind of self-control for the inference system. As we formulated the problem, this control has its own “action cost,” and this allows us to use the known solutions for controllable systems to identify the optimal feedback. The control gain $L$ is therefore a fundamental parameter, as it indicates whether it is best to send a prediction ($L \neq 0$) or not ($L = 0$). The control gain always takes the opposite sign as the product of prediction-multiplier and observation-multiplier, ensuring that the prediction is subtracted from the observation, which thereby reduces the feedforward cost. However, when the optimal control gain is 0, the prediction-multiplier $D$ also becomes 0 so feedback noise does not corrupt the observation if no prediction is sent.

Fig 2 shows how the optimal control gain, prediction-multiplier $D$ and observation-multiplier $E$ change with different parameters that define the constraints involved. We observe that there are cases where feedback and feedforward messages are useful, and others where messages are harmful.

5.1 Conditions for the Feedforward and Feedback Messages to be Useful

If the costs and noise are high, then it is not useful to send any messages forward at all. To understand this quantitatively, we consider what happens without feedback ($\dot{D} = 0$). Sending even an infinitesimal feedforward message about the observation to the brain is worth its feedforward energy cost if and only if

\[
(1 - A^2) \frac{U_{ff}}{U_s} < \frac{1}{1 + \frac{1}{\text{SNR}_o}}
\]

where $U_{ff} = W_f \sigma_f^2$ is the feedforward noise cost, i.e. the cost incurred by the noise variance in feedforward messages, $U_s = \frac{\sigma_o^2}{(1-A^2)}$ is the steady state signal power, and $\text{SNR}_o = \frac{\sigma_s^2}{(1-A^2) \sigma_f^2}$ is the observation Signal to Noise Ratio. When the left and right hand sides of Eq 13 are equal, the optimal strategy is indifferent between sending feedforward messages or not. Eq 13 is derived by finding when there exists a non-zero observation multiplier that minimizes the total cost in the absence of feedback. We know that the derivative of the total cost at the optimal non-zero $E$, when it exists, should be 0. We set this derivative to 0 and then use Descartes’ rule of signs to find when such a non-zero root exists. This yields the condition in Eq 13.

Next we consider the case where feedback is allowed. If the optimal prediction-multiplier is zero, then it is the same as no feedback, so by assumption the optimal observation-multiplier is non-zero if and only if feedforward is useful (Eq 13 holds). If the optimal prediction-multiplier is non-zero,
then naturally the feedforward evidence must also be non-zero to have any signal worth predicting. Furthermore, we also see that when sending feedback is optimal, it must be worth sending some feedforward messages even if the provision for sending feedback is cut off. These purely feedforward messages might need to be smaller — as small as the residuals when we had feedback — but sending at least some information is evidently worth the cost, since it was worth paying that feedforward cost even when noisy feedback corrupted the inference. Thus, mathematically, feedforward messages are useful if and only if Eq[13] is true, both with and without feedback.

Eq[13] implies that feedforward messages are worth their energy cost when either the observations are very reliable (high SNR), or when the relative cost of sending an arbitrarily small feedforward message is low (small $U_{fn}/U_o$).

Similarly, using reasoning described in Appendix[A.7] we find that feedback is valuable when

$$U_{bn} < \Phi(U_{fn}, A, \sigma_p^2, C^2, \sigma_o^2), \quad (14)$$

where $\Phi$ is a complicated function that involves solving for a quartic equation.

$U_{bn} = W_b \sigma_b^2$ is the feedback noise cost, i.e. the cost incurred by the noise variance in feedback messages. In Fig[A.3A], $\Phi$ (solid yellow line) is plotted as a function of the feedforward noise cost. Where Eq[14] holds as an equality (feedback and feedforward noise costs that correspond to points on the yellow line), an optimal observer is indifferent about sending feedback messages. Sending feedback is useful below that line, and harmful above it.

As stated above, when sending feedback is optimal (Eq[14] satisfied), it must be worth sending feedforward messages even if the provision for sending feedback is cut off (Eq[13] holds true). This is indeed observed in Fig[A.3A], where the dashed line is the locus of points where the optimal strategy is indifferent to sending feedforward messages: to the left, sending feedforward messages is useful, and to the right, it is not. As expected, the region where feedback is useful is also where feedforward messages are useful. Also, for very small feedback noise cost, the only case where sending feedback becomes harmful is when sending even an infinitesimal feedforward message is not useful either. As a result, the feedback indifference curve ends exactly at the precise feedforward noise cost where the optimal strategy is indifferent to sending feedforward messages. Fig[A.3B] shows a magnified version where feedforward and feedback products are near zero. At the origin, feedforward and feedback messages are free and/or noiseless. A noiseless message can be arbitrarily small and still convey information, so the cost can be arbitrarily small. In this case, there is nothing to gain or lose by subtracting predictions, so even free feedback makes no difference to costs or inferences. Thus the feedback indifference curve starts at the origin. Fig[A.3B] also demonstrates that for feedback to be useful, the feedback channel should be cheaper and/or less noisy than the feedforward channel. Note that this is true regardless of parameter values (world state timescale, measurement gain, etc.).

Figure 2: The best use of predictions and observations depends on the world state dynamics and channels’ noise and energetic costs. For tolerable feedback noise cost, as we increase either the A: feedforward noise, or the B: feedforward weight, the optimal strategy transitions from sending only feedforward, to predictive coding, back to only feedforward, and finally to no messages. For moderate feedforward noise cost, as we increase either the C: feedback noise, or the D: feedback weight, the optimal strategy transitions from predictive coding to feedforward messages only. When we increase either the E: measurement gain, or the F: process noise, or the H: world state timescale, the optimal strategy transitions from silence, to only feedback messages, to predictive coding. G: Increasing the observation noise leads to the opposite sequence of optimal strategies.
The exact solution for the optimization in Eq 9 depends on all the parameters that describe the dynamics (Eqs 1–7). However, from Eqs 13–14, we see that only certain combinations of parameters categorically determine if feedforward and feedback messages are useful. The relevant factors are feedback noise cost, feedforward noise cost, world state timescale, process noise variance, and the ratio of the measurement gain to the standard deviation of the observation noise. The feedforward (feedback) noise variance and feedforward (feedback) weights affect the optimal strategy only through their product, which we call the feedforward (feedback) noise cost. Increasing the channel noise means we need higher amplification and thus higher cost to achieve the same reliability; conversely, increasing the weight makes the channel more expensive for the same amount of amplification. Finally, the optimal strategy depends on the measurement gain and observation noise only through their ratio, \( \frac{\text{SNR}_o}{\text{SNR}} \), which determines the quality of observations.

Figure 3: Boundary curves divide the space of feedback and feedforward noise costs into regions of categorically different optimal strategies. A: Predictive coding is favored below the solid yellow line, feedforward efficient coding is favored above it, and no messages are favored to the right of the dashed line. B: The boundary curve determining whether feedback is useful lies below the line (cyan) along which the feedback and feedforward noise costs are equal, implying that for predictions to be useful the feedback channel must be cheaper and/or less noisy than the feedforward channel. C: With increasing predictability (thinner lines) of the world to be inferred, boundaries between coding strategies shift upwards and rightwards. As the predictability increases for a fixed value of channel parameters (dot), the optimal strategy transitions from sending no messages, to sending only feedforward messages, to sending and subtracting predictive feedback messages. D: An example of the shift in boundary curve with increasing predictability is shown for different world state timescales. As the timescale increases, the memory of the world state increases along with the SNR at the observation level, thereby increasing the predictability. E: A similar example is shown for different measurement gains. As the measurement gain increases, the observation SNR increases, thereby increasing the predictability.

5.2 Transitions in the Optimal Strategy

Having seen above how there are categorically different optimal strategies for computationally constrained inference, we now examine how individual parameters move the system between these strategies. We broadly group the parameters into three categories: feedforward, feedback, and sensory.

Feedforward parameters: We first consider the case of low to moderate feedback noise cost. Fig 4 illustrates the transition between optimal strategies as a function of the feedforward and feedback noise costs. The black line on Fig 4 left traces the transition as we increase the feedforward noise cost for a fixed feedback noise cost. For low values of the feedback noise cost, feedforward messages are almost free, so the system does not save appreciable resources by sending predictions; even worse, noisy feedback would corrupt the signal with noise. Thus for low feedforward noise costs it is optimal to send no predictions. As this cost increases, at some point it becomes equally valuable to send or withhold a feedback message. For higher feedforward noise costs, we cross the point of indifference, to where feedforward messages are important yet their channel is not economical by itself. Predictive feedback then becomes preferable, even when accounting for additional feedback noise.

As feedforward noise cost increases, reliable transmission through the channel becomes less affordable. As a consequence, the inference degrades. Upon increasing the feedforward noise cost beyond a certain point, the inference becomes so poor that it is no longer possible to make a good prediction worthy of the cost it incurs. Thus the system resorts to sending only feedforward messages.
Figure 4: Phase transition in the value of feedback. Left: Optimal control gain varies with channel parameters, specifically the noise cost for the feedback and feedforward channels. As the feedforward noise cost increases (black line), the optimal strategy transitions non-monotonically from sending only feedforward messages, to predictive coding with suppressive feedback, back to sending only feedforward messages, and eventually to sending no messages. The yellow curve on the panel is the phase transition for feedback: the locus of points where the optimal strategy is indifferent to sending feedback (green area) or not (red area). Near the critical point (colored circles), the loss function goes through a phase transition [34], seen at Right: The cost function has a minimum at Prediction-multiplier $D = 0$ for low feedforward noise cost, favoring no feedback (red). But as the feedforward noise cost increases from low to moderate values, this extremum switches to a maximum, with nearby minima that favor feedback with nonzero $D$ (green). Right at the transition point [34], the system becomes indifferent to feedback (yellow). Another phase transition occurs in the opposite direction as the feedforward noise cost increases further from moderate to high values.

For similar reasons, as the world becomes more predictable (Fig 3C), there is a wider range of feedforward and feedback noise costs for which sending predictions is optimal. The predictability can be increased either by lengthening the world state timescale, or by enhancing the observation SNR, enabling better inferences and thereby better predictions. Figs 3D–E demonstrates this for different world state timescales and measurement gains respectively. However, for large enough feedforward noise cost, sending even feedforward messages alone becomes too expensive/noisy, and so it is best to remain silent.

Fig 2A and B show how the optimal control gain $L$, prediction-multiplier $D$ and observation-multiplier $E$ change with feedforward noise and feedforward weight respectively. As only the product of noise variance and weight determines the transition in optimal strategy, we observe the same trend as either one of them increases. However, these parameters actually exhibit different effects away from the points of transitions. For example, when feedforward noise is close to 0, the system can save costs by attenuating the signal ($E \to 0$) and still beat the negligible feedforward noise. In contrast, in the extreme case that the feedforward messages are nearly free ($W_f \to 0$), the observation-multiplier increases arbitrarily ($E \to \infty$) to dominate any feedforward noise, improving the inference at no cost. These limiting cases provide helpful intuitions. Naturally, the challenging regime is in the middle, where there are real tradeoffs to make, and where feedback becomes relevant.

For the limiting case where feedback noise cost is extremely high, the feedback channel is too expensive/noisy to be used. Hence, as we slowly increase the feedforward noise cost from zero, we start by sending just the feedforward messages until the feedforward channel is too expensive/noisy, at which point we no longer send any messages.

**Feedback parameters:** We first consider the interesting case of low to moderate feedfoward noise cost. For low values of feedback noise cost we are in the regime where feedback is cheap and/or noiseless, and hence it is beneficial to send both predictive feedback and feedforward residual messages. But when the feedback noise cost becomes too high, sending predictions becomes too expensive/noisy, so it is best send only feedforward messages. This is shown in Fig 2C, D. Analogous to the feedforward case, although the same transition in optimal strategy is observed as we increase either the feedback noise or feedback weight, these parameters actually exhibit different effects away from that transition. For example, $L \to 0$ when feedback noise is close to 0, and $L \to -\infty$ when feedback weight is close to 0.

In the case of extremely high feedfoward noise cost, it is not worth sending even an infinitesimal feedforward message, so the optimal strategy is to not send any messages.
Sensory parameters: Fig 3C shows the boundary between strategies for three systems with different levels of predictability. For a fixed value of feedback and feedforward noise costs (dot), the optimal strategy changes with the predictability. With unpredictable dynamics (thick curve), the dot lies in the region where sending no messages is optimal, since the feedforward channel is relatively poor (right of the thick dashed line). For a slightly higher predictability, the dot lies within the region where feedforward-only messages are optimal (above medium curve, but left of the corresponding dashed line). And for even higher predictability, the dot lies in the region where predictive coding is optimal (below the thin curve). Hence, as the predictability increases, there is a transition from sending no messages, to sending just feedforward messages, to sending both feedback and feedforward messages.

Similarly, if either the measurement gain or the process noise increases, this would yield a higher observation SNR, which would then improve the inference and thereby predictability. Fig 2E–F shows the resultant transitions from no messages, to feedforward-only messages, then to predictive feedback, with increasing measurement gain or process noise. Increasing observation noise has the opposite effect, making observations less reliable and thereby reducing the predictability. Fig 2G shows the transitions in strategy with increasing observation noise. Finally, increasing the world state timescale increases the predictability since it increases both the memory of the system, and the observation SNR. Fig 2H reveals the familiar sequence of transitions in strategy, supporting our core intuitions about when feedback is valuable.

6 Discussion

In this paper, we define a new class of dynamic optimization tasks that more accurately capture essential biological constraints on inference in the brain, by including cost and noise for each recurrently connected computational element. We solve this optimization problem by modeling inference as a control problem with prediction as self-control. The resultant optimization provides nontrivial predictions for when we expect suppressive feedback as a function of biological constraints, computational costs, and world dynamics.

Predictive coding is a promising theory for brain computations [35–39], and a variety of experimental studies have indeed shown predictive suppression effects in neural responses [40–47]. However, neural responses vary in how much they are suppressed depending on a context and signal to noise ratio. Variants aiming to explain these effects all neglect the computational costs associated with predictive coding, even though those costs were part of the motivation for saving metabolic costs in the first place.

Although we contend that it is costly to send predictions, if these predictions are based on inferences that are already being computed for a task, then is it really an extra cost to send them as predictions? Yes, because distinct neurons are used to send feedforward and feedback signals, so the brain might pay costs twice for the same inference. When beneficial, the brain could avoid the duplicate feedback costs by silencing the feedback neurons, and send its inferences to higher brain areas only through its feedforward neurons. A related question arises for feedback suppression, which is presumably implemented through inhibitory neurons. What is the benefit of turning on an inhibitory neuron just in order to turn off an excitatory neuron? Excitatory neurons outnumber inhibitory neurons by 4:1, so few inhibitory neurons can suppress many excitatory ones, amounting to a potentially substantial savings. These biological constraints could be used in future elaborations of computationally constrained inference models.

One core prediction is that predictive coding grows more favorable when feedforward noise cost is greater than feedback noise cost. Why would such an asymmetry exist? Biologically, asymmetries in these noise costs can arise from differences in feedback and feedback anatomy or functional properties. Anatomically, feedback projections generally outnumber feedforward ones by 2:1, but the feedforward pathways compensate with greater weight, dominating at short cortical distances and leveling off at longer distances [48]. Functionally, the sparser, stronger feedforward channels therefore
have less ability to average away the noise, leading to a relatively higher amount of metabolically expensive activity caused by noise, and thus to a higher noise cost. This could establish conditions under which predictive feedback is useful.

Our mathematical system’s crucial theoretical parameters relate to biological quantities in three ways: as context-dependent parameters (time constant of the stimulus dynamics, sensory SNR), as neural parameters that could potentially be manipulated experimentally (feedforward and feedback SNR), and as developmentally-fixed parameters of the system (feedforward and feedback architecture). Testing our predicted dependence on these three types of parameters requires different considerations.

The context-dependent parameters are by far the easiest to manipulate experimentally. One can control the stimulus to adjust the observations’ SNR and the world state timescale, and measure whether any response suppression is modulated by these controlled parameters as shown in Fig 5.

The internal computational parameters like neural noise may be controllable through stimulus changes or experimental techniques of causal manipulation. Electrical or optogenetic stimulation could directly inject neural variability. Another approach could be based on the fact that neural noise variance tends to increase with firing rate. Thus, one could test our predictions about computational noise by elevating firing rates. Such methods could include providing a background sensory stimulus, or direct neural stimulation to increase baseline activity. In any case, it would be important to apply either natural manipulations or chronic unnatural ones to give the brain enough time and experience to optimize its computations.

For the developmentally fixed parameters like architecture, we cannot easily alter the system experimentally, and it may be unreasonable to assume that properties in a real biological system can be unambiguously mapped to any particular value in our abstract theoretical system. However, we can compare between brain systems or species with architectural difference, and test whether functional properties covary with those differences as predicted by our theory. Thus it may be fruitful to compare between brain areas with different architectures, such as 3-layer paleocortex (e.g. olfactory cortex) versus 6-layer neocortex (e.g. auditory or visual cortex), or within neocortical areas with different properties. It may also be fruitful to compare between organisms with different architectures (e.g. mammals versus reptiles). These architectures have different microcircuits with distinct feedforward and feedback projection neurons. For example, feedback in different visual and motor cortical systems tends to target different inhibitory cells [49] which have different noise levels [50, 51]. We predict that systems with more feedback noise (e.g. SOM versus VIP) would have less predictive suppression, as observed experimentally [49].

There are several interesting avenues for generalizing our theory. The proposed inference as control method can be extended to the more general case of observer taking external actions in addition to the internal predictions, in order to maximize external rewards while minimizing both external action costs (e.g. movements) and internal computational costs. This could be modeled as a typical LQG control problem [52] for external variables by including appropriate entries in matrices Q, R, and B_{aug} in addition to the internal controls we use for predictive coding. Though our results are limited to just a simple one dimensional linear dynamics with uncorrelated noise, our future work will explore these computational constraints in more complex multivariate and nonlinear tasks. Accounting for graph-structured inferences [53] and controllability [54] may provide additional constraints on the brain’s inference processes, and additional predictions for experiments.

Residuals between predictions and observations are useful not just for improving inferences, but also for learning, which this work does not address. In principle, a multivariate generalization could explain such computations as hierarchical inferences or adaptation where slower changes are also subject to prediction. However, the process of learning (as opposed to adaptation) occurs out of equilibrium with the environment, and accounting for transient responses under nonstationary statistics will require an extension to our theory. Overall, this work points a way towards expanding theories of predictive coding and efficient coding to unify inference, learning, and control in biological systems.

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References


A Appendix

A.1 Shoehorning the inference tracking dynamics as an LQG control problem

Substituting Eqs 1-2 and 4-5 in Eq 6

\[
\hat{\Delta}_t = \Delta_t + \eta_t
\]

\[
= (D \hat{p}_t^T + E \Delta_t^T) + \eta_t
\]

\[
= D \hat{p}_t^T + E (C x_t^T + \eta_t^C) + \eta_t
\]

\[
= D \hat{p}_t^T + E C x_t^T + E \eta_t^C + \eta_t
\]

\[
= D \hat{p}_t^T + E C (A x_{t-1}^T + \eta_t^A) + E \eta_t^C + \eta_t
\]

\[
= D \hat{p}_t^T + E C A x_{t-1}^T + E C \eta_t^C + E \eta_t^A + \eta_t
\]

\[
= D (p_t^T + \eta_t^A) + E C A x_{t-1}^T + E C \eta_t^C + E \eta_t^A + \eta_t
\]

\[
= E C A x_{t-1}^T + D p_t^T + E C \eta_t^C + E \eta_t^A + D \eta_t^A + \eta_t
\]

(15)

Combining Eqs 1 and 15 we write the dynamics of augmented state \( z_t = [x_t^T \hat{\Delta}_t^T]^T \) as in Eq 16

The noisy residual can now be written as a partial observation of the augmented state (Eq 17).

\[
z_t = \begin{bmatrix}
A_{aug} & z_{t-1} \\
0 & D
\end{bmatrix} + \begin{bmatrix}
 \eta_{aug}^{t-1} \\
 \eta_{aug}^t
\end{bmatrix}
\]

(16)

\[
\hat{\Delta}_t = \begin{bmatrix}
I \\
C_{aug}
\end{bmatrix} \begin{bmatrix}
 \hat{x}_t \\
 \hat{z}_t
\end{bmatrix}
\]

(17)

Rewriting Eqs 16-17 using concise notation, we get the LQG dynamics equations where prediction \( p \) is treated as the control.

\[
z_t = A_{aug} z_{t-1} + B_{aug} p_t + \eta_{aug}^{t-1}
\]

\[
\hat{\Delta}_t = C_{aug} z_t
\]

A.2 Feedforward and feedback energy costs expressed as the LQG state and control costs respectively

We express the feedforward and feedback energy costs as the LQG state and control costs respectively. For the derivation, we introduce the matrices \( Q = \begin{bmatrix} 0 & 0 \\ 0 & W_i \end{bmatrix} \), and \( R = W_b \). We take the feedback noise \( \eta_b \) as i.i.d \( \mathcal{N}(0, \Sigma_b) \).

\[
\min_p \lim_{T \to \infty} \frac{1}{T} \sum_{t=1}^T (\hat{\Delta}_t^T W_i \Delta_t^T + \hat{\Delta}_t^T W_b \eta_b^T W_b \eta_b^T)
\]

\[
= \min_p \lim_{T \to \infty} \frac{1}{T} \sum_{t=1}^T (\hat{\Delta}_t^T W_i \Delta_t^T + \hat{\Delta}_t^T W_b p_t^T + \eta_b^T W_b \eta_b)
\]

\[
= \min_p \lim_{T \to \infty} \frac{1}{T} \sum_{t=1}^T (\hat{\Delta}_t^T W_i \Delta_t^T + p_t^T W_b \eta_b + \eta_b^T W_b \eta_b) + \text{Tr}(W_b \Sigma_b)
\]

\[
= \min_p \lim_{T \to \infty} \frac{1}{T} \sum_{t=1}^T (z_t^T Q z_t + p_t^T R p_t) + \text{Tr}(W_b \Sigma_b)
\]

\[
= \min_p \lim_{T \to \infty} \frac{1}{T} \sum_{t=1}^T \begin{bmatrix}
\text{state cost} \\
\text{control cost}
\end{bmatrix}
\]
A.3 Minimizing the total energy cost also minimizes the inference cost, for a fixed \( D \& E \)

The LQG problem of interest is described by Eqs. \[10\] \[12\]. The separation principle states that the solution for LQG problem includes an estimation part and a control part, both of which jointly form the optimal solution even if treated separately. The estimation part of LQG solution minimizes the average squared norm error between estimated state \( \hat{z} \) and the true state \( z \), as shown in the left side of equality in Eq \[18\]. Note that at any time \( t \), we get to observe all the evidence up until that time (i.e. \( \hat{\Delta}^1, \hat{\Delta}^2, ..., \hat{\Delta}^t \)). This enables the simplification from Eq \[18\] to \[19\] because the optimal estimate \( \hat{\Delta}^t \) given \( \hat{\Delta}^t \) is trivially \( \hat{\Delta}^t \) itself. Hence, from Eq \[20\] we conclude that although we define the LQG objective function to be just the total energy cost, the LQG solution that minimizes the total energy cost also minimizes the inference cost for a fixed \( D \) and \( E \).

\[
\lim_{T \to \infty} \frac{1}{T} \sum_{t=1}^{T} (z^t - \hat{z}^t)^\top (z^t - \hat{z}^t) = \lim_{T \to \infty} \frac{1}{T} \sum_{t=1}^{T} \left[ \begin{array}{c} x^t \\ \hat{\Delta}^t \\ \end{array} \right]^\top \left( \begin{array}{c} \hat{\Delta}^t \\ \end{array} \right) - \left( \begin{array}{c} \hat{\Delta}^t \\ \end{array} \right) \right) (18)
\]

\[
= \lim_{T \to \infty} \frac{1}{T} \sum_{t=1}^{T} (x^t - \hat{x}^t)^\top (x^t - \hat{x}^t) (19)
\]

\[
= \text{Cost}_{\text{inf}} (20)
\]

A.4 LQG estimation solution to find \( F, G, \) and \( H \) in terms of \( D \) and \( E \)

The optimal estimate of the augmented state based on its noisy partial observations is given as

\[
\hat{z}^t = (I - K C_{\text{aug}}) A_{\text{aug}} \hat{z}^{t-1} + K \hat{\Delta}^t + (I - K C_{\text{aug}}) B_{\text{aug}} \eta^t (21)
\]

\[
K = \hat{\Sigma} C_{\text{aug}}^\top (C_{\text{aug}} \hat{\Sigma} C_{\text{aug}}^\top)^{-1},
\]

where \( \hat{\Sigma} \) is the solution to a discrete algebraic Riccati equation (Eq \[22\]), with \( W \) as the covariance of noise vector \( \eta_{\text{aug}} \).

\[
\hat{\Sigma} = A_{\text{aug}} \hat{\Sigma} A_{\text{aug}}^\top + W - A_{\text{aug}} \hat{\Sigma} C_{\text{aug}}^\top (C_{\text{aug}} \hat{\Sigma} C_{\text{aug}}^\top)^{-1} C_{\text{aug}} \hat{\Sigma} A_{\text{aug}}^\top (22)
\]

For brevity, we rewrite Eq \[21\] in terms of block matrices using the following substitutions,

\[
F_{\text{aug}} = (I - K C_{\text{aug}}) A_{\text{aug}}, \quad H_{\text{aug}} = (I - K C_{\text{aug}}) B_{\text{aug}}
\]

\[
\left[ \begin{array}{c} \hat{\Delta}^t \\ \end{array} \right] = \left[ \begin{array}{c} (F_{\text{aug}})_{11} \\ (F_{\text{aug}})_{21} \\ (F_{\text{aug}})_{22} \end{array} \right] \hat{\Delta}^{t-1} + \left[ \begin{array}{c} (K)_{1} \\ (K)_{2} \end{array} \right] \hat{\Delta}^t + \left[ \begin{array}{c} (H_{\text{aug}})_{1} \\ (H_{\text{aug}})_{2} \end{array} \right] \eta^t (23)
\]

yielding

\[
\hat{x}^t = (F_{\text{aug}})_{11} \hat{x}^{t-1} + (F_{\text{aug}})_{12} \hat{\Delta}^{t-1} + (K)_{1} \hat{\Delta}^t + (H_{\text{aug}})_{1} \eta^t (24)
\]

\[
\hat{\Delta}^t = (F_{\text{aug}})_{21} \hat{x}^{t-1} + (F_{\text{aug}})_{22} \hat{\Delta}^{t-1} + (K)_{2} \hat{\Delta}^t + (H_{\text{aug}})_{2} \eta^t.
\]

Since the states are Markovian, consequently the optimal estimates are Markovian as well. This implies that \( \hat{x}^t \) given \( \hat{x}^{t-1} \), does not depend on \( \hat{\Delta}^{t-1} \). Likewise, \( \hat{\Delta}^t \) given \( \hat{\Delta}^t \), does not depend on \( \hat{\Delta}^{t-1} \), \( \hat{\Delta}^{t-1} \), and \( \eta^t \). The above two arguments can be used to deduce that

\[
(F_{\text{aug}})_{12} = 0, \quad (F_{\text{aug}})_{21} = 0, \quad (F_{\text{aug}})_{22} = 0 \quad (K)_{2} = I, \quad (H_{\text{aug}})_{2} = 0.
\]

which we also verified empirically for the one dimensional case. Substituting \( (F_{\text{aug}})_{12} = 0 \) in Eq \[24\] and comparing it with Eq \[7\] we get the optimal solutions for \( F, G, \) and \( H \) in terms of \( D \) and \( E \), denoted as \( F', G', \) and \( H' \) respectively.

\[
F' = (F_{\text{aug}})_{11}, \quad G' = (K)_{1}, \quad H' = (H_{\text{aug}})_{1}
\]

A.5 LQG control solution to find \( L \) in terms of \( D \) and \( E \)

The optimal LQG control is given as

\[
p^t = L_{\text{aug}} \hat{x}^{t-1} (25)
\]

\[
L_{\text{aug}} = -(R + B_{\text{aug}}^\top P_{\text{aug}})^{-1} B_{\text{aug}}^\top P \quad A_{\text{aug}} (26)
\]
where $P$ is the solution of a discrete algebraic Riccati equation (Eq 27),

$$ P = Q + A^\top_{\text{aug}} P A_{\text{aug}} - A^\top_{\text{aug}} P B_{\text{aug}} (R + B^\top_{\text{aug}} P B_{\text{aug}})^{-1} B^\top_{\text{aug}} P A_{\text{aug}} \quad (27) $$

As shown in Eq 16, the last set of columns in $A_{\text{aug}}$ are all zero vectors. As a consequence, since $A_{\text{aug}}$ is the last multiplier in the right side of equality in Eq 23, the last set of columns of $L_{\text{aug}}$ would also be zero vectors. More specifically, Eq 25 can be further simplified by writing $L_{\text{aug}}$ in terms of block matrices in the following way

$$ p^t = [(L_{\text{aug}})_1, (L_{\text{aug}})_2] = [(L_{\text{aug}})_1, (L_{\text{aug}})_2] = \hat{x}^{t-1} + (L_{\text{aug}})_2 \hat{A}^{t-1}, \text{ then } (L_{\text{aug}})_2 = 0 $$

Hence, the optimal prediction is linearly related to the estimate through $(L_{\text{aug}})_1$. For consistency in notations, we denote $(L_{\text{aug}})_1$ as $L'$, yielding

$$ p^t = L' \hat{x}^{t-1}, \text{ where } L' = (L_{\text{aug}})_1. $$

### A.6 Closed form expressions for total cost in terms of $D$ and $E$

The optimal inference cost for fixed $D$ and $E$, which is the same as the augmented state’s estimation error, is $\text{Cost}_{\text{inf}}' = \text{Tr}(\Sigma)$. Where $\Sigma$ is the augmented state’s estimation error covariance matrix, such that

$$ \Sigma = \hat{\Sigma} - \hat{\Sigma} C_{\text{aug}}^\top (C_{\text{aug}} \hat{\Sigma} C_{\text{aug}}^\top)^{-1} C_{\text{aug}} \hat{\Sigma}. \quad (28) $$

The optimal total energy cost for a given $D$ and $E$, which is the optimal LQG cost, is given as

$$ \text{Cost}_{\text{energy}}' = \text{Tr}(Q \Sigma) + \text{Tr}(P(\Sigma - \Sigma)). $$

As $\Sigma$ is the error covariance matrix in estimating $z'$, and since the noisy residual $\hat{A}^{t-1}$ is fully observable at any time point, the corresponding lower block matrix in $\Sigma$ will be zero. Also, by definition in Eq 12, we know that the upper block matrix in $Q$ is zero. As a consequence, $\text{Tr}(Q \Sigma)$ would always be zero. Resulting in

$$ \text{Cost}_{\text{energy}}' = \text{Tr}(P(\Sigma - \Sigma)). $$

Combining the inference cost and energy cost, we have the total cost in terms of $D$ and $E$ as

$$ \text{Cost}_{\text{tot}}' = \text{Tr}(\Sigma) + \text{Tr}(P(\Sigma - \Sigma)) \quad (29) $$

### A.7 Condition for useful feedback

It can be algebraically shown that the total cost is an even function in both $D$ and $E$ and hence can be written as a function of $\hat{D} = D^2$ and $\hat{E} = E^2$. This limits the function domain to non-negative values, thereby reducing the search space for numerical optimization. We empirically observe that the cost function now has just one minimum when plotted with $\hat{D}$ and $\hat{E}$, and that the negative of gradient at any point always directs toward this minimum.

Let $\hat{E}'$ denote the optimal $\hat{E}$ that minimizes the total cost at $\hat{D} = 0$. $\hat{E}'$ can be computed by equating the derivative of cost with respect to $\hat{E}$ to 0, at $\hat{D} = 0$ (Eq 30).

$$ \frac{\partial \text{Cost}_{\text{tot}}'}{\partial \hat{E}} \bigg|_{\hat{D} = 0, \hat{E} = \hat{E}'} = 0 \quad (30) $$

We define $\psi$ as the derivative of total cost with respect to $\hat{D}$, evaluated at $\hat{D} = 0$ and $\hat{E} = \hat{E}'$ (Eq 31).

$$ \psi = \frac{\partial \text{Cost}_{\text{tot}}'}{\partial \hat{D}} \bigg|_{\hat{D} = 0, \hat{E} = \hat{E}'} \quad (31) $$

Since the negative of gradient always points to the minimum, the following holds true. If $\psi$ is negative, then the negative of gradient points towards non-zero $\hat{D}$, implying the optimal $\hat{D}$ is non-zero. However, given that the domain of $\hat{D}$ is non-negative, if $\psi$ is non-negative then the optimal $\hat{D}$ is 0. Therefore, the optimal $\hat{D}$ is non-zero if and only if $\psi < 0$. These conditions can be concisely written as

$$ U_{\text{bn}} < \Phi(U_{\text{fn}}, A, \sigma_p^2, C^2, \sigma_a^2). \quad (32) $$

where $\Phi$ is a complicated function involving the roots $\hat{E}'$ of the quartic equation Eq 30 substituted into Eq 31. Ultimately we use these analytic expressions to solve numerically for the remaining conditions on the optimal prediction-multiplier $\hat{D}$ and observation-multiplier $E$. 

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