

Brain-like Variational Inference

Hadi Vafaii^{1,*}

Dekel Galor^{1,*}

Jacob L. Yates¹

* co-first authors, correspondence to vafaii@berkeley.edu

¹Redwood Center for Theoretical Neuroscience, UC Berkeley

Abstract

Inference in both brains and machines can be formalized by optimizing a shared objective: maximizing the evidence lower bound (ELBO) in machine learning, or minimizing variational free energy (\mathcal{F}) in neuroscience (ELBO = $-\mathcal{F}$). While this equivalence suggests a unifying framework, it leaves open how inference is implemented in neural systems. Here, we introduce FOND (*Free energy Online Natural-gradient Dynamics*), a framework that derives neural inference dynamics from three principles: (1) natural gradients on \mathcal{F} , (2) online belief updating, and (3) iterative refinement. We apply FOND to derive iP-VAE (*iterative Poisson variational autoencoder*), a recurrent spiking neural network that performs variational inference through membrane potential dynamics, replacing amortized encoders with iterative inference updates. Theoretically, iP-VAE yields several desirable features such as emergent normalization via lateral competition, and hardware-efficient integer spike count representations. Empirically, iP-VAE outperforms both standard VAEs and Gaussian-based predictive coding models in sparsity, reconstruction, and biological plausibility, and scales to complex color image datasets such as CelebA. iP-VAE also exhibits strong generalization to out-of-distribution inputs, exceeding hybrid iterative-amortized VAEs. These results demonstrate how deriving inference algorithms from first principles can yield concrete architectures that are simultaneously biologically plausible and empirically effective.

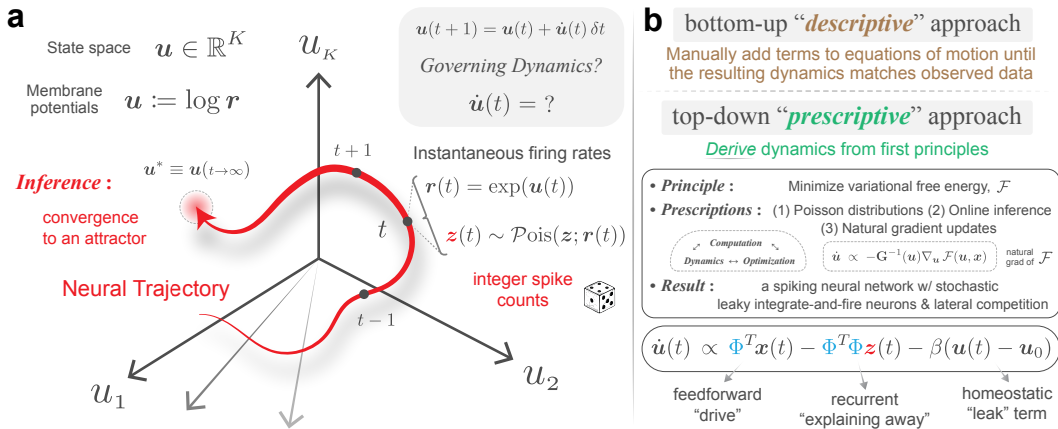


Figure 1: Inferential and dynamical accounts of perception are unified under variational inference. **(a)** Perception is framed as a dynamical process of convergence to attractors in a neural state space, where membrane potentials evolve and generate spikes along the way. **(b)** Our prescriptive approach derives neural dynamics by minimizing free energy via natural gradient descent, yielding a spiking neural network with lateral competition. The resulting architectures are principled and empirically effective. Code, data, and model checkpoints are available here: <https://github.com/hadivafaii/IterativeVAE>

1 Introduction

Artificial intelligence and theoretical neuroscience share a foundational principle: understanding the world requires inferring hidden causes behind sensory observations (early work: [1–3]; modern interpretations: [4–9]). This principle is formalized through Bayesian posterior inference [10–12], with *variational inference* [4, 13–17] offering an optimization-based approximation. Variational inference employs an identical objective function across both fields, albeit under different names. In machine learning, it is called *evidence lower bound* (ELBO), which forms the basis of variational autoencoders (VAEs; [18–21]); whereas, neuroscience refers to it as *variational free energy* (\mathcal{F}), which subsumes predictive coding [22, 23] and is presented as a unified theory of brain function [24]. ELBO is exactly equal to negative free energy ($\text{ELBO} = -\mathcal{F}$; [25]), and this mathematical equivalence offers a powerful common language for describing both artificial and biological intelligence [26].

Despite this promising connection, neither ELBO nor \mathcal{F} have proven particularly prescriptive for developing specific algorithms or architectures [27, 28]. Instead, the pattern often works in reverse: effective methods are discovered empirically, then later recognized as instances of these principles. In machine learning, diffusion models were originally motivated by non-equilibrium statistical mechanics [29], and only later understood as a form of ELBO maximization [30, 31]. Similarly, in neuroscience, *predictive coding* (PC; [22]) was first proposed as a heuristic model for minimizing prediction errors [32], before being reinterpreted as \mathcal{F} minimization [23, 33]. This pattern of post-hoc theoretical justification, rather than theory-driven derivation, is common across both disciplines.

Then why pursue a general theory at all? A unifying framework offers several advantages: it clarifies the design choices underlying successful models, explains why they work, and guides the development of new models. The recent *Bayesian learning rule* (BLR; [34]) exemplifies this potential. It re-interprets a broad class of learning algorithms as instances of variational inference, optimized via natural gradient descent [35] over approximate posteriors q_{λ} . By varying the form of q_{λ} and the associated approximations, BLR not only recovers a wide range of algorithms—from SGD and Adam to Dropout—but, crucially, it also offers a principled recipe for designing new ones [34]. Thus, BLR transforms a post-hoc theoretical justification into a prescriptive framework for algorithm design.

In variational inference, the prescriptive choices are specifying q_{λ} and how to optimize the variational parameters, λ . The machine learning community has embraced *amortized inference* [18, 19, 36–38], where a neural network is trained to produce λ in a single forward pass for each input sample. In contrast, neuroscience models have traditionally favored *iterative inference* methods [22, 39], which align more naturally with the recurrent [40–44] and adaptive [45–49] processing observed in cortical circuits (but see Gershman and Goodman [36] for a counterpoint). Despite this fundamental divide in methodology, systematic comparisons between iterative and amortized inference variants remain scarce, particularly when evaluated against biologically relevant metrics.

In this paper, we introduce *Free energy Online Natural-gradient Dynamics* (**FOND**), a framework for deriving brain-like inference dynamics from \mathcal{F} minimization. As a concrete application of FOND, we derive a novel family of iterative VAE architectures that perform inference via natural gradient descent on \mathcal{F} —including a spiking variant, the *iterative Poisson VAE* (**iP-VAE**)—with distinct computational and biological advantages. The paper is organized as follows:

- In section 2 and the associated appendix A, we review and synthesize existing models from machine learning and neuroscience, showing how they can be unified under the variational inference framework via specific choices of distributions and inference methods (Fig. 2).
- In sections 3 and 4, and the associated appendix B, we derive neural dynamics as natural gradient descent on free energy. This yields a novel family of iterative VAEs, including the iP-VAE, which performs online Bayesian inference through membrane potential dynamics, with emergent lateral competition, explaining away dynamics, and divisive normalization.
- In section 5, we show that iterative inference consistently outperforms amortized methods, with iP-VAE achieving the best reconstruction-sparsity trade-off, while using $25\times$ fewer parameters and integer-valued spike counts. Appendix C shows that iP-VAE: (i) exhibits emergent cortical response properties, (ii) generalizes better to out-of-distribution data, and (iii) scales to complex color image datasets such as ImageNet32, CIFAR-10, and CelebA.
- In section 6, and the associated appendix D, we relate our results to recent advances in sequence modeling, and discuss how expressive nonlinearities, emergent normalization, and effective stochastic depth contribute to iP-VAE’s computational strengths.

2 Background and Related Work

Notation and conventions. We start with a generative model that assigns probabilistic beliefs to observations, $\mathbf{x} \in \mathbb{R}^M$ (e.g., images), through invoking K -dimensional latent variables, \mathbf{z} : $p_\theta(\mathbf{x}) = \int p_\theta(\mathbf{x}, \mathbf{z}) d\mathbf{z} = \int p_\theta(\mathbf{x}|\mathbf{z})p_\theta(\mathbf{z}) d\mathbf{z}$, where θ are its adaptable parameters (e.g., neural network weights or synaptic connection strengths in the brain). Throughout this work, we color-code the **generative** and **inference** model components as **blue** and **red**, respectively.

Variational inference and the ELBO objective. Following the *perception-as-inference* framework [1, 2], we formalize perception as Bayesian posterior inference. In appendix A.1, we provide a historical background, and in appendix A.2, we review the challenges associated with posterior inference. We overcome these challenges by approximating the true but often intractable posterior, $p_\theta(\mathbf{z}|\mathbf{x})$, using another distribution, $q_\phi(\mathbf{z}|\mathbf{x})$, referred to as the *approximate* (or *variational*) posterior. In appendix A.3, we provide more details about how *variational inference* [15, 17] approximates the inference process, and derive the standard *Evidence Lower Bound* (ELBO) objective [13, 15, 17]:

$$\underbrace{\log p_\theta(\mathbf{x})}_{\text{model evidence}} = \underbrace{\mathbb{E}_{\mathbf{z} \sim q_\phi(\mathbf{z}|\mathbf{x})} \left[\log \frac{p_\theta(\mathbf{x}, \mathbf{z})}{q_\phi(\mathbf{z}|\mathbf{x})} \right]}_{\text{ELBO}(\mathbf{x}; \theta, \phi)} + \underbrace{\mathcal{D}_{\text{KL}}(q_\phi(\mathbf{z}|\mathbf{x}) \parallel p_\theta(\mathbf{z}|\mathbf{x}))}_{\text{Kullback-Leibler (KL) divergence}}. \quad (1)$$

Importantly, maximizing the ELBO minimizes the intractable Kullback-Leibler (KL) divergence between the approximate and true posterior. This can be seen by taking gradients of eq. (1) with respect to ϕ . The model evidence on the left-hand side does not depend on ϕ , making the gradients of the two terms on the right additive inverses. Thus, ELBO maximization directly enhances the quality of posterior inference. In theoretical neuroscience, the negative ELBO is referred to as variational free energy (\mathcal{F}), which is the mathematical quantity central to the *free energy principle* [24, 25].

In the remainder of this section, we demonstrate how diverse models across machine learning and neuroscience emerge as instances of \mathcal{F} minimization through two fundamental design choices:

- 1. Choice of distributions** (appendix A.4):
(i) approximate posterior $q_\phi(\mathbf{z}|\mathbf{x})$, (ii) prior $p_\theta(\mathbf{z})$, and (iii) likelihood $p_\theta(\mathbf{x}|\mathbf{z})$
- 2. Choice of inference method** (appendix A.8):
(i) *amortized* (e.g., learned neural network) vs. (ii) *iterative* (e.g., gradient descent)

Variational Autoencoder (VAE) model family. Variational Autoencoders (VAEs) transform the abstract ELBO objective into practical deep learning architectures [18–20]. The standard Gaussian VAE (\mathcal{G} -VAE) exemplifies this approach by assuming factorized Gaussian distributions for all three distributions, with the approximate posterior $q_\phi(\mathbf{z}|\mathbf{x})$ implemented as a neural network that maps each input \mathbf{x} to posterior parameters: $\text{enc}(\mathbf{x}; \phi) \rightarrow (\boldsymbol{\mu}(\mathbf{x}), \boldsymbol{\sigma}^2(\mathbf{x}))$. This *amortization* of inference—using a single network to approximate posteriors across the entire dataset—is a defining characteristic of VAEs. Alternative distribution choices are also possible; for instance, replacing both prior and posterior with Poisson distributions yields the Poisson VAE (\mathcal{P} -VAE; [50]), which better aligns with neural spike-count statistics [51–53]. We derive the VAE loss in appendix A.5, and discuss both \mathcal{G} -VAE and \mathcal{P} -VAE extensively in appendices A.6 and A.7.

Sparse coding and predictive coding as variational inference. Two major cornerstones of theoretical neuroscience, sparse coding (SC; [54]) and predictive coding (PC; [22]), can also be derived as instances of ELBO maximization (or equivalently, \mathcal{F} minimization), given specific distributional choices [33, 55, 56]. SC and PC share two key characteristics that distinguish them from standard VAEs. First, they both use a Dirac-delta distribution for the approximate posterior, effectively collapsing it to a point estimate. But they differ in their prior assumptions: PC employs a Gaussian prior, while SC uses a sparsity-promoting prior (e.g., Laplace; Fig. 2). Second, instead of amortized inference as in VAEs, both PC and SC employ iterative inference, better aligning with the recurrent nature of neural computation [40–44]. See appendix A.8 for an in-depth comparison, and appendix A.9 for a pedagogical derivation of the Rao and Ballard [22] objective as \mathcal{F} minimization.

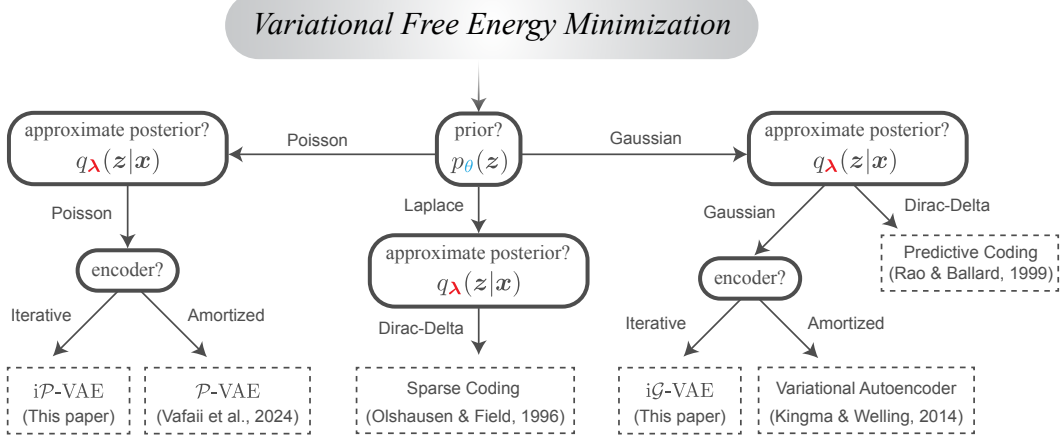


Figure 2: A wide range of models across machine learning and theoretical neuroscience can be unified under free energy (\mathcal{F}) minimization. Different distributional and optimization choices result in different models (appendix A.10). Motivated by this unification potential, we introduce **FOND**, a framework for deriving brain-like inference algorithms from first principles (section 3). We apply FOND to derive a family of iterative VAE architectures, including the spiking **iP-VAE** (section 4).

Online inference through natural gradient descent. In a recent landmark paper, Khan and Rue [34] proposed the *Bayesian learning rule* (BLR), unifying seemingly disparate learning algorithms as instances of variational inference optimized via natural gradient descent [35, 57] on a Bayesian objective which reduces to the ELBO when the likelihood is known [58, 59]. BLR’s generality extends naturally to sequential settings [60], where beliefs must be updated online as data arrives. In such settings, a rolling update scheme—where the posterior at each step becomes the prior for the next (Fig. 7)—provides a simple yet effective approach to continual belief revision [60].

Summary so far. In this background section, and the corresponding appendix A, we reviewed how seemingly different models across machine learning and neuroscience can be understood as instances of \mathcal{F} minimization (Fig. 2). The differences among them arise from the choices we make on the distributions and the inference methods (appendix A.10).

3 FOND: Free energy Online Natural-gradient Dynamics

Building on the unification potential shown above, we introduce FOND, a framework for deriving inference dynamics from \mathcal{F} minimization. Unlike post-hoc interpretations of existing models, FOND adopts a top-down approach: it starts from theoretical principles and derives architectures, making explicit the connection between design choices and computational properties.

A two-level framework: flexible choices and fixed prescriptions. FOND operates at two distinct levels. First, the modeler makes *flexible choices* about distributions and their parameterizations—decisions that define the inference problem. Second, once these choices are made, FOND applies *fixed prescriptions* that fully determine the inference dynamics.

This structure mirrors prescriptive theories in physics [61–64]. To derive dynamics from first principles, one must specify: (a) the dynamical variables of interest, and (b) the equations governing their evolution (see appendix B.1). In FOND, (a) corresponds to flexible choices, while (b) follows from fixed prescriptions.

Flexible choices — what the modeler decides. The modeler must choose:

- **Distributions:** Variational family and conditional likelihood (appendix A.4)
- **Parameterization:** Choice of dynamical variables that parameterize the variational distribution

These modeling decisions determine *what* is being optimized, but not *how* optimization proceeds.

Fixed prescriptions — what FOND determines. Once the flexible choices are made, the inference dynamics are *fully determined* by FOND’s three core prescriptions:

FOND prescriptions	
(1)	Natural gradients: Dynamics follow natural gradients of \mathcal{F}
(2)	Online: Inference updates beliefs sequentially from streaming data
(3)	Iterative: Inference refines estimates through recurrent updates

Why natural gradients? Natural gradient descent follows the steepest descent path in the space of probability distributions [35], achieving maximal free energy reduction per unit of distance (measured via Fisher information metric [57, 65]). This provides the most efficient optimization trajectory.

Why online? Biological perception requires adaptive priors that evolve with experience. Static inference cannot account for phenomena like *serial dependence*, where recent stimuli systematically bias current perception [46], or *learned helplessness*, where beliefs about agency are updated by experience [66, 67]. Online inference enables time-evolving priors that capture such effects (Fig. 7).

Why iterative? Perception follows an “analysis-by-synthesis” loop [68]: hypotheses generate predictions (synthesis), errors refine hypotheses (analysis). Iterative inference implements this closed-loop error-correction, adapting estimates when initial predictions fail. Amortized inference, by contrast, commits to a single forward pass—an open-loop guess that cannot recover when it errs, making it brittle on novel or ambiguous inputs. The brain appears to implement this kind of iterative refinement: macaque visual cortex requires an additional $\sim 30\text{ms}$ of recurrent processing to recognize challenging images [42], and neural codes for faces dynamically evolve over hundreds of milliseconds—a process termed “code switching” [44]. Thus, iterative refinement is motivated both computationally (enabling error correction) and empirically (matching neural dynamics).

Demonstrating FOND: iterative VAE architectures. To demonstrate FOND’s utility, we derive three iterative VAE models by making different flexible choices while applying the same fixed prescriptions:

- $i\mathcal{P}$ -VAE: Poisson distributions with log-rate parameterization
- $i\mathcal{G}$ -VAE: Gaussian distributions with mean and log-std parameterization
- $i\mathcal{G}_\varphi$ -VAE: like Gaussian, but with post-sampling nonlinearity $\varphi(\cdot)$

See Table 1 for complete specifications. In what follows, we present the theoretical derivations, evaluate empirical performance, and discuss implications for neuroscience and machine learning.

4 $i\mathcal{P}$ -VAE: Deriving a Spiking Inference Model from Variational Principles

In this section, we apply the FOND framework to derive brain-like inference dynamics from first principles. We begin by identifying the key prescriptive choices required for deriving these dynamics. We then introduce Poisson assumptions and derive membrane potential updates as natural gradient descent on variational free energy (\mathcal{F}), leading to the iterative Poisson VAE ($i\mathcal{P}$ -VAE) architecture.

Three distributional choices. To fully specify \mathcal{F} , we must choose an approximate posterior, a prior, and a conditional likelihood. We use Poisson distributions for both posterior and prior, as it leads to more brain-like integer-valued spike count representations (see appendix B.2 for a discussion). Later in the appendix, we show how this derivation extends to Gaussian posteriors with optional nonlinearities applied after sampling, illustrating the generality and flexibility of FOND.

For the likelihood, we assume factorized Gaussians throughout this work (a standard modeling choice in both sparse coding [54] and predictive coding [22]). In the main text, for pedagogical clarity, we focus on linear decoders, $p_\theta(\mathbf{x}|\mathbf{z}) = \mathcal{N}(\mathbf{x}; \Phi\mathbf{z}, \mathbf{I})$, where Φ is commonly referred to as the *dictionary* in sparse coding literature. In the appendix, we show how our results naturally extend to nonlinear decoders with learned variance [69], and we explore these extensions both theoretically and empirically.

Parameterization choices. For a neurally plausible model, we choose the dynamic variables to be real-valued membrane potentials, $\mathbf{u} \in \mathbb{R}^K$, where K is the number of neurons. To generate spike counts from \mathbf{u} , we assume the canonical Poisson parameterization, defining firing rates as $\mathbf{r} := \exp(\mathbf{u})$ (Fig. 1a). This choice is both mathematically convenient, since it avoids constrained optimization over a strictly positive variable, and biologically motivated, as the spiking threshold of real neurons is well-approximated by expansive nonlinearities [70, 71].

Under the assumption that dynamics, computation, and optimization are three expressions of the same underlying *process* [72–75] (i.e., *inference* \Leftrightarrow *dynamics*), membrane potentials evolve to minimize variational free energy (\mathcal{F}). To respect the curved geometry of distribution space, this optimization is implemented via natural gradient descent [34, 57, 76] (Fig. 1b).

Poisson variational free energy. Given a Poisson posterior and prior, and a factorized Gaussian likelihood with a linear decoder, the free energy (negative ELBO from eq. (1)) takes the form:

$$\mathcal{F}(\mathbf{x}; \Phi, \mathbf{u}_0, \mathbf{u}) = \underbrace{\mathbb{E}_{\mathbf{z} \sim q(\mathbf{z}|\mathbf{x})} \left[\frac{1}{2} \|\mathbf{x} - \Phi \mathbf{z}\|_2^2 \right]}_{\mathcal{L}_{\text{recon.}}: \text{reconstruction term (distortion)}} + \beta \underbrace{\sum_{i=1}^K (e^{\mathbf{u}} \odot (\mathbf{u} - \mathbf{u}_0) - (e^{\mathbf{u}} - e^{\mathbf{u}_0}))_i}_{\mathcal{L}_{\text{KL}}: \text{KL term (coding rate)}}, \quad (2)$$

where $\mathbf{u}_0 \in \mathbb{R}^K$ and $\mathbf{u} \in \mathbb{R}^K$ are the prior and posterior membrane potentials, K is the latent dimensionality, \odot represents the element-wise (Hadamard) product, and β is a positive coefficient that controls the *rate-distortion* trade-off [77, 78]. See appendix B.3 for a detailed derivation.

Next, we compute the gradient of \mathcal{F} with respect to the variational parameters, i.e., $\nabla_{\mathbf{u}} \mathcal{F}$.

Free energy gradient: the reconstruction term. $\mathcal{L}_{\text{recon.}}$ is the expected value of the prediction errors under the approximate posterior. Since this expectation is intractable in general, we follow standard practice in variational inference and approximate it using a single Monte Carlo sample [34, 60]: $\mathcal{L}_{\text{recon.}} \approx \frac{1}{2} \|\mathbf{x} - \Phi \mathbf{z}(\mathbf{u})\|_2^2$, where $\mathbf{z}(\mathbf{u}) \sim q_{\mathbf{u}}(\mathbf{z}|\mathbf{x})$.

Since the reconstruction loss depends on the sample \mathbf{z} , which is a stochastic function of the firing rate $\mathbf{r} = \exp(\mathbf{u})$, we propagate gradients through both the exponential nonlinearity and the sampling process (i.e., $\mathbf{u} \rightarrow \mathbf{r} \rightarrow \mathbf{z} \rightarrow \mathcal{L}_{\text{recon.}}$). We apply the chain rule twice to get:

$$\nabla_{\mathbf{u}} \mathcal{L}_{\text{recon.}} = \frac{\partial \mathbf{r}}{\partial \mathbf{u}} \frac{\partial \mathbf{z}}{\partial \mathbf{r}} \frac{\partial}{\partial \mathbf{z}} \mathcal{L}_{\text{recon.}} \approx e^{\mathbf{u}} \odot \frac{\partial \mathbf{z}}{\partial \mathbf{r}} \odot (-\Phi^T (\mathbf{x} - \Phi \mathbf{z}(\mathbf{u}))). \quad (3)$$

We further simplify the expression by applying the straight-through gradient estimator [79], treating $\partial \mathbf{z} / \partial \mathbf{r} \approx \mathbf{I}$ for the purpose of deriving inference equations. During model training, however, we update the generative model parameters by utilizing the Poisson reparameterization algorithm [50]. This straight-through approximation of the sample gradient yields:

$$\nabla_{\mathbf{u}} \mathcal{L}_{\text{recon.}} \approx e^{\mathbf{u}} \odot (-\Phi^T (\mathbf{x} - \Phi \mathbf{z}(\mathbf{u}))). \quad (4)$$

Free energy gradient: the KL term. The KL-term gradient is easily computed from eq. (2): $\nabla_{\mathbf{u}} \mathcal{L}_{\text{KL}} = e^{\mathbf{u}} \odot (\mathbf{u} - \mathbf{u}_0)$. Combine it with the reconstruction-term gradient from eq. (4) to get:

$$\nabla_{\mathbf{u}} \mathcal{F}(\mathbf{x}; \Phi, \mathbf{u}_0, \mathbf{u}) \approx e^{\mathbf{u}} \odot [-\Phi^T (\mathbf{x} - \Phi \mathbf{z}(\mathbf{u})) + \beta (\mathbf{u} - \mathbf{u}_0)]. \quad (5)$$

Natural gradients: applying Fisher preconditioning. FOND prescribes that neural dynamics follow natural gradients of the free energy, $\dot{\mathbf{u}} := -\mathbf{G}^{-1}(\mathbf{u}) \nabla_{\mathbf{u}} \mathcal{F}$, where \mathbf{G} is the Fisher information matrix. For Poisson distributions in the canonical form, we have: $\mathbf{G}(\mathbf{u}) = \exp(\mathbf{u})$ (see appendix B.4 for a derivation). Combining this result with eq. (5) yields:

$$\dot{\mathbf{u}} \propto \underbrace{\Phi^T \mathbf{x}}_{\text{feedforward "drive"}} - \underbrace{\Phi^T \Phi \mathbf{z}(\mathbf{u})}_{\text{recurrent "explaining away"}} - \underbrace{\beta (\mathbf{u} - \mathbf{u}_0)}_{\text{homeostatic "leak" term}} \quad (6)$$

This concludes the derivation of our core theoretical result underlying the iP-VAE architecture. Natural gradient descent on \mathcal{F} yields circuit dynamics that share important characteristics with neural models developed since the early 1970s [80–83], while offering a notable biological advantage over

standard predictive coding (PC). Namely, recurrent interactions in $i\mathcal{P}$ -VAE (eq. (6)) occur through discrete spikes \mathbf{z} , rather than continuous membrane potentials as in PC (eq. (16)), better aligning with how real neurons communicate [84]. In appendix B.5, we interpret each term in the dynamics and explain the rationale behind its naming. In appendix B.6, we extend the derivation to nonlinear decoders; and in appendix B.7, we extend to Gaussian posteriors with optional nonlinearities. Finally, appendix B.8 explores this biological distinction with standard PC in more detail.

Online inference: adding time. Perception is an ongoing process that requires continually updating beliefs as data arrives, rather than reverting to a fixed prior in the distant past. To model this sequential process, we adopt a rolling update scheme, where the current posterior becomes the next prior (Fig. 7, [60]). Combining this online structure with the dynamics from eq. (6), we arrive at the following discrete-time update rule:

$$\mathbf{u}_{t+1} = \mathbf{u}_t + \Phi^T \mathbf{x} - \Phi^T \Phi \mathbf{z}_t, \quad (7)$$

where \mathbf{u}_t and \mathbf{u}_{t+1} are interpreted as the prior and posterior membrane potentials at time t (Fig. 5).

Notably, the leak term in eq. (6)—which stems from the KL term in eq. (2)—disappears in this discrete-time update. This is because we perform only a single step per time point in the online setting, where the prior evolves continuously over time (Fig. 7). In appendix B.9, we derive the general form of free energy for sequences, and in appendix B.10, we explain why the KL contribution vanishes in the single-update limit.

Lateral competition as a stabilizing mechanism. The recurrent connectivity matrix, $\mathbf{W} := \Phi^T \Phi$, has a stabilizing effect. To demonstrate this, we transform the discrete-time dynamics in eq. (7) from membrane potentials to firing rates, yielding the following multiplicative update for neuron i :

$$\mathbf{r}_{t+1,i} = \mathbf{r}_{t,i} \frac{\exp(\Phi^T \mathbf{x})_i}{\exp(\mathbf{W}_{ii} \mathbf{z}_{t,i}) \prod_{j=1, j \neq i}^K \exp(\mathbf{W}_{ij} \mathbf{z}_{t,j})}, \quad (8)$$

where $\mathbf{r}_t = \exp(\mathbf{u}_t)$ are firing rates, and $\mathbf{z}_t \sim \mathcal{P}\text{ois}(\mathbf{z}; \mathbf{r}_t)$ are sampled spikes. The resulting denominator reveals a form of multiplicative divisive normalization: co-active neurons suppress each other proportionally to their spike output.

As seen in eq. (8), the recurrent term $\mathbf{W} \mathbf{z}_t$ acts as a stabilizing force in two ways. First, its diagonal entries are positive (i.e., $\mathbf{W}_{ii} = \|\Phi_{\cdot i}\|_2^2 > 0$); therefore, neurons that spike strongly receive self-suppression, dampening activity at the next time point. Second, the off-diagonal entries couple neurons with overlapping tuning. Due to this coupling, vigorously active neurons extend suppressive influence toward their similarly-tuned neighbors (i.e., when $\mathbf{W}_{ij} > 0$), preventing excess activity. In addition to stabilization, such competitive interactions also underlie the sparsification dynamics observed in cortical circuits [85–87], and are widely regarded as a hallmark of sparse coding [39, 88].

In sum, we have shown that natural gradient descent on free energy, combined with biologically motivated assumptions, leads to principled and interpretable neural dynamics. As our next step, we apply the theoretical derivations (eq. (6), appendix B.7, and Fig. 5) to design specific instances of iterative VAEs within the broader FOND framework. These include: the iterative Poisson VAE ($i\mathcal{P}$ -VAE), the iterative Gaussian VAE ($i\mathcal{G}$ -VAE), and the iterative Gaussian-relu VAE ($i\mathcal{G}_{\text{relu}}$ -VAE).

5 Experiments

We evaluate the family of iterative VAE models introduced in this work ($i\mathcal{P}$ -VAE, $i\mathcal{G}$ -VAE, $i\mathcal{G}_{\text{relu}}$ -VAE; Table 1). These models share identical inference dynamics derived in section 4 and appendix B.7, differing only in their latent variable distributions (Poisson vs. Gaussian) and an optional nonlinearity (e.g., relu [89]) applied after sampling from the posterior. This systematic comparison helps isolate the relative influence of each component on learning brain-like representations that generalize. To evaluate the impact of inference methods, we compare these iterative models to their amortized counterparts (\mathcal{P} -VAE, \mathcal{G} -VAE, $\mathcal{G}_{\text{relu}}$ -VAE), all implemented with identical convolutional encoders.

We also compare to classic normative models in neuroscience, including two predictive coding models, standard PC [22] and incremental PC (iPC; [90]), and the locally competitive algorithm (LCA; [39]), a sparse coding model that can be viewed as a deterministic, non-spiking precursor to $i\mathcal{P}$ -VAE. See Table 1 for a summary of models, and Fig. 2 for a visualization of the model tree. Additional comparisons to hybrid iterative-amortized VAEs [91, 92] are presented in the appendix.

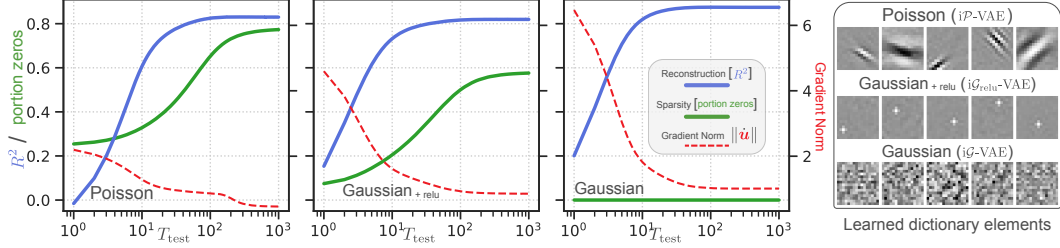


Figure 3: All iterative VAEs converge beyond the training regime ($T_{\text{train}} = 16$). $i\mathcal{P}$ -VAE outperforms $i\mathcal{G}_{\text{relu}}$ -VAE in sparsity, while $i\mathcal{G}$ -VAE achieves superior reconstruction but with dense representations. $i\mathcal{P}$ -VAE maintains reasonable reconstruction performance, despite using constrained representations (sparse, integer-valued spike count). The sparsification dynamics of both $i\mathcal{P}$ -VAE and $i\mathcal{G}_{\text{relu}}$ -VAE resemble those observed in the mouse visual cortex [106] (appendix C.3). All models are trained on 16×16 natural image patches, and the traces are averages over the entire test set. The right panel displays representative dictionary elements (Φ); see Fig. 11 for the complete set of $K = 512$ features.

Learning to infer. To learn the model parameters, we use a training scheme that accumulates gradients across the entire inference trajectory and applies a single update at the end. Specifically, we perform T_{train} inference steps per input batch and optimize model weights using the accumulated gradients across all steps (not just the final state). This procedure is analogous to backpropagation through time [93, 94], and T_{train} can be interpreted as the effective model “depth” [43, 95–97] (Fig. 5). We find that the choice of T_{train} has a significant effect on quantitative metrics, making it an important hyperparameter to track. We explore various T_{train} , but report performance using the same $T_{\text{test}} = 1,000$ steps.

Hyperparameters. In addition to T_{train} , we explore various β values [78], which controls the reconstruction-KL trade-off (eq. (2)). For $i\mathcal{P}$ -VAE and \mathcal{P} -VAE [50], varying β traces out a reconstruction-sparsity landscape, loosely analogous to a rate-distortion curve [77]. In the main paper, all models have a latent dimensionality of $K = 512$, with linear decoders comprised of a single dictionary, $\Phi \in \mathbb{R}^{M \times K}$, where M is the input dimensionality (i.e., number of pixels). In the appendix, we explore more general nonlinear decoder architectures and different latent dimensionalities. See appendix C.1 for additional implementation, hyperparameter, and training details.

Tasks and Datasets. We evaluate models in several ways, including convergence behavior, reconstruction–sparsity trade-off, downstream classification, and out-of-distribution (OOD; [98, 99]) generalization. We train and evaluate models on two datasets: (1) whitened 16×16 natural image patches from the van Hateren dataset [100], used to assess convergence and reconstruction–sparsity trade-offs; (2) MNIST [101], used for reconstruction, classification, and OOD generalization tests. A good portion of these results, including the OOD ones, are presented in the appendix, as our primary focus in this paper is theoretical, and these results warrant their focused exploration in future work.

Performance metrics. We define model *representations* as samples drawn from the posterior at each time point (e.g., $\mathbf{z}(t)$ in Fig. 1a), and quantify performance using the following metrics. For reconstruction, we compute the coefficient of determination (R^2) between the input image, \mathbf{x} , and its reconstruction, $\hat{\mathbf{x}} = \Phi \mathbf{z}$. $R^2(\mathbf{x}, \hat{\mathbf{x}})$ quantifies the proportion of input variance explained and yields a dimensionality-independent score bounded from above ($R^2 \leq 1$, typically in $[0, 1]$ for effective models). For sparsity, we use the proportion of zeros in the sampled latents: $\text{torch.mean}(\mathbf{z} == 0)$. This is a simple but informative proxy for energy efficiency in hardware implementations [102–105].

$i\mathcal{P}$ -VAE converges to sparser states while maintaining competitive reconstruction performance. We frame inference as convergence to attractor states (Fig. 1a) that faithfully represent inputs, achieving high-fidelity reconstruction with sparsity. To evaluate convergence quality, we train iterative VAEs using $T_{\text{train}} = 16$, and monitor inference process across $T_{\text{test}} = 1,000$ iterations, tracking three metrics averaged over the test set: (1) reconstruction fidelity via R^2 , (2) sparsity via the proportion of zeros, and (3) proximity to the attractor via gradient norm $\|\dot{\mathbf{u}}\| \propto \|\mathbf{G}^{-1}(\mathbf{u}) \nabla_{\mathbf{u}} \mathcal{F}\|$ calculated across the latent dimension ($K = 512$). These metrics collectively characterize convergence dynamics and allow us to evaluate attractor quality (Fig. 3).

We determine convergence by detecting when the R^2 trace flattens and remains stable (details in appendix C.2). For $i\mathcal{P}$ -VAE, $i\mathcal{G}_{\text{relu}}$ -VAE, and $i\mathcal{G}$ -VAE, respectively, we observe convergence times of 95, 75, and 69 iterations. At the final state ($t = 1,000$), these models achieve R^2 values of 0.83, 0.82, and 0.87, with latents exhibiting 77%, 58%, and 0% zeros (Fig. 3). $i\mathcal{P}$ -VAE achieves superior sparsity compared to both Gaussian models, while $i\mathcal{G}$ -VAE achieves the best overall R^2 . Throughout inference, the gradient norm $\|\dot{\mathbf{u}}\|$ steadily decreases but plateaus around 0.5, 0.9, and 1.0, respectively, likely due to gradient variance induced by stochastic inference dynamics.

$i\mathcal{P}$ -VAE learns V1-like features. Analysis of the learned features reveals that $i\mathcal{P}$ -VAE develops V1-like Gabor filters [107–110], while $i\mathcal{G}_{\text{relu}}$ -VAE learns localized pixel-like patterns and $i\mathcal{G}$ -VAE learns unstructured features (see right panel in Fig. 3, and Fig. 11 for complete dictionaries). Additionally, when tested with drifting gratings of varying contrasts, $i\mathcal{P}$ -VAE exhibits contrast-dependent response latency characteristic of V1 neurons [111, 112] (Fig. 8), possibly a consequence of the normalization dynamics that emerge from our theoretical derivations (eq. (8)). We explore these cortex-like properties further in appendix C.3. In summary, these results suggest $i\mathcal{P}$ -VAE learns brain-like representations while achieving the best reconstruction-sparsity compromise.

$i\mathcal{P}$ -VAE achieves the best overall reconstruction-sparsity trade-off. To assess the robustness of $i\mathcal{P}$ -VAE’s performance across hyperparameter settings, we systematically explore combinations of $T_{\text{train}} \in [8, 16, 32]$, and β values proportional to training iterations (ranging from $0.5 \times$ to $4.0 \times T_{\text{train}}$). To compare across inference methods, we include amortized counterparts with identical β selection criteria but using $T_{\text{train}} = 1$. Finally, we also include LCA [39] due to its theoretical similarity to $i\mathcal{P}$ -VAE (eq. (6)). See appendices C.1.1 to C.1.4 for architectural and training details for all models.

Figure 4a positions all models within a unified sparsity-reconstruction landscape, enabling direct comparison of performance metrics and revealing hyperparameter sensitivity. This representation can be interpreted through the lens of rate-distortion theory [77], where R^2 corresponds to inverse distortion and sparsity to inverse coding rate. The optimal point represents perfect reconstruction ($R^2 = 1.0$) using only zeros (sparsity = 1.0). This unachievable ideal is marked with a gold star.

For $i\mathcal{P}$ -VAE, varying T_{train} and β traces a characteristic curve where increased sparsity trades off against reconstruction quality at $T_{\text{train}} = 8$, with this trade-off improving at higher training iterations ($T_{\text{train}} = 16, 32$). LCA and $i\mathcal{G}_{\text{relu}}$ -VAE exhibit a similar pattern, but $i\mathcal{G}_{\text{relu}}$ -VAE consistently underperforms $i\mathcal{P}$ -VAE in both metrics, confirming Fig. 3. $i\mathcal{G}$ -VAE achieves comparable R^2 values to high- T_{train} $i\mathcal{P}$ -VAE fits but with zero sparsity. These extensive evaluations confirm that both $i\mathcal{P}$ -VAE and LCA achieve the best overall reconstruction-sparsity trade-offs among the tested models.

Finally, for fair comparison with LCA’s *maximum a posteriori* (MAP) estimation, we evaluated VAE models with deterministic decoding, where $i\mathcal{P}$ -VAE slightly outperforms LCA (Fig. 9). We also confirm that higher β values increase $i\mathcal{P}$ -VAE sparsity as theoretically predicted [50] (Fig. 10 and appendix C.4). For the effect of latent dimensionality on performance, see appendix C.5.

Iterative VAEs unanimously outperform their amortized counterparts. To quantify overall performance as a single metric, we compute the Euclidean distance from each model to the optimal point (the gold star at $R^2 = 1.0$, sparsity = 1.0), with lower distances indicating better performance. Figure 4b shows that iterative VAE models ($i\mathcal{G}$ -VAE, $i\mathcal{G}_{\text{relu}}$ -VAE, $i\mathcal{P}$ -VAE) consistently outperform their amortized counterparts (\mathcal{G} -VAE, $\mathcal{G}_{\text{relu}}$ -VAE, and \mathcal{P} -VAE), despite the latter employing deep convolutional encoders with orders of magnitude more parameters. As predicted by theory (comparing eq. (6) with the LCA dynamics [39]), the performance of LCA and $i\mathcal{P}$ -VAE are statistically indistinguishable, though $i\mathcal{P}$ -VAE exhibits lower variability across hyperparameter settings.

For clarity in the reconstruction-sparsity analysis, we omit PC and iPC as their dense Gaussian latents are effectively represented by $i\mathcal{G}$ -VAE. Extended experiments on MNIST (appendix C.6) show that iterative VAEs outperform PCNs in reconstruction metrics, with $i\mathcal{P}$ -VAE achieving the best reconstruction-sparsity trade-off (Table 3). Interestingly, in downstream classification, \mathcal{P} -VAE reaches $\sim 98\%$ accuracy, comparable to supervised PCNs [113]. See appendix C.6 for more details.

Iterative VAEs match the inference runtime of their amortized counterparts. Despite requiring $\sim 2 \times$ training time (appendix C.1.4), iterative models achieve competitive inference speeds for large batches, matching amortized performance before continuing to superior trade-offs (appendix C.7).

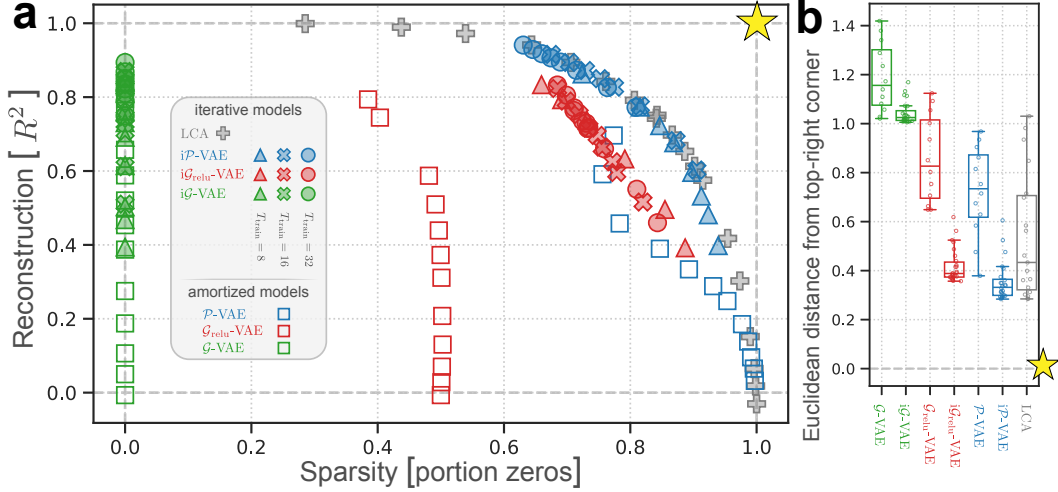


Figure 4: Reconstruction-sparsity trade-off across model families. **(a)** Performance landscape showing reconstruction quality (R^2) versus sparsity (proportion of zeros). Different symbols indicate model variants (triangles: $T_{train} = 8$, crosses: $T_{train} = 16$, circles: $T_{train} = 32$, empty squares: amortized VAEs, plus: LCA), with colors denoting model architectures. The gold star marks the theoretical optimum. **(b)** Overall performance measured as Euclidean distance from the optimum point. Iterative models (right side) consistently outperform their amortized counterparts (left side), with iP -VAE and LCA achieving the best overall performance. See also related Figs. 9 and 10.

iP -VAE exhibits strong out-of-distribution (OOD) generalization. While the main results use linear decoders ($\hat{x} = \Phi z$), our framework easily extends to deep, nonlinear decoders. In appendix B.6, we develop the theory; and in appendix C.8, we train nonlinear iP -VAE models with multilayer perceptron and convolutional decoders—interpretable as *deep sparse coding*—and compare them to hybrid iterative-amortized VAEs [91, 92]. For both within-dataset perturbations (Fig. 14) and cross-dataset settings (Figs. 13, 15 and 16), iP -VAE consistently outperforms alternatives in OOD reconstruction and classification accuracy (Fig. 14). These results suggest that iP -VAE learns a compositional code (Fig. 17), a hypothesis we aim to study more systematically in future work.

iP -VAE scales to complex color image datasets and generates realistic images. In appendix C.9, we demonstrate practical utility by scaling iP -VAE to high-dimensional color images (CelebA, CIFAR-10, tiny ImageNet); and, in appendix C.10, we show that iP -VAE successfully generates realistic MNIST samples through an iterative procedure.

6 Conclusions and Discussion

In this paper, we introduced FOND, a framework for deriving brain-like inference dynamics from variational principles. We then applied FOND to derive a new family of iterative VAE models, including the iP -VAE, a spiking model that performs inference in its membrane potential dynamics. iP -VAE’s success likely stems from three key attributes: (1) exponential nonlinearities and (2) emergent normalization, similar to recent advances in sequence modeling [114]; and (3) effective stochastic depth through temporal unrolling, which also explains the effectiveness of hierarchical VAEs [115]. Further, iP -VAE’s weight reuse and its sparse, integer-valued spike count representations enable efficient hardware implementation [116]. While we focused on variational inference, equally important sampling-based approaches offer complementary perspectives [117–122]. Future work should explore acceleration techniques for iterative inference [114], biologically plausible learning rules [123], predictive dynamics for non-stationary sequences [124], hierarchical extensions [125, 126], and neural data applications [127–129]. We extend upon these points in appendices D.1 to D.5.

In sum, this work connects the prescriptive model development philosophy of FOND with practical algorithms that exhibit brain-like behavior and deliver empirical benefits in machine learning.

7 Code and data

Our code, data, and model checkpoints are available here: <https://github.com/hadivafaii/IterativeVAE>.

8 Author contributions

All authors conceived of the project and developed the core theoretical framework. H.V. conducted the formal analysis, implemented the primary models, and generated figures and tables. D.G. implemented baseline comparisons. All authors contributed to writing the manuscript.

9 Acknowledgments

We would like to thank Bruno Olshausen, Richard D. Lange, and Ralf M. Haefner for fruitful discussions. This work was supported by the National Institute of Health under award number NEI EY032179. This material is also based upon work supported by the National Science Foundation Graduate Research Fellowship Program under Grant No. DGE-1752814 (DG). Any opinions, findings, conclusions, or recommendations expressed in this material are those of the author(s) and do not necessarily reflect the views of the National Science Foundation. Additionally, DG was funded by the Center for Innovation in Vision and Optics. We thank the developers of the software packages used in this project, including PyTorch [130], NumPy [131], SciPy [132], scikit-learn [133], pandas [134], matplotlib [135], and seaborn [136].

References

- [1] Alhazen. *Book of optics (Kitab Al-Manazir)*. 1011–1021 AD. URL: <https://archive.org/details/TheOpticsOfIbnAlHaythamBooksI>.
- [2] Hermann Von Helmholtz. *Handbuch der physiologischen Optik*. Vol. 9. Voss, 1867. URL: <https://archive.org/details/handbuchderphysi00helm>.
- [3] Kenneth J. W. Craik. *The Nature of Explanation*. Cambridge, UK: Cambridge University Press, 1943. URL: <https://archive.org/details/natureofexplanat0000crai/page/n5/mode/2up>.
- [4] Peter Dayan et al. “The Helmholtz machine”. In: *Neural Computation* 7.5 (1995), pp. 889–904. DOI: 10.1162/neco.1995.7.5.889.
- [5] Tai Sing Lee and David Mumford. “Hierarchical Bayesian inference in the visual cortex”. In: *JOSA A* 20.7 (2003), pp. 1434–1448. DOI: 10.1364/JOSAA.20.001434.
- [6] Horace Barlow. “Redundancy reduction revisited”. In: *Network: computation in neural systems* 12.3 (2001), p. 241. DOI: 10.1080/net.12.3.241.253.
- [7] Bruno A. Olshausen. “Perception as an Inference Problem”. In: *The Cognitive Neurosciences (5th edition)* (2014). Ed. by Michael Gazzaniga and George R. Mangun. DOI: 10.7551/mitpress/9504.003.0037. URL: <http://rctn.org/bruno/papers/perception-as-inference.pdf>.
- [8] David Ha and Jürgen Schmidhuber. “World models”. In: (2018). arXiv: 1803.10122v4 [cs.LG].
- [9] Danijar Hafner et al. *Action and Perception as Divergence Minimization*. 2022. arXiv: 2009.01791 [cs.AI].
- [10] Thomas Bayes. “An essay towards solving a problem in the doctrine of chances”. In: *Philosophical Transactions of the Royal Society of London* 53 (1763), pp. 370–418. DOI: 10.1098/rstl.1763.0053.
- [11] Pierre-Simon Laplace. *A Philosophical Essay on Probabilities*. Originally published in French in 1814 as *Essai philosophique sur les probabilités*. Courcier, 1812. URL: <https://dn790006.ca.archive.org/0/items/philosophicaless00lapliala/philosophicaless00lapliala.pdf>.
- [12] Kevin P Murphy. *Machine Learning: A Probabilistic Perspective*. MIT Press, 2012. URL: <https://probml.github.io/pml-book/book0.html>.

- [13] Radford M. Neal and Geoffrey E. Hinton. “A View of the Em Algorithm that Justifies Incremental, Sparse, and other Variants”. In: *Learning in Graphical Models*. Ed. by Michael I. Jordan. Dordrecht: Springer Netherlands, 1998, pp. 355–368. ISBN: 978-94-011-5014-9. DOI: 10.1007/978-94-011-5014-9_12.
- [14] Arnold Zellner and. “Optimal Information Processing and Bayes’s Theorem”. In: *The American Statistician* 42.4 (1988), pp. 278–280. DOI: 10.1080/00031305.1988.10475585.
- [15] Michael I Jordan et al. “An introduction to variational methods for graphical models”. In: *Machine learning* 37 (1999), pp. 183–233. DOI: 10.1023/A:1007665907178.
- [16] Dimitris G Tzikas et al. “The variational approximation for Bayesian inference”. In: *IEEE Signal Processing Magazine* 25.6 (2008), pp. 131–146. DOI: 10.1109/MSP.2008.929620.
- [17] David M. Blei et al. “Variational Inference: A Review for Statisticians”. In: *Journal of the American Statistical Association* 112.518 (2017), pp. 859–877. DOI: 10.1080/01621459.2017.1285773.
- [18] Diederik P Kingma and Max Welling. “Auto-encoding variational bayes”. In: (2014). arXiv: 1312.6114v11 [stat.ML].
- [19] Danilo Jimenez Rezende et al. “Stochastic backpropagation and approximate inference in deep generative models”. In: *International Conference on Machine Learning*. PMLR. 2014, pp. 1278–1286. URL: <https://proceedings.mlr.press/v32/rezende14.html>.
- [20] Diederik P Kingma and Max Welling. “An introduction to variational autoencoders”. In: *Foundations and Trends® in Machine Learning* 12.4 (2019), pp. 307–392. DOI: 10.1561/22000000056.
- [21] Joseph Marino. “Predictive coding, variational autoencoders, and biological connections”. In: *Neural Computation* 34.1 (2022), pp. 1–44. DOI: 10.1162/neco_a_01458.
- [22] Rajesh PN Rao and Dana H Ballard. “Predictive coding in the visual cortex: a functional interpretation of some extra-classical receptive-field effects”. In: *Nature Neuroscience* 2.1 (1999), pp. 79–87. DOI: 10.1038/4580.
- [23] Karl Friston. “A theory of cortical responses”. In: *Philosophical transactions of the Royal Society B: Biological Sciences* 360.1456 (2005), pp. 815–836. DOI: 10.1098/rstb.2005.1622.
- [24] Karl Friston. “The free-energy principle: a unified brain theory?” In: *Nature Reviews Neuroscience* 11.2 (2010), pp. 127–138. DOI: 10.1038/nrn2787.
- [25] Rafal Bogacz. “A tutorial on the free-energy framework for modelling perception and learning”. In: *Journal of Mathematical Psychology* 76 (2017). Model-based Cognitive Neuroscience, pp. 198–211. ISSN: 0022-2496. DOI: <https://doi.org/10.1016/j.jmp.2015.11.003>.
- [26] Beren Millidge. *Applications of the Free Energy Principle to Machine Learning and Neuroscience*. 2021. arXiv: 2107.00140 [cs.AI].
- [27] Samuel J Gershman. “What does the free energy principle tell us about the brain?” In: *arXiv:1901.07945* (2019). URL: <https://arxiv.org/abs/1901.07945>.
- [28] Mel Andrews. “The math is not the territory: navigating the free energy principle”. In: *Biology & Philosophy* 36.3 (2021), p. 30. DOI: 10.1007/s10539-021-09807-0.
- [29] Jascha Sohl-Dickstein et al. “Deep unsupervised learning using nonequilibrium thermodynamics”. In: *International conference on machine learning*. PMLR. 2015, pp. 2256–2265.
- [30] Diederik P Kingma and Ruiqi Gao. “Understanding Diffusion Objectives as the ELBO with Simple Data Augmentation”. In: *Thirty-seventh Conference on Neural Information Processing Systems*. 2023. URL: <https://openreview.net/forum?id=NnMEadcdyD>.
- [31] Calvin Luo. *Understanding Diffusion Models: A Unified Perspective*. 2022. arXiv: 2208.11970 [cs.LG].
- [32] Mandyam Veerambudi Srinivasan et al. “Predictive coding: a fresh view of inhibition in the retina”. In: *Proceedings of the Royal Society of London. Series B. Biological Sciences* 216.1205 (1982), pp. 427–459. DOI: 10.1098/rspb.1982.0085.
- [33] Beren Millidge et al. *Predictive Coding: a Theoretical and Experimental Review*. 2022. arXiv: 2107.12979 [cs.AI].
- [34] Mohammad Emtiyaz Khan and Håvard Rue. “The Bayesian Learning Rule”. In: *Journal of Machine Learning Research* 24.281 (2023), pp. 1–46. URL: <http://jmlr.org/papers/v24/22-0291.html>.

- [35] Shun-ichi Amari. “Natural Gradient Works Efficiently in Learning”. In: *Neural Computation* 10.2 (Feb. 1998), pp. 251–276. ISSN: 0899-7667. DOI: 10.1162/089976698300017746.
- [36] Samuel Gershman and Noah Goodman. “Amortized inference in probabilistic reasoning”. In: *Proceedings of the annual meeting of the cognitive science society*. Vol. 36. 36. 2014. URL: <https://escholarship.org/uc/item/34j1h7k5>.
- [37] Brandon Amos. “Tutorial on Amortized Optimization”. In: *Foundations and Trends® in Machine Learning* 16.5 (2023), pp. 592–732. ISSN: 1935-8237. DOI: 10.1561/22000000102.
- [38] Ankush Ganguly et al. “Amortized Variational Inference: A Systematic Review”. In: *Journal of Artificial Intelligence Research* 78 (2023), pp. 167–215. DOI: 10.1613/jair.1.14258.
- [39] Christopher J Rozell et al. “Sparse coding via thresholding and local competition in neural circuits”. In: *Neural Computation* 20.10 (2008), pp. 2526–2563. DOI: 10.1162/neco.2008.03-07-486.
- [40] Victor A.F. Lamme and Pieter R. Roelfsema. “The distinct modes of vision offered by feedforward and recurrent processing”. In: *Trends in Neurosciences* 23.11 (2000), pp. 571–579. ISSN: 0166-2236. DOI: [https://doi.org/10.1016/S0166-2236\(00\)01657-X](https://doi.org/10.1016/S0166-2236(00)01657-X).
- [41] Tim C Kietzmann et al. “Recurrence is required to capture the representational dynamics of the human visual system”. In: *Proceedings of the National Academy of Sciences* 116.43 (2019), pp. 21854–21863. DOI: 10.1073/pnas.1905544116.
- [42] Kohitij Kar et al. “Evidence that recurrent circuits are critical to the ventral stream’s execution of core object recognition behavior”. In: *Nature neuroscience* 22.6 (2019), pp. 974–983. DOI: 10.1038/s41593-019-0392-5.
- [43] Ruben S van Bergen and Nikolaus Kriegeskorte. “Going in circles is the way forward: the role of recurrence in visual inference”. In: *Current Opinion in Neurobiology* 65 (2020). Whole-brain interactions between neural circuits, pp. 176–193. ISSN: 0959-4388. DOI: <https://doi.org/10.1016/j.conb.2020.11.009>.
- [44] Yuelin Shi et al. “Rapid, concerted switching of the neural code in inferotemporal cortex”. In: *bioRxiv* (2023). DOI: 10.1101/2023.12.06.570341.
- [45] Adam Kohn. “Visual adaptation: physiology, mechanisms, and functional benefits”. In: *Journal of neurophysiology* 97.5 (2007), pp. 3155–3164. DOI: 10.1152/jn.00086.2007.
- [46] Jason Fischer and David Whitney. “Serial dependence in visual perception”. In: *Nature neuroscience* 17.5 (2014), pp. 738–743. DOI: 10.1038/nn.3689.
- [47] Guido Marco Cicchini et al. “Serial dependence in perception”. In: *Annual Review of Psychology* 75 (2024), pp. 129–154. DOI: 10.1146/annurev-psych-021523-104939.
- [48] Jennifer J Freyd and Ronald A Finke. “Representational momentum”. In: *Journal of Experimental Psychology: Learning, Memory, and Cognition* 10.1 (1984), p. 126. DOI: 10.1037/0278-7393.10.1.126.
- [49] Floris P De Lange et al. “How do expectations shape perception?” In: *Trends in cognitive sciences* 22.9 (2018), pp. 764–779. DOI: 10.1016/j.tics.2018.06.002.
- [50] Hadi Vafaii et al. “Poisson Variational Autoencoder”. In: *The Thirty-eighth Annual Conference on Neural Information Processing Systems*. 2024. URL: <https://openreview.net/forum?id=ektPEcqGLb>.
- [51] David J Tolhurst et al. “The statistical reliability of signals in single neurons in cat and monkey visual cortex”. In: *Vision research* 23.8 (1983), pp. 775–785. DOI: 10.1016/0042-6989(83)90200-6.
- [52] AF Dean. “The variability of discharge of simple cells in the cat striate cortex”. In: *Experimental Brain Research* 44.4 (1981), pp. 437–440. DOI: 10.1007/BF00238837.
- [53] Alexandre Pouget et al. “Information processing with population codes”. In: *Nature Reviews Neuroscience* 1.2 (2000), pp. 125–132. DOI: 10.1038/35039062.
- [54] Bruno A Olshausen and David J Field. “Emergence of simple-cell receptive field properties by learning a sparse code for natural images”. In: *Nature* 381.6583 (1996), pp. 607–609. DOI: 10.1038/381607a0.
- [55] Bruno A Olshausen. “Learning linear, sparse, factorial codes”. In: (1996). URL: <https://dspace.mit.edu/bitstream/handle/1721.1/7184/AIM-1580.pdf>.
- [56] Peter Dayan and Laurence F Abbott. “Theoretical Neuroscience”. In: (2001). URL: <https://mitpress.mit.edu/9780262041997/theoretical-neuroscience/>.

- [57] Mohammad Emtiyaz Khan and Didrik Nielsen. “Fast yet simple natural-gradient descent for variational inference in complex models”. In: *2018 International Symposium on Information Theory and Its Applications (ISITA)*. IEEE, 2018, pp. 31–35. DOI: 10.23919/ISITA.2018.8664326.
- [58] Olivier Catoni. *PAC-Bayesian Supervised Classification: The Thermodynamics of Statistical Learning*. Institute of Mathematical Statistics Lecture Notes—Monograph Series. IMS, 2007. DOI: 10.1214/074921707000000391. URL: <https://arxiv.org/abs/0712.0248>.
- [59] P. G. Bissiri et al. “A general framework for updating belief distributions”. In: *Journal of the Royal Statistical Society: Series B (Statistical Methodology)* 78.5 (2016), pp. 1103–1130. DOI: <https://doi.org/10.1111/rssb.12158>.
- [60] Matt Jones et al. “Bayesian Online Natural Gradient (BONG)”. In: *The Thirty-eighth Annual Conference on Neural Information Processing Systems*. 2024. URL: <https://openreview.net/forum?id=E7en5Dy02G>.
- [61] L.D. Landau and E.M. Lifshitz. *The Classical Theory of Fields*. 4th. Vol. 2. Course of Theoretical Physics. Pergamon Press, 1975. URL: <https://perso.crans.org/sylvainrey/Biblio%20Physique/Physique/%C3%89lectromagn%C3%A9tisme/%5BLandau%2C%20Lifshitz%5D%2002%20The%20Classical%20Theory%20of%20Fields.pdf>.
- [62] Steven Weinberg. “Effective field theory, past and future”. In: *International Journal of Modern Physics A* 31.06 (2016), p. 1630007. DOI: 10.1142/S0217751X16300076.
- [63] Jakob Schwichtenberg. *No-Nonsense Quantum Field Theory: A Student-Friendly Introduction*. No-Nonsense Books, 2020. ISBN: 9783948763015. URL: <http://www.stat.ucla.edu/~ywu/QFT0.pdf>.
- [64] Jakob Schwichtenberg. *Physics from symmetry*. Springer, 2018. DOI: 10.1007/978-3-319-66631-0.
- [65] James Martens. “New Insights and Perspectives on the Natural Gradient Method”. In: *Journal of Machine Learning Research* 21.146 (2020), pp. 1–76. URL: <http://jmlr.org/papers/v21/17-678.html>.
- [66] Martin E Seligman and Steven F Maier. “Failure to escape traumatic shock.” In: *Journal of experimental psychology* 74.1 (1967), p. 1. DOI: 10.1037/h0024514.
- [67] Charisse Nixon. *Learned Helplessness*. Nov. 2007. URL: <https://www.youtube.com/watch?v=gFmF0mprTt0>.
- [68] Alan Yuille and Daniel Kersten. “Vision as Bayesian inference: analysis by synthesis?” In: *Trends in Cognitive Sciences* 10.7 (2006), pp. 301–308. DOI: 10.1016/j.tics.2006.05.002.
- [69] Oleh Rybkin et al. “Simple and Effective VAE Training with Calibrated Decoders”. In: *Proceedings of the 38th International Conference on Machine Learning*. Ed. by Marina Meila and Tong Zhang. Vol. 139. Proceedings of Machine Learning Research. PMLR, June 2021, pp. 9179–9189. URL: <https://proceedings.mlr.press/v139/rybkin21a.html>.
- [70] Nicholas J Priebe et al. “The contribution of spike threshold to the dichotomy of cortical simple and complex cells”. In: *Nature neuroscience* 7.10 (2004), pp. 1113–1122. DOI: 10.1038/nn1310.
- [71] Nicolas Fourcaud-Trocmé et al. “How spike generation mechanisms determine the neuronal response to fluctuating inputs”. In: *Journal of neuroscience* 23.37 (2003), pp. 11628–11640. DOI: 10.1523/JNEUROSCI.23-37-11628.2003.
- [72] Alfred North Whitehead. *Process and Reality: An Essay in Cosmology*. 1929. URL: <https://archive.org/details/processrealitygi00alfr>.
- [73] J J Hopfield. “Neural networks and physical systems with emergent collective computational abilities.” In: *Proceedings of the National Academy of Sciences* 79.8 (1982), pp. 2554–2558. DOI: 10.1073/pnas.79.8.2554.
- [74] Karl Friston et al. “Active Inference: A Process Theory”. In: *Neural Computation* 29.1 (Jan. 2017), pp. 1–49. ISSN: 0899-7667. DOI: 10.1162/NECO_a_00912.
- [75] Saurabh Vyas et al. “Computation Through Neural Population Dynamics”. In: *Annual Review of Neuroscience* 43. Volume 43, 2020 (2020), pp. 249–275. ISSN: 1545-4126. DOI: <https://doi.org/10.1146/annurev-neuro-092619-094115>.
- [76] Shun-ichi Amari and Hiroshi Nagaoka. *Methods of information geometry*. Vol. 191. American Mathematical Soc., 2000. DOI: 10.1090/mmono/191.

- [77] Alexander Alemi et al. “Fixing a Broken ELBO”. In: *Proceedings of the 35th International Conference on Machine Learning*. Ed. by Jennifer Dy and Andreas Krause. Vol. 80. Proceedings of Machine Learning Research. PMLR, July 2018, pp. 159–168. URL: <https://proceedings.mlr.press/v80/alemi18a.html>.
- [78] Irina Higgins et al. “beta-VAE: Learning Basic Visual Concepts with a Constrained Variational Framework”. In: *International Conference on Learning Representations*. 2017. URL: <https://openreview.net/forum?id=Sy2fzU9gl>.
- [79] Yoshua Bengio et al. “Estimating or Propagating Gradients Through Stochastic Neurons for Conditional Computation”. In: (2013). arXiv: 1308.3432 [cs.LG].
- [80] Shun-Ichi Amari. “Characteristics of random nets of analog neuron-like elements”. In: *IEEE Transactions on systems, man, and cybernetics* 5 (1972), pp. 643–657. DOI: 10.1109/TSMC.1972.4309193.
- [81] Wulfram Gerstner and Werner M. Kistler. *Spiking Neuron Models: Single Neurons, Populations, Plasticity*. Cambridge, UK: Cambridge University Press, 2002. ISBN: 9780521890793. DOI: 10.1017/CB09780521890793.
- [82] Wulfram Gerstner et al. *Neuronal dynamics: From single neurons to networks and models of cognition*. Cambridge University Press, 2014. DOI: 10.1017/CB09781107447615.
- [83] Daniel B Rubin et al. “The stabilized supralinear network: a unifying circuit motif underlying multi-input integration in sensory cortex”. In: *Neuron* 85.2 (2015), pp. 402–417. DOI: 10.1016/j.neuron.2014.12.026.
- [84] Eric R. Kandel et al. *Principles of Neural Science*. 5th ed. New York: McGraw Hill, 2000. URL: <https://archive.org/details/PrinciplesOfNeuralScienceFifthKANDEL>.
- [85] Ho Ko et al. “The emergence of functional microcircuits in visual cortex”. In: *Nature* 496.7443 (2013), pp. 96–100. DOI: 10.1038/nature12015.
- [86] Selmaan N Chettih and Christopher D Harvey. “Single-neuron perturbations reveal feature-specific competition in V1”. In: *Nature* 567.7748 (2019), pp. 334–340. DOI: 10.1038/s41586-019-0997-6.
- [87] Zhuokun Ding et al. “Functional connectomics reveals general wiring rule in mouse visual cortex”. In: *Nature* 640.8058 (2025), pp. 459–469. DOI: 10.1038/s41586-025-08840-3.
- [88] Karol Gregor and Yann LeCun. “Learning fast approximations of sparse coding”. In: *Proceedings of the 27th international conference on international conference on machine learning*. 2010, pp. 399–406. URL: <https://icml.cc/Conferences/2010/papers/449.pdf>.
- [89] James C. R. Whittington et al. “Disentanglement with Biological Constraints: A Theory of Functional Cell Types”. In: *The Eleventh International Conference on Learning Representations*. 2023. URL: https://openreview.net/forum?id=9Z_GfhZnGH.
- [90] Tommaso Salvatori et al. “A Stable, Fast, and Fully Automatic Learning Algorithm for Predictive Coding Networks”. In: *The Twelfth International Conference on Learning Representations*. 2024. URL: <https://openreview.net/forum?id=RyUvzda8GH>.
- [91] Joe Marino et al. “Iterative Amortized Inference”. In: *Proceedings of the 35th International Conference on Machine Learning*. Ed. by Jennifer Dy and Andreas Krause. Vol. 80. Proceedings of Machine Learning Research. PMLR, July 2018, pp. 3403–3412. URL: <https://proceedings.mlr.press/v80/marino18a.html>.
- [92] Yoon Kim et al. “Semi-Amortized Variational Autoencoders”. In: *Proceedings of the 35th International Conference on Machine Learning*. Ed. by Jennifer Dy and Andreas Krause. Vol. 80. Proceedings of Machine Learning Research. PMLR, July 2018, pp. 2678–2687. URL: <https://proceedings.mlr.press/v80/kim18e.html>.
- [93] Paul J Werbos. “Backpropagation through time: what it does and how to do it”. In: *Proceedings of the IEEE* 78.10 (1990), pp. 1550–1560. DOI: 10.1109/5.58337.
- [94] Timothy P Lillicrap and Adam Santoro. “Backpropagation through time and the brain”. In: *Current Opinion in Neurobiology* 55 (2019). Machine Learning, Big Data, and Neuroscience, pp. 82–89. ISSN: 0959-4388. DOI: <https://doi.org/10.1016/j.conb.2019.01.011>. URL: <https://www.sciencedirect.com/science/article/pii/S0959438818302009>.
- [95] Stanisław Jastrzębski et al. *Residual Connections Encourage Iterative Inference*. 2018. arXiv: 1710.04773 [cs.CV].

- [96] Qianli Liao and Tomaso Poggio. *Bridging the Gaps Between Residual Learning, Recurrent Neural Networks and Visual Cortex*. 2020. arXiv: 1604.03640 [cs.LG].
- [97] Avi Schwarzschild. “Deep Thinking Systems: Logical Extrapolation With Recurrent Neural Networks”. PhD thesis. UMD, 2023, p. 124. URL: <https://www.proquest.com/dissertations-theses/deep-thinking-systems-logical-extrapolation-with/docview/2830027656/se-2>.
- [98] Kaiyang Zhou et al. “Domain generalization: A survey”. In: *IEEE Transactions on Pattern Analysis and Machine Intelligence* 45.4 (2022), pp. 4396–4415. DOI: 10.1109/TPAMI.2022.3195549.
- [99] Jindong Wang et al. “Generalizing to unseen domains: A survey on domain generalization”. In: *IEEE transactions on knowledge and data engineering* 35.8 (2022), pp. 8052–8072. DOI: 10.1109/TKDE.2022.3178128.
- [100] J. H. van Hateren and A. van der Schaaf. “Independent component filters of natural images compared with simple cells in primary visual cortex”. In: *Proceedings of the Royal Society of London. Series B: Biological Sciences* 265.1394 (1998), pp. 359–366. DOI: 10.1098/rspb.1998.0303.
- [101] Yann LeCun et al. “Gradient-based learning applied to document recognition”. In: *Proceedings of the IEEE* 86.11 (1998), pp. 2278–2324. DOI: 10.1109/5.726791.
- [102] Song Han et al. “EIE: Efficient inference engine on compressed deep neural network”. In: *ACM SIGARCH Computer Architecture News* 44.3 (2016), pp. 243–254. DOI: 10.1145/3007787.3001163.
- [103] Vivienne Sze et al. *Efficient processing of deep neural networks*. Springer, 2020. DOI: 10.1007/978-3-031-01766-7.
- [104] Amir Gholami et al. “A survey of quantization methods for efficient neural network inference”. In: *Low-power computer vision*. Chapman and Hall/CRC, 2022, pp. 291–326. DOI: 10.1201/9781003162810-13.
- [105] Itay Hubara et al. “Binarized Neural Networks”. In: *Advances in Neural Information Processing Systems*. Ed. by D. Lee et al. Vol. 29. Curran Associates, Inc., 2016. URL: https://proceedings.neurips.cc/paper_files/paper/2016/hash/d8330f857a17c53d217014ee776bfd50-Abstract.html.
- [106] S. Amin Moosavi et al. “Temporal dynamics of energy-efficient coding in mouse primary visual cortex”. In: *bioRxiv* (2024). DOI: 10.1101/2024.12.17.628997.
- [107] S. Marçelja. “Mathematical description of the responses of simple cortical cells*”. In: *J. Opt. Soc. Am.* 70.11 (Nov. 1980), pp. 1297–1300. DOI: 10.1364/JOSA.70.001297.
- [108] David H. Hubel and Torsten N. Wiesel. “Receptive fields of single neurones in the cat’s striate cortex”. In: *The Journal of Physiology* 148 (1959). DOI: 10.1113/jphysiol.1959.sp006308.
- [109] David H. Hubel and Torsten N. Wiesel. “Receptive fields and functional architecture of monkey striate cortex”. In: *The Journal of Physiology* 195 (1968). DOI: 10.1113/jphysiol.1968.sp008455.
- [110] Jiakun Fu et al. “Heterogeneous orientation tuning in the primary visual cortex of mice diverges from Gabor-like receptive fields in primates”. In: *Cell reports* 43.8 (2024). DOI: 10.1016/j.celrep.2024.114639.
- [111] Matteo Carandini et al. “Linearity and normalization in simple cells of the macaque primary visual cortex”. In: *Journal of Neuroscience* 17.21 (1997), pp. 8621–8644. DOI: 10.1523/JNEUROSCI.17-21-08621.1997.
- [112] Duane G Albrecht et al. “Visual cortex neurons of monkeys and cats: temporal dynamics of the contrast response function”. In: *Journal of neurophysiology* 88.2 (2002), pp. 888–913. DOI: 10.1152/jn.2002.88.2.888.
- [113] Luca Pinchetti et al. “Benchmarking Predictive Coding Networks – Made Simple”. In: *The Thirteenth International Conference on Learning Representations*. 2025. URL: <https://openreview.net/forum?id=sahQq2sH5x>.
- [114] Maximilian Beck et al. “xLSTM: Extended Long Short-Term Memory”. In: *The Thirty-eighth Annual Conference on Neural Information Processing Systems*. 2024. URL: <https://openreview.net/forum?id=ARAxPPIAhq>.

- [115] Rewon Child. “Very Deep {VAE}s Generalize Autoregressive Models and Can Outperform Them on Images”. In: *International Conference on Learning Representations*. 2021. URL: <https://openreview.net/forum?id=RLRXCV6DbEJ>.
- [116] C. D. Schuman et al. “Opportunities for neuromorphic computing algorithms and applications”. In: *Nature Computational Science* (2022). DOI: 10.1038/s43588-022-00223-2.
- [117] Patrik Hoyer and Aapo Hyvärinen. “Interpreting Neural Response Variability as Monte Carlo Sampling of the Posterior”. In: *Advances in Neural Information Processing Systems*. Ed. by S. Becker et al. Vol. 15. MIT Press, 2002. URL: https://proceedings.neurips.cc/paper_files/paper/2002/hash/a486cd07e4ac3d270571622f4f316ec5-Abstract.html.
- [118] Gergő Orbán et al. “Neural variability and sampling-based probabilistic representations in the visual cortex”. In: *Neuron* 92.2 (2016), pp. 530–543. DOI: 10.1016/j.neuron.2016.09.038.
- [119] Paul Masset et al. “Natural gradient enables fast sampling in spiking neural networks”. In: *Advances in Neural Information Processing Systems*. Ed. by S. Koyejo et al. Vol. 35. Curran Associates, Inc., 2022, pp. 22018–22034. URL: https://proceedings.neurips.cc/paper_files/paper/2022/hash/8a0fd48510590071e3c129a79b8b8527-Abstract-Conference.html.
- [120] Michael Y.-S. Fang et al. “Learning and Inference in Sparse Coding Models With Langevin Dynamics”. In: *Neural Computation* 34.8 (July 2022), pp. 1676–1700. ISSN: 0899-7667. DOI: 10.1162/neco_a_01505.
- [121] Gaspard Oliviers et al. “Learning probability distributions of sensory inputs with Monte Carlo predictive coding”. In: *PLOS Computational Biology* 20.10 (Oct. 2024), pp. 1–34. DOI: 10.1371/journal.pcbi.1012532.
- [122] Eli Zachary Sennesh et al. “Divide-and-Conquer Predictive Coding: a structured Bayesian inference algorithm”. In: *The Thirty-eighth Annual Conference on Neural Information Processing Systems*. 2024. URL: <https://openreview.net/forum?id=dxwIaCVkWU>.
- [123] Joel Zylberberg et al. “A Sparse Coding Model with Synaptically Local Plasticity and Spiking Neurons Can Account for the Diverse Shapes of V1 Simple Cell Receptive Fields”. In: *PLOS Computational Biology* 7.10 (Oct. 2011), pp. 1–12. DOI: 10.1371/journal.pcbi.1002250.
- [124] Gerardo Duran-Martin et al. “A unifying framework for generalised Bayesian online learning in non-stationary environments”. In: *Transactions on Machine Learning Research* (2025). ISSN: 2835-8856. URL: <https://openreview.net/forum?id=osesw2V10u>.
- [125] Hadi Vafaii et al. “Hierarchical VAEs provide a normative account of motion processing in the primate brain”. In: *Thirty-seventh Conference on Neural Information Processing Systems*. 2023. URL: <https://openreview.net/forum?id=1w0kHN9JK8>.
- [126] Ferenc Csikor et al. “Top-down perceptual inference shaping the activity of early visual cortex”. In: *bioRxiv* (2025). DOI: 10.1101/2023.11.29.569262.
- [127] Martin Schrimpf et al. “Brain-score: Which artificial neural network for object recognition is most brain-like?” In: *BioRxiv* (2018), p. 407007. DOI: 10.1101/407007.
- [128] Eric Y Wang et al. “Foundation model of neural activity predicts response to new stimulus types”. In: *Nature* 640.8058 (2025), pp. 470–477. DOI: 10.1038/s41586-025-08829-y.
- [129] Chengrui Li et al. “A Differentiable Partially Observable Generalized Linear Model with Forward-Backward Message Passing”. In: *Forty-first International Conference on Machine Learning*. 2024. URL: <https://openreview.net/forum?id=2FKzbEE24s>.
- [130] Adam Paszke et al. “PyTorch: An Imperative Style, High-Performance Deep Learning Library”. In: *Advances in Neural Information Processing Systems*. Vol. 32. Curran Associates, Inc., 2019. URL: https://papers.nips.cc/paper_files/paper/2019/hash/bdbca288fee7f92f2bfa9f7012727740-Abstract.html.
- [131] Charles R. Harris et al. “Array programming with NumPy”. In: *Nature* 585.7825 (Sept. 2020), pp. 357–362. DOI: 10.1038/s41586-020-2649-2.
- [132] Pauli Virtanen et al. “SciPy 1.0: Fundamental Algorithms for Scientific Computing in Python”. In: *Nature Methods* 17 (2020), pp. 261–272. DOI: 10.1038/s41592-019-0686-2.
- [133] Fabian Pedregosa et al. “Scikit-learn: Machine learning in Python”. In: *the Journal of machine Learning research* 12 (2011), pp. 2825–2830. DOI: 10.5555/1953048.2078195.

- [134] The pandas development team. “pandas-dev/pandas: Pandas”. Version latest. In: (Feb. 2020). DOI: 10.5281/zenodo.3509134.
- [135] John D Hunter. “Matplotlib: A 2D graphics environment”. In: *Computing in science & engineering* 9.03 (2007), pp. 90–95. DOI: 10.1109/MCSE.2007.55.
- [136] Michael L Waskom. “Seaborn: statistical data visualization”. In: *Journal of Open Source Software* 6.60 (2021), p. 3021. DOI: 10.21105/joss.03021.
- [137] Immanuel Kant. *Critique of Pure Reason*. Translated by Paul Guyer and Allen W. Wood, Cambridge University Press. 1781. DOI: 10.1017/CB09780511804649.
- [138] Aristotle. *Posterior Analytics*. Trans. by Jonathan Barnes. Originally written c. 350 BCE. Oxford: Oxford University Press, 1994. URL: <https://classics.mit.edu/Aristotle/posterior.1.i.html>.
- [139] John Locke. *An essay concerning human understanding*. Ed. by Peter H. Nidditch. Oxford University Press, 1690. DOI: 10.1093/actrade/9780198243861.book.1.
- [140] Alison Gopnik et al. *The Scientist in the Crib: What Early Learning Tells Us About the Mind*. HarperCollins, 2004. URL: <http://alisingopnik.com/TheScientistInTheCrib.htm>.
- [141] Plato. *Meno*. Trans. by G.M.A. Grube. Originally written c. 380 BCE. Indianapolis: Hackett Publishing, 1976. URL: <https://classics.mit.edu/Plato/meno.html>.
- [142] Elizabeth S. Spelke and Katherine D. Kinzler. “Core knowledge”. In: *Developmental Science* 10.1 (2007). DOI: <https://doi.org/10.1111/j.1467-7687.2007.00569.x>.
- [143] Anthony M Zador. “A critique of pure learning and what artificial neural networks can learn from animal brains”. In: *Nature Communications* 10.1 (2019), p. 3770. DOI: 10.1038/s41467-019-11786-6.
- [144] Edwin Garrigues Boring. “Sensation and perception in the history of experimental psychology.” In: (1942). URL: https://ia801507.us.archive.org/12/items/in.ernet.dli.2015.52372/2015.52372.Sensation-And-Perception-In-The-History-Of-Experimental-Psychology_text.pdf.
- [145] Richard Langton Gregory. “Perceptions as hypotheses”. In: *Philosophical Transactions of the Royal Society of London. B, Biological Sciences* 290.1038 (1980), pp. 181–197. DOI: 10.1098/RSTB.1980.0090.
- [146] Andy Clark. “Whatever next? Predictive brains, situated agents, and the future of cognitive science”. In: *Behavioral and brain sciences* 36.3 (2013), pp. 181–204. DOI: 10.1017/S0140525X12000477.
- [147] David C Knill and Alexandre Pouget. “The Bayesian brain: the role of uncertainty in neural coding and computation”. In: *Trends in Neurosciences* 27.12 (2004), pp. 712–719. DOI: 10.1016/j.tins.2004.10.007.
- [148] Karl Friston. “The free-energy principle: a rough guide to the brain?” In: *Trends in cognitive sciences* 13.7 (2009), pp. 293–301. DOI: 10.1016/j.neuron.2016.03.020.
- [149] Karl Friston et al. “The free energy principle made simpler but not too simple”. In: *Physics Reports* 1024 (2023). The free energy principle made simpler but not too simple, pp. 1–29. ISSN: 0370-1573. DOI: <https://doi.org/10.1016/j.physrep.2023.07.001>.
- [150] Bruno A. Olshausen and David J. Field. “Sparse coding with an overcomplete basis set: A strategy employed by V1?” In: *Vision Research* 37.23 (1997), pp. 3311–3325. ISSN: 0042-6989. DOI: 10.1016/S0042-6989(97)00169-7.
- [151] Bruno A Olshausen and David J Field. “Sparse coding of sensory inputs”. In: *Current opinion in neurobiology* 14.4 (2004), pp. 481–487. DOI: 10.1016/j.conb.2004.07.007.
- [152] William Lotter et al. “Deep Predictive Coding Networks for Video Prediction and Unsupervised Learning”. In: *International Conference on Learning Representations*. 2017. URL: <https://openreview.net/forum?id=B1ewdt9xe>.
- [153] Christopher L. Buckley et al. “The free energy principle for action and perception: A mathematical review”. In: *Journal of Mathematical Psychology* 81 (2017), pp. 55–79. ISSN: 0022-2496. DOI: <https://doi.org/10.1016/j.jmp.2017.09.004>.
- [154] Joy A. Thomas Thomas M. Cover. *Elements of Information Theory*. 2nd ed. Wiley-Interscience, 2006. DOI: 10.1002/047174882X.
- [155] Naftali Tishby et al. *The information bottleneck method*. 2000. arXiv: physics/0004057 [physics.data-an].

- [156] L. D. Landau and E. M. Lifshitz. *Statistical Physics, Part 1*. 3rd. Oxford: Pergamon Press, 1980. URL: <https://ia902908.us.archive.org/31/items/ost-physics-landaulifshitz-statisticalphysics/LandauLifshitz-StatisticalPhysics.pdf>.
- [157] E. T. Jaynes. *Probability Theory: The Logic of Science*. Cambridge: Cambridge University Press, 2003. URL: <http://www.med.mcgill.ca/epidemiology/hanley/bios601/GaussianModel/JaynesProbabilityTheory.pdf>.
- [158] Geoffrey E Hinton and Richard Zemel. “Autoencoders, Minimum Description Length and Helmholtz Free Energy”. In: *Advances in Neural Information Processing Systems*. Ed. by J. Cowan et al. Vol. 6. Morgan-Kaufmann, 1993. URL: <https://proceedings.neurips.cc/paper/1993/hash/9e3cfc48eccf81a0d57663e129aef3cb-Abstract.html>.
- [159] Bin Dai and David Wipf. *Diagnosing and Enhancing VAE Models*. 2019. arXiv: 1903.05789 [cs.LG].
- [160] Casper Kaae Sønderby et al. “Ladder Variational Autoencoders”. In: *Advances in Neural Information Processing Systems*. Vol. 29. Curran Associates, Inc., 2016. URL: https://papers.nips.cc/paper_files/paper/2016/hash/6ae07dcb33ec3b7c814df797cbda0f87-Abstract.html.
- [161] Arash Vahdat and Jan Kautz. “NVAE: A Deep Hierarchical Variational Autoencoder”. In: *Advances in Neural Information Processing Systems*. Vol. 33. Curran Associates, Inc., 2020, pp. 19667–19679. URL: https://papers.nips.cc/paper_files/paper/2020/hash/e3b21256183cf7c2c7a66be163579d37-Abstract.html.
- [162] Jakub Tomczak and Max Welling. “VAE with a VampPrior”. In: *Proceedings of the Twenty-First International Conference on Artificial Intelligence and Statistics*. Ed. by Amos Storkey and Fernando Perez-Cruz. Vol. 84. Proceedings of Machine Learning Research. PMLR, Apr. 2018, pp. 1214–1223. URL: <https://proceedings.mlr.press/v84/tomczak18a.html>.
- [163] Eric Nalisnick and Padhraic Smyth. “Stick-Breaking Variational Autoencoders”. In: *International Conference on Learning Representations*. 2017. URL: <https://openreview.net/forum?id=S1jmAotxg>.
- [164] Gabriel Loaiza-Ganem and John P Cunningham. “The continuous Bernoulli: fixing a pervasive error in variational autoencoders”. In: *Advances in Neural Information Processing Systems*. Ed. by H. Wallach et al. Vol. 32. Curran Associates, Inc., 2019. URL: https://proceedings.neurips.cc/paper_files/paper/2019/file/f82798ec8909d23e55679ee26bb26437-Paper.pdf.
- [165] Chethan Pandarinath et al. “Inferring single-trial neural population dynamics using sequential auto-encoders”. In: *Nature methods* 15.10 (2018), pp. 805–815. DOI: 10.1038/s41592-018-0109-9.
- [166] He Zhao et al. “Variational Autoencoders for Sparse and Overdispersed Discrete Data”. In: *Proceedings of the Twenty Third International Conference on Artificial Intelligence and Statistics*. Ed. by Silvia Chiappa and Roberto Calandra. Vol. 108. Proceedings of Machine Learning Research. PMLR, Aug. 2020, pp. 1684–1694. URL: <https://proceedings.mlr.press/v108/zhao20c.html>.
- [167] Tim Salimans et al. “PixelCNN++: Improving the PixelCNN with Discretized Logistic Mixture Likelihood and Other Modifications”. In: *International Conference on Learning Representations*. 2017. URL: <https://openreview.net/forum?id=BJrFC6ceg>.
- [168] Danilo Rezende and Shakir Mohamed. “Variational Inference with Normalizing Flows”. In: *Proceedings of the 32nd International Conference on Machine Learning*. Ed. by Francis Bach and David Blei. Vol. 37. Proceedings of Machine Learning Research. Lille, France: PMLR, July 2015, pp. 1530–1538. URL: <https://proceedings.mlr.press/v37/rezende15.html>.
- [169] Durk P Kingma et al. “Improved Variational Inference with Inverse Autoregressive Flow”. In: *Advances in Neural Information Processing Systems*. Ed. by D. Lee et al. Vol. 29. Curran Associates, Inc., 2016. URL: https://proceedings.neurips.cc/paper_files/paper/2016/hash/ddeebdeefdb7e7e7a697e1c3e3d8ef54-Abstract.html.
- [170] Eric Jang et al. “Categorical Reparameterization with Gumbel-Softmax”. In: *International Conference on Learning Representations*. 2017. URL: <https://openreview.net/forum?id=rkE3y85ee>.

- [171] Chris J. Maddison et al. “The Concrete Distribution: A Continuous Relaxation of Discrete Random Variables”. In: *International Conference on Learning Representations*. 2017. URL: <https://openreview.net/forum?id=S1jE5L5gl>.
- [172] Jason Tyler Rolfe. “Discrete Variational Autoencoders”. In: *International Conference on Learning Representations*. 2017. URL: <https://openreview.net/forum?id=ryMxXPfex>.
- [173] Arash Vahdat et al. “DVAE++: Discrete Variational Autoencoders with Overlapping Transformations”. In: *Proceedings of the 35th International Conference on Machine Learning*. Ed. by Jennifer Dy and Andreas Krause. Vol. 80. Proceedings of Machine Learning Research. PMLR, July 2018, pp. 5035–5044. URL: <https://proceedings.mlr.press/v80/vahdat18a.html>.
- [174] Yookoon Park et al. “Variational Laplace Autoencoders”. In: *Proceedings of the 36th International Conference on Machine Learning*. Ed. by Kamalika Chaudhuri and Ruslan Salakhutdinov. Vol. 97. Proceedings of Machine Learning Research. PMLR, June 2019, pp. 5032–5041. URL: <https://proceedings.mlr.press/v97/park19a.html>.
- [175] Akash Srivastava and Charles Sutton. “Autoencoding Variational Inference For Topic Models”. In: *International Conference on Learning Representations*. 2017. URL: <https://openreview.net/forum?id=BybtVK9lg>.
- [176] Emile Mathieu et al. “Continuous Hierarchical Representations with Poincaré Variational Auto-Encoders”. In: *Advances in Neural Information Processing Systems*. Vol. 32. Curran Associates, Inc., 2019. URL: https://proceedings.neurips.cc/paper_files/paper/2019/file/0ec04cb3912c4f08874dd03716f80df1-Paper.pdf.
- [177] Tim R. Davidson et al. *Hyperspherical Variational Auto-Encoders*. 2022. arXiv: 1804.00891 [stat.ML].
- [178] Juno Kim et al. “ t^3 -Variational Autoencoder: Learning Heavy-tailed Data with Student’s t and Power Divergence”. In: *The Twelfth International Conference on Learning Representations*. 2024. URL: <https://openreview.net/forum?id=RzN1ECeo0B>.
- [179] Yixuan Zhang et al. *Negative Binomial Variational Autoencoders for Overdispersed Latent Modeling*. 2025. arXiv: 2508.05423 [cs.LG].
- [180] Robbe LT Goris et al. “Partitioning neuronal variability”. In: *Nature neuroscience* 17.6 (2014), pp. 858–865. DOI: 10.1038/nn.3711.
- [181] Hayden R. Johnson et al. *Inferring response times of perceptual decisions with Poisson variational autoencoders*. 2025. arXiv: 2511.11480 [q-bio.NC].
- [182] George Cybenko. “Approximation by superpositions of a sigmoidal function”. In: *Mathematics of control, signals and systems* 2.4 (1989), pp. 303–314. DOI: 10.1007/BF02551274.
- [183] Chris Cremer et al. “Inference Suboptimality in Variational Autoencoders”. In: *Proceedings of the 35th International Conference on Machine Learning*. Ed. by Jennifer Dy and Andreas Krause. Vol. 80. Proceedings of Machine Learning Research. PMLR, July 2018, pp. 1078–1086. URL: <https://proceedings.mlr.press/v80/cremer18a.html>.
- [184] Charles O’Neill et al. *Compute Optimal Inference and Provable Amortisation Gap in Sparse Autoencoders*. 2025. arXiv: 2411.13117 [cs.LG].
- [185] Rahul Krishnan et al. “On the challenges of learning with inference networks on sparse, high-dimensional data”. In: *Proceedings of the Twenty-First International Conference on Artificial Intelligence and Statistics*. Ed. by Amos Storkey and Fernando Perez-Cruz. Vol. 84. Proceedings of Machine Learning Research. PMLR, Apr. 2018, pp. 143–151. URL: <https://proceedings.mlr.press/v84/krishnan18a.html>.
- [186] Matthew D. Hoffman et al. “Stochastic Variational Inference”. In: *Journal of Machine Learning Research* 14.40 (2013), pp. 1303–1347. URL: <http://jmlr.org/papers/v14/hoffman13a.html>.
- [187] Arthur P Dempster et al. “Maximum likelihood from incomplete data via the EM algorithm”. In: *Journal of the royal statistical society: series B (methodological)* 39.1 (1977), pp. 1–22. DOI: 10.1111/j.2517-6161.1977.tb01600.x.
- [188] Christopher M. Bishop. *Pattern Recognition and Machine Learning*. New York: Springer, 2006. URL: <https://www.microsoft.com/en-us/research/wp-content/uploads/2006/01/Bishop-Pattern-Recognition-and-Machine-Learning-2006.pdf>.

- [189] Martin J. Wainwright and Michael I. Jordan. “Graphical Models, Exponential Families, and Variational Inference”. In: *Foundations and Trends® in Machine Learning* 1.1–2 (2008), pp. 1–305. ISSN: 1935-8237. DOI: 10.1561/22000000001. URL: <http://dx.doi.org/10.1561/22000000001>.
- [190] Thomas P. Minka. *Expectation Propagation for approximate Bayesian inference*. 2013. arXiv: 1301.2294 [cs.AI].
- [191] Timothy Hospedales et al. “Meta-learning in neural networks: A survey”. In: *IEEE transactions on pattern analysis and machine intelligence* 44.9 (2021), pp. 5149–5169. DOI: 10.1109/TPAMI.2021.3079209.
- [192] Edgar Douglas Adrian and Yngve Zotterman. “The impulses produced by sensory nerve-endings: Part II. The response of a Single End-Organ”. In: *The Journal of Physiology* (1926), pp. 151–71. DOI: 10.1113/jphysiol.1926.sp002281.
- [193] Malvin C Teich. “Fractal character of the auditory neural spike train”. In: *IEEE Transactions on Biomedical Engineering* 36.1 (1989), pp. 150–160. DOI: 10.1109/10.16460.
- [194] Michael N Shadlen and William T Newsome. “The variable discharge of cortical neurons: implications for connectivity, computation, and information coding”. In: *Journal of neuroscience* 18.10 (1998), pp. 3870–3896. DOI: 10.1523/JNEUROSCI.18-10-03870.1998.
- [195] Fred Rieke et al. *Spikes: exploring the neural code*. MIT press, 1999. URL: <https://mitpress.mit.edu/9780262181747/spikes/>.
- [196] Wilson Truccolo et al. “A point process framework for relating neural spiking activity to spiking history, neural ensemble, and extrinsic covariate effects”. In: *Journal of neurophysiology* 93.2 (2005), pp. 1074–1089. DOI: 10.1152/jn.00697.2004.
- [197] Zachary F Mainen and Terrence J Sejnowski. “Reliability of spike timing in neocortical neurons”. In: *Science* 268.5216 (1995), pp. 1503–1506. DOI: 10.1126/science.7770778.
- [198] Daniel A Butts et al. “Nonlinear computations shaping temporal processing of precortical vision”. In: *Journal of Neurophysiology* 116.3 (2016), pp. 1344–1357. DOI: 10.1152/jn.00878.2015.
- [199] Alison I. Weber and Jonathan W. Pillow. “Capturing the Dynamical Repertoire of Single Neurons with Generalized Linear Models”. In: *Neural Computation* 29.12 (Dec. 2017), pp. 3260–3289. ISSN: 0899-7667. DOI: 10.1162/neco_a_01021.
- [200] Shun-ichi Amari. *Information geometry and its applications*. Vol. 194. Springer, 2016. DOI: 10.1007/978-4-431-55978-8.
- [201] S. M. Sherman and R. W. Guillery. “Functional organization of thalamocortical relays”. In: *Journal of Neurophysiology* 76.3 (1996). PMID: 8890259, pp. 1367–1395. DOI: 10.1152/jn.1996.76.3.1367.
- [202] P. Adams et al. “The role of the thalamus in the flow of information to the cortex”. In: *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 357.1428 (2002), pp. 1695–1708. DOI: 10.1098/rstb.2002.1161.
- [203] Colin Blakemore and Elisabeth A Tobin. “Lateral inhibition between orientation detectors in the cat’s visual cortex”. In: *Experimental brain research* 15 (1972), pp. 439–440. DOI: 10.1007/BF00234129.
- [204] Arthur Szlam et al. “Structured sparse coding via lateral inhibition”. In: *Advances in Neural Information Processing Systems*. Ed. by J. Shawe-Taylor et al. Vol. 24. Curran Associates, Inc., 2011. URL: https://proceedings.neurips.cc/paper_files/paper/2011/file/fae0b27c451c728867a567e8c1bb4e53-Paper.pdf.
- [205] Hillel Adesnik and Massimo Scanziani. “Lateral competition for cortical space by layer-specific horizontal circuits”. In: *Nature* 464.7292 (2010), pp. 1155–1160. DOI: 10.1038/nature08935.
- [206] Liqun Luo. “Architectures of neuronal circuits”. In: *Science* 373.6559 (2021). DOI: 10.1126/science.abg7285.
- [207] Joseph Del Rosario et al. “Lateral inhibition in V1 controls neural and perceptual contrast sensitivity”. In: *Nature Neuroscience* (2025), pp. 1–12. DOI: 10.1038/s41593-025-01888-4.
- [208] Jan Benda and Andreas V. M. Herz. “A Universal Model for Spike-Frequency Adaptation”. In: *Neural Computation* 15.11 (Nov. 2003), pp. 2523–2564. ISSN: 0899-7667. DOI: 10.1162/089976603322385063.

- [209] Arthur Hobson. “A new theorem of information theory”. In: *Journal of Statistical Physics* 1 (1969), pp. 383–391. DOI: 10.1007/BF01106578.
- [210] Christof Koch. *Biophysics of Computation: Information Processing in Single Neurons*. Oxford University Press, Nov. 1998. ISBN: 9780195104912. DOI: 10.1093/oso/9780195104912.001.0001.
- [211] Kaiming He et al. “Deep Residual Learning for Image Recognition”. In: *Proceedings of the IEEE Conference on Computer Vision and Pattern Recognition (CVPR)*. June 2016. URL: https://openaccess.thecvf.com/content_cvpr_2016/html/He_Deep_Residual_Learning_CVPR_2016_paper.html.
- [212] Angeliki Giannou et al. “Looped Transformers as Programmable Computers”. In: *Proceedings of the 40th International Conference on Machine Learning*. Ed. by Andreas Krause et al. Vol. 202. Proceedings of Machine Learning Research. PMLR, July 2023, pp. 11398–11442. URL: <https://proceedings.mlr.press/v202/giannou23a.html>.
- [213] Liu Yang et al. “Looped Transformers are Better at Learning Learning Algorithms”. In: *The Twelfth International Conference on Learning Representations*. 2024. URL: <https://openreview.net/forum?id=HHbRxoDTxE>.
- [214] Ying Fan et al. “Looped Transformers for Length Generalization”. In: *The Thirteenth International Conference on Learning Representations*. 2025. URL: <https://openreview.net/forum?id=2edigk8yoU>.
- [215] Trenton Bricken et al. “Emergence of Sparse Representations from Noise”. In: *Proceedings of the 40th International Conference on Machine Learning*. Ed. by Andreas Krause et al. Vol. 202. Proceedings of Machine Learning Research. PMLR, July 2023, pp. 3148–3191. URL: <https://proceedings.mlr.press/v202/bricken23a.html>.
- [216] Michael Teti. *LCA-PyTorch*. [Computer Software] <https://doi.org/10.11578/dc.20230728.4>. June 2023. DOI: 10.11578/dc.20230728.4. URL: <https://doi.org/10.11578/dc.20230728.4>.
- [217] Diederik P Kingma and Jimmy Ba. “Adam: A method for stochastic optimization”. In: (2014). arXiv: 1412.6980 [cs.LG].
- [218] Ilya Loshchilov and Frank Hutter. “SGDR: Stochastic Gradient Descent with Warm Restarts”. In: *International Conference on Learning Representations*. 2017. URL: <https://openreview.net/forum?id=Skq89Sccx>.
- [219] Samuel R. Bowman et al. “Generating Sentences from a Continuous Space”. In: *Proceedings of the 20th SIGNLL Conference on Computational Natural Language Learning*. Berlin, Germany: Association for Computational Linguistics, Aug. 2016, pp. 10–21. DOI: 10.18653/v1/K16-1002.
- [220] Hao Fu et al. “Cyclical Annealing Schedule: A Simple Approach to Mitigating KL Vanishing”. In: *Proceedings of the 2019 Conference of the North American Chapter of the Association for Computational Linguistics: Human Language Technologies, Volume 1 (Long and Short Papers)*. Minneapolis, Minnesota: Association for Computational Linguistics, June 2019, pp. 240–250. DOI: 10.18653/v1/N19-1021.
- [221] Y. Lecun et al. “Gradient-based learning applied to document recognition”. In: *Proceedings of the IEEE* 86.11 (1998), pp. 2278–2324. DOI: 10.1109/5.726791.
- [222] Mengchen Zhu and Christopher J Rozell. “Visual nonclassical receptive field effects emerge from sparse coding in a dynamical system”. In: *PLoS computational biology* 9.8 (2013), e1003191. DOI: 10.1371/journal.pcbi.1003191.
- [223] Matteo Carandini and David J Heeger. “Normalization as a canonical neural computation”. In: *Nature reviews neuroscience* 13.1 (2012), pp. 51–62. DOI: 10.1038/nrn3136.
- [224] Gregory Cohen et al. “EMNIST: Extending MNIST to handwritten letters”. In: *2017 international joint conference on neural networks (IJCNN)*. IEEE. 2017, pp. 2921–2926. DOI: 10.1109/IJCNN.2017.7966217.
- [225] Brenden M Lake et al. “Human-level concept learning through probabilistic program induction”. In: *Science* 350.6266 (2015), pp. 1332–1338. DOI: 10.1126/science.aab3050.
- [226] Patryk Chrabaszcz et al. *A Downsampled Variant of ImageNet as an Alternative to the CIFAR datasets*. 2017. arXiv: 1707.08819 [cs.CV].

- [227] Muhammad Ghifary et al. “Domain Generalization for Object Recognition With Multi-Task Autoencoders”. In: *Proceedings of the IEEE International Conference on Computer Vision (ICCV)*. Dec. 2015. URL: https://openaccess.thecvf.com/content_iccv_2015/html/Ghifary_Domain_Generalization_for_ICCV_2015_paper.html.
- [228] Honglak Lee et al. “Sparse deep belief net model for visual area V2”. In: *Advances in neural information processing systems* 20 (2007). URL: https://papers.nips.cc/paper_files/paper/2007/file/4daa3db355ef2b0e64b472968cb70f0d-Paper.pdf.
- [229] Robin Rombach et al. “High-Resolution Image Synthesis With Latent Diffusion Models”. In: *Proceedings of the IEEE/CVF Conference on Computer Vision and Pattern Recognition (CVPR)*. June 2022, pp. 10684–10695. URL: https://openaccess.thecvf.com/content/CVPR2022/html/Rombach_High-Resolution_Image_Synthesis_With_Latent_Diffusion_Models_CVPR_2022_paper.
- [230] Ling Yang et al. *Diffusion Models: A Comprehensive Survey of Methods and Applications*. 2024. arXiv: 2209.00796 [cs.LG]. URL: <https://arxiv.org/abs/2209.00796>.
- [231] Horace B Barlow et al. “Possible principles underlying the transformation of sensory messages”. In: *Sensory communication* 1.01 (1961), pp. 217–233.
- [232] Robert Price. “A useful theorem for nonlinear devices having Gaussian inputs”. In: *IRE Transactions on Information Theory* 4.2 (1958), pp. 69–72. DOI: 10.1109/TIT.1958.1057444.
- [233] Georges Bonnet. “Transformations des signaux aléatoires a travers les systemes non linéaires sans mémoire”. In: *Annales des Télécommunications*. Vol. 19. 9. Springer. 1964, pp. 203–220. DOI: 10.1007/BF03014720.
- [234] Edgar Adrian. “The activity of the nerve fibres”. In: *Nobel lecture* (1932). URL: <https://www.nobelprize.org/prizes/medicine/1932/adrian/lecture/>.
- [235] Donald H Perkel and Theodore H Bullock. “Neural coding”. In: *Neurosciences Research Program Bulletin* (1968). URL: <https://ntrs.nasa.gov/citations/19690022317>.
- [236] Ehud Zohary et al. “Correlated neuronal discharge rate and its implications for psychophysical performance”. In: *Nature* 370.6485 (1994), pp. 140–143. DOI: 10.1038/370140a0.
- [237] Vivienne Sze et al. “Efficient processing of deep neural networks: A tutorial and survey”. In: *Proceedings of the IEEE* 105.12 (2017), pp. 2295–2329. DOI: 10.1109/JPROC.2017.2761740.
- [238] Yu-Hsin Chen et al. “Eyeriss: An energy-efficient reconfigurable accelerator for deep convolutional neural networks”. In: *IEEE journal of solid-state circuits* 52.1 (2016), pp. 127–138. DOI: 10.1109/JSSC.2016.2616357.
- [239] Xuexing Du et al. “A generalized Spiking Locally Competitive Algorithm for multiple optimization problems”. In: *Neurocomputing* 624 (2025), p. 129392. ISSN: 0925-2312. DOI: <https://doi.org/10.1016/j.neucom.2025.129392>.
- [240] W. K. Hastings. “Monte Carlo sampling methods using Markov chains and their applications”. In: *Biometrika* 57.1 (Apr. 1970), pp. 97–109. ISSN: 0006-3444. DOI: 10.1093/biomet/57.1.97.
- [241] Alan E. Gelfand and Adrian F. M. Smith and. “Sampling-Based Approaches to Calculating Marginal Densities”. In: *Journal of the American Statistical Association* 85.410 (1990), pp. 398–409. DOI: 10.1080/01621459.1990.10476213.
- [242] Steve Brooks et al. *Handbook of markov chain monte carlo*. CRC press, 2011. DOI: 10.1201/b10905.
- [243] Christian A. Naesseth et al. “Elements of Sequential Monte Carlo”. In: *Foundations and Trends® in Machine Learning* 12.3 (2019), pp. 307–392. ISSN: 1935-8237. DOI: 10.1561/22000000074. URL: <http://dx.doi.org/10.1561/22000000074>.
- [244] József Fiser et al. “Statistically optimal perception and learning: from behavior to neural representations”. In: *Trends in cognitive sciences* 14.3 (2010), pp. 119–130. DOI: 10.1016/j.tics.2010.01.003.
- [245] Lars Buesing et al. “Neural Dynamics as Sampling: A Model for Stochastic Computation in Recurrent Networks of Spiking Neurons”. In: *PLOS Computational Biology* 7.11 (Nov. 2011), pp. 1–22. DOI: 10.1371/journal.pcbi.1002211.
- [246] Ralf M Haefner et al. “Perceptual decision-making as probabilistic inference by neural sampling”. In: *Neuron* 90.3 (2016), pp. 649–660. DOI: 10.1016/j.neuron.2016.03.020.

- [247] Rodrigo Echeveste et al. “Cortical-like dynamics in recurrent circuits optimized for sampling-based probabilistic inference”. In: *Nature neuroscience* 23.9 (2020), pp. 1138–1149. DOI: 10.1038/s41593-020-0671-1.
- [248] Camille Rullán Buxó and Cristina Savin. “A sampling-based circuit for optimal decision making”. In: *Advances in Neural Information Processing Systems*. Vol. 34. Curran Associates, Inc., 2021, pp. 14163–14175. URL: <https://proceedings.neurips.cc/paper/2021/hash/76444b3132fda0e2aca778051d776f1c-Abstract.html>.
- [249] Cristina Savin and Sophie Deneve. “Spatio-temporal Representations of Uncertainty in Spiking Neural Networks”. In: *Advances in Neural Information Processing Systems*. Ed. by Z. Ghahramani et al. Vol. 27. Curran Associates, Inc., 2014. URL: https://proceedings.neurips.cc/paper_files/paper/2014/file/02a12643ae21d984b93c9df82a9d2152-Paper.pdf.
- [250] Dylan Festa et al. “Neuronal variability reflects probabilistic inference tuned to natural image statistics”. In: *Nature communications* 12.1 (2021), p. 3635. DOI: 10.1038/s41467-021-23838-x.
- [251] Suhas Shrinivasan et al. “Taking the neural sampling code very seriously: A data-driven approach for evaluating generative models of the visual system”. In: *Advances in Neural Information Processing Systems*. Ed. by A. Oh et al. Vol. 36. Curran Associates, Inc., 2023, pp. 21945–21959. URL: https://proceedings.neurips.cc/paper_files/paper/2023/hash/458d9f2dd5c7565af60143630dc62f10-Abstract-Conference.html.
- [252] Wen-Hao Zhang et al. “Sampling-based Bayesian inference in recurrent circuits of stochastic spiking neurons”. In: *Nature communications* 14.1 (2023), p. 7074. DOI: 10.1038/s41467-023-41743-3.
- [253] Ralf M. Haefner et al. *How does the brain compute with probabilities?* 2024. arXiv: 2409.02709 [q-bio.NC].
- [254] Yashar Ahmadian et al. “Analysis of the Stabilized Supralinear Network”. In: *Neural Computation* 25.8 (Aug. 2013), pp. 1994–2037. ISSN: 0899-7667. DOI: 10.1162/NECO_a_00472.
- [255] Guillaume Hennequin et al. “The dynamical regime of sensory cortex: stable dynamics around a single stimulus-tuned attractor account for patterns of noise variability”. In: *Neuron* 98.4 (2018), pp. 846–860. DOI: 10.1016/j.neuron.2018.04.017.
- [256] Yi-An Ma et al. “A Complete Recipe for Stochastic Gradient MCMC”. In: *Advances in Neural Information Processing Systems*. Ed. by C. Cortes et al. Vol. 28. Curran Associates, Inc., 2015. URL: https://proceedings.neurips.cc/paper_files/paper/2015/hash/9a4400501febb2a95e79248486a5f6d3-Abstract.html.
- [257] Tim Salimans et al. “Markov Chain Monte Carlo and Variational Inference: Bridging the Gap”. In: *Proceedings of the 32nd International Conference on Machine Learning*. Ed. by Francis Bach and David Blei. Vol. 37. Proceedings of Machine Learning Research. Lille, France: PMLR, July 2015, pp. 1218–1226. URL: <https://proceedings.mlr.press/v37/salimans15.html>.
- [258] Richard D. Lange et al. “Interpolating between sampling and variational inference with infinite stochastic mixtures”. In: *Proceedings of the Thirty-Eighth Conference on Uncertainty in Artificial Intelligence*. Ed. by James Cussens and Kun Zhang. Vol. 180. Proceedings of Machine Learning Research. PMLR, Aug. 2022, pp. 1063–1073. URL: <https://proceedings.mlr.press/v180/lange22a.html>.
- [259] Jason Wei et al. “Chain-of-Thought Prompting Elicits Reasoning in Large Language Models”. In: *Advances in Neural Information Processing Systems*. Ed. by S. Koyejo et al. Vol. 35. Curran Associates, Inc., 2022, pp. 24824–24837. URL: https://proceedings.neurips.cc/paper_files/paper/2022/hash/9d5609613524ecf4f15af0f7b31abca4-Abstract-Conference.html.
- [260] Shunyu Yao et al. “Tree of Thoughts: Deliberate Problem Solving with Large Language Models”. In: *Advances in Neural Information Processing Systems*. Ed. by A. Oh et al. Vol. 36. Curran Associates, Inc., 2023, pp. 11809–11822. URL: https://proceedings.neurips.cc/paper_files/paper/2023/hash/271db9922b8d1f4dd7aaef84ed5ac703-Abstract-Conference.html.
- [261] Aayush Karan and Yilun Du. *Reasoning with Sampling: Your Base Model is Smarter Than You Think*. 2025. arXiv: 2510.14901 [cs.LG].
- [262] Guan Wang et al. *Hierarchical Reasoning Model*. 2025. arXiv: 2506.21734 [cs.AI].

- [263] Yeskendir Koishekenov et al. *Encode, Think, Decode: Scaling test-time reasoning with recursive latent thoughts*. 2025. arXiv: 2510.07358 [cs.LG].
- [264] Dileep George et al. “A generative vision model that trains with high data efficiency and breaks text-based CAPTCHAs”. In: *Science* 358.6368 (2017), eaag2612. DOI: 10.1126/science.aag2612.
- [265] Dileep George et al. “A detailed theory of thalamic and cortical microcircuits for predictive visual inference”. In: *Science Advances* 11.6 (2025), eadr6698. DOI: 10.1126/sciadv.adr6698.
- [266] Francois Chollet et al. *ARC Prize 2024: Technical Report*. 2025. arXiv: 2412.04604 [cs.AI].
- [267] Isaac Liao and Albert Gu. *ARC-AGI Without Pretraining*. Mar. 2025. URL: https://iliao2345.github.io/blog_posts/arc_agi_without_pretraining/arc_agi_without_pretraining.html.
- [268] Yuxi Liu et al. *The Serial Scaling Hypothesis*. 2025. arXiv: 2507.12549 [cs.LG].
- [269] Tri Dao et al. “FlashAttention: Fast and Memory-Efficient Exact Attention with IO-Awareness”. In: *Advances in Neural Information Processing Systems*. Ed. by S. Koyejo et al. Vol. 35. Curran Associates, Inc., 2022, pp. 16344–16359. URL: https://proceedings.neurips.cc/paper_files/paper/2022/hash/67d57c32e20fd0a7a302cb81d36e40d5-Abstract-Conference.html.
- [270] Albert Gu and Tri Dao. “Mamba: Linear-Time Sequence Modeling with Selective State Spaces”. In: *First Conference on Language Modeling*. 2024. URL: <https://openreview.net/forum?id=tEYskw1VY2>.
- [271] Thomas Schmied et al. *A Large Recurrent Action Model: xLSTM enables Fast Inference for Robotics Tasks*. 2025. arXiv: 2410.22391 [cs.LG].
- [272] Reiner Pope et al. “Efficiently Scaling Transformer Inference”. In: *Proceedings of Machine Learning and Systems*. Ed. by D. Song et al. Vol. 5. Curran, 2023, pp. 606–624. URL: https://proceedings.mlsys.org/paper_files/paper/2023/hash/c4be71ab8d24cdfb45e3d06dbfca2780-Abstract-mlsys2023.html.
- [273] Charlie Chen et al. *Accelerating Large Language Model Decoding with Speculative Sampling*. 2023. arXiv: 2302.01318 [cs.CL].
- [274] Stephen Grossberg. “Competitive learning: From interactive activation to adaptive resonance”. In: *Cognitive Science* 11.1 (1987), pp. 23–63. ISSN: 0364-0213. DOI: [https://doi.org/10.1016/S0364-0213\(87\)80025-3](https://doi.org/10.1016/S0364-0213(87)80025-3).
- [275] Guillaume Bellec et al. “A solution to the learning dilemma for recurrent networks of spiking neurons”. In: *Nature communications* 11.1 (2020), p. 3625. DOI: 10.1038/s41467-020-17236-y.
- [276] Alexandre Payeur et al. “Burst-dependent synaptic plasticity can coordinate learning in hierarchical circuits”. In: *Nature neuroscience* 24.7 (2021), pp. 1010–1019. DOI: 10.1038/s41593-021-00857-x.
- [277] James C. R. Whittington and Rafal Bogacz. “An Approximation of the Error Backpropagation Algorithm in a Predictive Coding Network with Local Hebbian Synaptic Plasticity”. In: *Neural Computation* 29.5 (May 2017), pp. 1229–1262. ISSN: 0899-7667. DOI: 10.1162/NECO_a_00949.
- [278] Sen Song et al. “Highly Nonrandom Features of Synaptic Connectivity in Local Cortical Circuits”. In: *PLOS Biology* 3.3 (Mar. 2005). DOI: 10.1371/journal.pbio.0030068.
- [279] James CR Whittington and Rafal Bogacz. “Theories of error back-propagation in the brain”. In: *Trends in cognitive sciences* 23.3 (2019), pp. 235–250. DOI: 10.1016/j.tics.2018.12.005.
- [280] Timothy P Lillicrap et al. “Backpropagation and the brain”. In: *Nature Reviews Neuroscience* 21.6 (2020), pp. 335–346. DOI: 10.1038/s41583-020-0277-3.
- [281] Katharina Dobs et al. “Brain-like functional specialization emerges spontaneously in deep neural networks”. In: *Science Advances* 8.11 (2022), eabl8913. DOI: 10.1126/sciadv.abl8913.
- [282] Wulfram Gerstner et al. “Eligibility traces and plasticity on behavioral time scales: experimental support of neohebbian three-factor learning rules”. In: *Frontiers in neural circuits* 12 (2018), p. 53. DOI: 10.3389/fncir.2018.00053.

- [283] Timothy P Lillicrap et al. “Random synaptic feedback weights support error backpropagation for deep learning”. In: *Nature communications* 7.1 (2016), p. 13276. DOI: 10.1038/ncomms13276.
- [284] Tahereh Toosi and Elias Issa. “Brain-like Flexible Visual Inference by Harnessing Feedback Feedforward Alignment”. In: *Advances in Neural Information Processing Systems*. Ed. by A. Oh et al. Vol. 36. Curran Associates, Inc., 2023, pp. 56979–56997. URL: https://proceedings.neurips.cc/paper_files/paper/2023/file/b29ec434e049fb96f3c4245a405ee976-Paper-Conference.pdf.
- [285] Andre M Bastos et al. “Canonical microcircuits for predictive coding”. In: *Neuron* 76.4 (2012), pp. 695–711. DOI: 10.1016/j.neuron.2012.10.038.
- [286] Anastasia Dimakou et al. “The predictive nature of spontaneous brain activity across scales and species”. In: *Neuron* (2025). DOI: 10.1016/j.neuron.2025.02.009.
- [287] Belle Liu et al. “Predictive encoding of motion begins in the primate retina”. In: *Nature neuroscience* 24.9 (2021), pp. 1280–1291. DOI: 10.1038/s41593-021-00899-1.
- [288] Georg B Keller and Thomas D Mrsic-Flogel. “Predictive processing: a canonical cortical computation”. In: *Neuron* 100.2 (2018). DOI: 10.1016/j.neuron.2018.10.003.
- [289] Tsai-Wen Chen et al. “A Map of Anticipatory Activity in Mouse Motor Cortex”. In: *Neuron* 94 (2017), 866–879.e4. DOI: 10.1016/j.neuron.2017.05.005.
- [290] Linxing Preston Jiang and Rajesh P. N. Rao. “Dynamic predictive coding: A model of hierarchical sequence learning and prediction in the neocortex”. In: *PLOS Computational Biology* 20.2 (Feb. 2024), pp. 1–30. DOI: 10.1371/journal.pcbi.1011801.
- [291] David Ha et al. “HyperNetworks”. In: *International Conference on Learning Representations*. 2017. URL: <https://openreview.net/forum?id=rkpACe1lx>.
- [292] Beren Millidge et al. “Predictive coding networks for temporal prediction”. In: *PLOS Computational Biology* 20.4 (Apr. 2024), pp. 1–31. DOI: 10.1371/journal.pcbi.1011183.
- [293] Pierre-Étienne H Fiquet and Eero P Simoncelli. “A polar prediction model for learning to represent visual transformations”. In: *Thirty-seventh Conference on Neural Information Processing Systems*. 2023. URL: <https://openreview.net/forum?id=hyPUZX03Ks>.
- [294] Olivier J Hénaff et al. “Perceptual straightening of natural videos”. In: *Nature neuroscience* 22.6 (2019), pp. 984–991. DOI: 10.1038/s41593-019-0377-4.
- [295] Daniel J Felleman and David C Van Essen. “Distributed hierarchical processing in the primate cerebral cortex”. In: *Cerebral Cortex* 1.1 (1991), pp. 1–47. DOI: 10.1093/CERCOR/1.1.1.
- [296] Richard D Lange et al. “Bayesian encoding and decoding as distinct perspectives on neural coding”. In: *Nature Neuroscience* 26.12 (2023), pp. 2063–2072. DOI: 10.1038/s41593-023-01458-6.
- [297] William Bechtel and Leonardo Bich. “Grounding cognition: heterarchical control mechanisms in biology”. In: *Philosophical Transactions of the Royal Society B: Biological Sciences* 376.1820 (2021), p. 20190751. DOI: 10.1098/rstb.2019.0751.
- [298] Jeff Hawkins et al. *Hierarchy or Heterarchy? A Theory of Long-Range Connections for the Sensorimotor Brain*. 2025. arXiv: 2507.05888 [q-bio.NC].
- [299] Jay Hegde and Daniel J Felleman. “Reappraising the functional implications of the primate visual anatomical hierarchy”. In: *The Neuroscientist* 13.5 (2007), pp. 416–421. DOI: 10.1177/1073858407305201.
- [300] Tommaso Salvatori et al. “Learning on Arbitrary Graph Topologies via Predictive Coding”. In: *Advances in Neural Information Processing Systems*. Ed. by S. Koyejo et al. Vol. 35. Curran Associates, Inc., 2022, pp. 38232–38244. URL: https://proceedings.neurips.cc/paper_files/paper/2022/hash/f9f54762cbb4fe4dbffdd4f792c31221-Abstract-Conference.html.
- [301] Jacob A. Westerberg and Pieter R. Roelfsema. “Hierarchical interactions between sensory cortices defy predictive coding”. In: *Trends in Cognitive Sciences* (2025). ISSN: 1364-6613. DOI: 10.1016/j.tics.2025.09.018.
- [302] Victor Boutin et al. “Pooling strategies in V1 can account for the functional and structural diversity across species”. In: *PLOS Computational Biology* 18.7 (July 2022), pp. 1–21. DOI: 10.1371/journal.pcbi.1010270.

- [303] Kuniyiko Fukushima. “Neocognitron: A self-organizing neural network model for a mechanism of pattern recognition unaffected by shift in position”. In: *Biological cybernetics* 36.4 (1980), pp. 193–202. DOI: 10.1007/BF00344251.
- [304] Eugene M. Izhikevich. “Polychronization: Computation with Spikes”. In: *Neural Computation* 18.2 (Feb. 2006), pp. 245–282. ISSN: 0899-7667. DOI: 10.1162/089976606775093882.
- [305] Camille E. Rullán Buxó and Jonathan W. Pillow. “Poisson balanced spiking networks”. In: *PLOS Computational Biology* 16.11 (Nov. 2020), pp. 1–27. DOI: 10.1371/journal.pcbi.1008261. URL: <https://doi.org/10.1371/journal.pcbi.1008261>.
- [306] Yusi Chen et al. “Predictive sequence learning in the hippocampal formation”. In: *Neuron* 112.15 (2024), pp. 2645–2658. DOI: 10.1016/j.neuron.2024.05.024.
- [307] T. Anderson Keller et al. *A Spacetime Perspective on Dynamical Computation in Neural Information Processing Systems*. 2024. arXiv: 2409.13669 [q-bio.NC].
- [308] Daniel LK Yamins et al. “Performance-optimized hierarchical models predict neural responses in higher visual cortex”. In: *Proceedings of the National Academy of Sciences* 111.23 (2014), pp. 8619–8624. DOI: 10.1073/pnas.1403112111.
- [309] Matteo Carandini et al. “Do we know what the early visual system does?” In: *Journal of Neuroscience* 25.46 (2005), pp. 10577–10597. DOI: 10.1523/JNEUROSCI.3726-05.2005.
- [310] Michael C.-K. Wu et al. “COMPLETE FUNCTIONAL CHARACTERIZATION OF SENSORY NEURONS BY SYSTEM IDENTIFICATION”. In: *Annual Review of Neuroscience* 29. Volume 29, 2006 (2006), pp. 477–505. ISSN: 1545-4126. DOI: <https://doi.org/10.1146/annurev.neuro.29.051605.113024>.
- [311] Bruno A. Olshausen and David J. Field. “How Close Are We to Understanding V1?” In: *Neural Computation* 17.8 (Aug. 2005), pp. 1665–1699. ISSN: 0899-7667. DOI: 10.1162/0899766054026639.
- [312] Nancy Kanwisher et al. “Using artificial neural networks to ask ‘why’ questions of minds and brains”. In: *Trends in Neurosciences* (2023). DOI: 10.1016/j.tins.2022.12.008.
- [313] Fabian H Sinz et al. “Engineering a less artificial intelligence”. In: *Neuron* 103.6 (2019), pp. 967–979. DOI: 10.1016/j.neuron.2019.08.034.
- [314] Mackenzie Weygandt Mathis et al. “Decoding the brain: From neural representations to mechanistic models”. In: *Cell* 187.21 (2024), pp. 5814–5832. DOI: 10.1016/j.cell.2024.08.051.

Appendix: Brain-like Variational Inference

A	Extended Background: Philosophical, Historical, and Theoretical	29
A.1	Perception as inference	29
A.2	Bayesian posterior inference	29
A.3	Variational inference and deriving the ELBO objective	29
A.4	Three distributions, one ELBO	30
A.5	Two ways to carve up the ELBO	31
A.6	Gaussian Variational Autoencoder (\mathcal{G} -VAE)	31
A.7	Poisson Variational Autoencoder (\mathcal{P} -VAE)	32
A.8	Amortized versus iterative variational inference	32
A.9	Predictive coding as variational inference	34
A.10	Variational free energy minimization unifies machine learning and neuroscience . .	35
B	Extended Theory: Motivations, Derivations, and Discussions	36
B.1	What do we mean by “prescriptive”?	36
B.2	Why Poisson?	37
B.3	Poisson Kullback–Leibler (KL) divergence	37
B.4	Fisher information matrix	38
B.5	Interpreting the terms in Poisson dynamics equations	41
B.6	Extension to nonlinear decoders	42
B.7	Extension to Gaussian posteriors	42
B.8	Biological interpretation of the standard predictive coding dynamics	45
B.9	Free energy for sequences	46
B.10	Static versus online inference	46
C	Extended Experiments: Methodological Details and Additional Results	48
C.1	Architecture, Hyperparameter, and Training details	48
C.2	Convergence detection procedure	49
C.3	$i\mathcal{P}$ -VAE exhibits cortex-like dynamics: contrast-dependent response latency	51
C.4	Reconstruction-sparsity with deterministic MAP decoding, and dependence on β .	51
C.5	Reconstruction-sparsity performance across latent dimensionalities	53
C.6	Reconstruction performance and downstream classification accuracy on MNIST . .	55
C.7	Runtime comparison: iterative versus amortized inference	56
C.8	$i\mathcal{P}$ -VAE exhibits strong out-of-distribution (OOD) generalization	58
C.9	$i\mathcal{P}$ -VAE scales up to complex, high-dimensional color image datasets	63
C.10	$i\mathcal{P}$ -VAE generates novel samples through an iterative procedure	64
D	Extended Discussion	65
D.1	A summary of our prescriptive framework, and how it relates to BLR and BONG .	65
D.2	Three possible explanations for the effectiveness of $i\mathcal{P}$ -VAE	67
D.3	Hardware-efficient implementation and real-world deployment potential of $i\mathcal{P}$ -VAE	67
D.4	Relationship to sampling-based inference methods	68
D.5	Limitations and future work	69

A Extended Background: Philosophical, Historical, and Theoretical

In this appendix, we present additional background information that complements the main text (section 2). First, we explore the historical and philosophical perspectives underlying our work. We then connect these foundations to recent developments while providing pedagogical explanations of essential statistical concepts. Finally, we review existing machine learning and neuroscience models as instances of free energy minimization, culminating in a model taxonomy shown in Fig. 2.

A.1 Perception as inference

The idea that perception is an inferential (rather than passive) process has been around for centuries. Early thinkers described it as a process of “unconscious inference” about the hidden causes of sensory inputs [1, 2]. This inference relies on two key components: (i) incoming sensory data, and (ii) *a priori* knowledge about the environment [137]. Prior world knowledge can be acquired either through subjective experience [138–140], or innately built in through evolutionary and developmental processes [141–143]. As recognized in early psychology [144], and later formalized in theoretical and computational frameworks, perception emerges when these two sources—sensory evidence and prior expectations—are integrated to infer the most likely state of the world. Thus, brains actively “construct” their perceptions [3, 145].

This framework remains a major cornerstone of theoretical neuroscience, and has inspired many influential theories across the field [5–7, 22–24, 32, 54, 146–149]. Although these theories go by different names, they are unified by the core idea of “*perception-as-inference*”. Of particular relevance to our work are *sparse coding* [54, 55, 150, 151], *predictive coding* [22, 33, 146, 152], and the *free energy principle* [23–25, 148, 149, 153].

Ideas such as *variational inference* from statistics [4, 14–17] and *variational autoencoders* (VAEs) from machine learning [18–20] closely parallel those from theoretical neuroscience. While there has been increasing dialogue between these fields, opportunities remain for deeper integration. Our work speaks directly to this overlap by offering a theoretical synthesis of these ideas (Fig. 2), as well as introducing a new family of brain-inspired machine learning architectures with practical benefits.

A.2 Bayesian posterior inference

In statistical terms, perception can be modeled as a problem of Bayesian posterior inference [10–12]. We start with a generative model, $p_\theta(\mathbf{x})$, that assigns probabilistic beliefs to observations, $\mathbf{x} \in \mathbb{R}^M$ (e.g., images), through invoking K -dimensional latent variables, \mathbf{z} :

$$\underbrace{p_\theta(\mathbf{x})}_{\substack{\text{marginal likelihood} \\ \text{(a.k.a model evidence)}}} = \underbrace{\int p_\theta(\mathbf{x}, \mathbf{z}) d\mathbf{z}}_{\substack{\text{joint} \\ \text{distribution}}} = \int \underbrace{p_\theta(\mathbf{x}|\mathbf{z})}_{\substack{\text{conditional} \\ \text{likelihood}}} \underbrace{p_\theta(\mathbf{z})}_{\text{prior}} d\mathbf{z}, \quad (9)$$

where θ are the adaptable parameters of the generative model (e.g., neural network weights or synaptic connection strengths in the brain). Here, $p_\theta(\mathbf{z})$ represents prior beliefs over latent causes, and $p_\theta(\mathbf{x}|\mathbf{z})$ is the conditional likelihood of observations given latents.

Posterior inference inverts this generative process to determine which latent configurations are most likely given an observation. Apply Bayes’ rule to get:

$$\underbrace{p_\theta(\mathbf{z}|\mathbf{x})}_{\text{posterior}} = \frac{p_\theta(\mathbf{x}, \mathbf{z})}{p_\theta(\mathbf{x})} = \frac{p_\theta(\mathbf{x}|\mathbf{z})p_\theta(\mathbf{z})}{p_\theta(\mathbf{x})} = \frac{p_\theta(\mathbf{x}|\mathbf{z})p_\theta(\mathbf{z})}{\int p_\theta(\mathbf{x}|\mathbf{z})p_\theta(\mathbf{z}) d\mathbf{z}}. \quad (10)$$

This posterior distribution is analytically intractable in all but the simplest cases due to the integration over all latent configurations in the denominator. This necessitates approximate inference methods.

A.3 Variational inference and deriving the ELBO objective

Variational inference is a powerful approximate inference method that transforms the posterior inference problem, eq. (10), into an optimization task [15–17]. Specifically, one introduces a variational density, $q_\phi(\mathbf{z}|\mathbf{x})$, parameterized by ϕ , which approximates the true posterior. The goal is to minimize the Kullback-Leibler (KL) divergence between $q_\phi(\mathbf{z}|\mathbf{x})$ and the true posterior $p_\theta(\mathbf{z}|\mathbf{x})$.

This optimization leads to the standard *Evidence Lower Bound* (ELBO) objective [15, 17], which can be derived starting from the model evidence as follows:

$$\begin{aligned}
\log p_\theta(\mathbf{x}) &= \log p_\theta(\mathbf{x}) \int q_\phi(\mathbf{z}|\mathbf{x}) d\mathbf{z} \\
&= \int q_\phi(\mathbf{z}|\mathbf{x}) \log p_\theta(\mathbf{x}) d\mathbf{z} \\
&= \mathbb{E}_{\mathbf{z} \sim q_\phi(\mathbf{z}|\mathbf{x})} \left[\log p_\theta(\mathbf{x}) \right] \\
&= \mathbb{E}_{\mathbf{z} \sim q_\phi(\mathbf{z}|\mathbf{x})} \left[\log p_\theta(\mathbf{x}) + \log p_\theta(\mathbf{z}|\mathbf{x}) - \log p_\theta(\mathbf{z}|\mathbf{x}) \right] \\
&= \mathbb{E}_{\mathbf{z} \sim q_\phi(\mathbf{z}|\mathbf{x})} \left[\log \frac{p_\theta(\mathbf{x}) p_\theta(\mathbf{z}|\mathbf{x})}{p_\theta(\mathbf{z}|\mathbf{x})} \right] \\
&= \mathbb{E}_{\mathbf{z} \sim q_\phi(\mathbf{z}|\mathbf{x})} \left[\log \frac{p_\theta(\mathbf{x}, \mathbf{z})}{p_\theta(\mathbf{z}|\mathbf{x})} \right] \tag{11} \\
&= \mathbb{E}_{\mathbf{z} \sim q_\phi(\mathbf{z}|\mathbf{x})} \left[\log \frac{p_\theta(\mathbf{x}, \mathbf{z}) q_\phi(\mathbf{z}|\mathbf{x})}{p_\theta(\mathbf{z}|\mathbf{x}) q_\phi(\mathbf{z}|\mathbf{x})} \right] \\
&= \mathbb{E}_{\mathbf{z} \sim q_\phi(\mathbf{z}|\mathbf{x})} \left[\log \frac{p_\theta(\mathbf{x}, \mathbf{z})}{q_\phi(\mathbf{z}|\mathbf{x})} + \log \frac{q_\phi(\mathbf{z}|\mathbf{x})}{p_\theta(\mathbf{z}|\mathbf{x})} \right] \\
&= \mathbb{E}_{\mathbf{z} \sim q_\phi(\mathbf{z}|\mathbf{x})} \left[\log \frac{p_\theta(\mathbf{x}, \mathbf{z})}{q_\phi(\mathbf{z}|\mathbf{x})} \right] + \mathbb{E}_{\mathbf{z} \sim q_\phi(\mathbf{z}|\mathbf{x})} \left[\log \frac{q_\phi(\mathbf{z}|\mathbf{x})}{p_\theta(\mathbf{z}|\mathbf{x})} \right] \\
&= \underbrace{\mathbb{E}_{\mathbf{z} \sim q_\phi(\mathbf{z}|\mathbf{x})} \left[\log \frac{p_\theta(\mathbf{x}, \mathbf{z})}{q_\phi(\mathbf{z}|\mathbf{x})} \right]}_{\text{ELBO}(\mathbf{x}; \theta, \phi)} + \mathcal{D}_{\text{KL}}(q_\phi(\mathbf{z}|\mathbf{x}) \parallel p_\theta(\mathbf{z}|\mathbf{x})).
\end{aligned}$$

This concludes our derivation of eq. (1). All we did was multiply by one twice (once by inserting $\int q_\phi(\mathbf{z}|\mathbf{x}) d\mathbf{z}$ and once by introducing the ratio $\frac{q_\phi(\mathbf{z}|\mathbf{x})}{q_\phi(\mathbf{z}|\mathbf{x})}$) followed by a few algebraic rearrangements.

Importantly, eq. (1) holds for any $q_\phi(\mathbf{z}|\mathbf{x})$ that defines a proper probability density. Compared to the typical derivation using Jensen’s inequality [15], this derivation yields a stronger result [20]: An exact decomposition of the model evidence into the ELBO plus the KL divergence between the approximate and true posterior.

A direct consequence of this equality is that taking gradients of eq. (1) with respect to ϕ shows that maximizing the ELBO minimizes the KL divergence, since the model evidence on the left-hand side is independent of ϕ . Thus, ELBO maximization improves posterior inference quality, corresponding to more accurate perception under the perception-as-inference framework (appendix A.1).

A.4 Three distributions, one ELBO

To fully specify the ELBO in eq. (1), we must make choices about the approximate posterior $q_\phi(\mathbf{z}|\mathbf{x})$ and the joint distribution $p_\theta(\mathbf{x}, \mathbf{z})$, which further decomposes as $p_\theta(\mathbf{x}, \mathbf{z}) = p_\theta(\mathbf{z}) p_\theta(\mathbf{x}|\mathbf{z})$. Therefore, we are faced with a total of three independent distributional choices: approximate posterior, prior, and likelihood ¹.

In both neuroscience and machine learning, it is common practice to assume all three distributions are Gaussian. These critical assumptions are frequently adopted by convention rather than through theoretical justification. We emphasize that these distributions are entirely at the discretion of the modeler, and there are no fundamental constraints requiring them to be Gaussian in all cases.

¹In the online inference setting, both the prior and approximate posterior (typically) become one family, reducing the independent choices into two: approximate posterior, and likelihood.

A.5 Two ways to carve up the ELBO

There are two common ways of expressing and interpreting the ELBO. The first, more popular in the machine learning community, is the VAE loss decomposition [20]:

$$\begin{aligned}
\text{ELBO}(\mathbf{x}; \theta, \phi) &= \mathbb{E}_{\mathbf{z} \sim q_\phi(\mathbf{z}|\mathbf{x})} \left[\log \frac{p_\theta(\mathbf{x}|\mathbf{z})p_\theta(\mathbf{z})}{q_\phi(\mathbf{z}|\mathbf{x})} \right] \\
&= \mathbb{E}_{\mathbf{z} \sim q_\phi(\mathbf{z}|\mathbf{x})} \left[\log p_\theta(\mathbf{x}|\mathbf{z}) \right] + \mathbb{E}_{\mathbf{z} \sim q_\phi(\mathbf{z}|\mathbf{x})} \left[\log \frac{p_\theta(\mathbf{z})}{q_\phi(\mathbf{z}|\mathbf{x})} \right] \\
&= \underbrace{\mathbb{E}_{\mathbf{z} \sim q_\phi(\mathbf{z}|\mathbf{x})} \left[\log p_\theta(\mathbf{x}|\mathbf{z}) \right]}_{\text{Reconstruction term (distortion)}} - \underbrace{\mathcal{D}_{\text{KL}}(q_\phi(\mathbf{z}|\mathbf{x}) \parallel p_\theta(\mathbf{z}))}_{\text{KL term (coding rate)}}.
\end{aligned} \tag{12}$$

This view emphasizes reconstruction fidelity and latent space regularization. The reconstruction term can be interpreted as a *distortion measure*, quantifying how well the latent code \mathbf{z} can explain the input \mathbf{x} through the generative model. The KL term, by contrast, acts as an *information rate*, measuring how much input-dependent information is encoded in the posterior $q_\phi(\mathbf{z}|\mathbf{x})$ beyond what is already present in the prior $p_\theta(\mathbf{z})$. In other words, the KL quantifies the *coding cost* of representing \mathbf{x} via \mathbf{z} , and reflects the capacity of the latent space to capture novel, stimulus-specific structure. This interpretation is closely related to classical *rate-distortion theory* [154, 155], and has been formalized in the context of VAEs by Alemi et al. [77].

The second view, more aligned with theoretical neuroscience and physics, splits (negative) ELBO as:

$$-\text{ELBO}(\mathbf{x}; \theta, \phi) \equiv \mathcal{F}(\mathbf{x}; \theta, \phi) = \underbrace{\mathbb{E}_{\mathbf{z} \sim q_\phi(\mathbf{z}|\mathbf{x})} \left[-\log p_\theta(\mathbf{x}, \mathbf{z}) \right]}_{\text{Energy}} - \underbrace{\mathcal{H}[q_\phi(\mathbf{z}|\mathbf{x})]}_{\text{Entropy}}, \tag{13}$$

where $\mathcal{H}[q] = -\int q \log q$ is the Shannon entropy.

This carving is analogous to the concept of *Helmholtz free energy* from statistical physics [156–158], where minimizing free energy involves reducing energy while preserving entropy (i.e., maintaining uncertainty). Below, we will use this decomposition to show that the predictive coding objective of Rao and Ballard [22] can be directly derived from eq. (13) under specific distributional assumptions.

A.6 Gaussian Variational Autoencoder (\mathcal{G} -VAE)

The standard Gaussian VAE (\mathcal{G} -VAE) represents a foundational model in the VAE family, where all three distributions are factorized Gaussians [20]. To simplify the model, the prior is typically fixed as a standard normal distribution with zero mean and unit variance: $p_\theta(\mathbf{z}) = \mathcal{N}(\mathbf{0}, \mathbf{1})$.

The key innovation of VAEs lies in how they parameterize the approximate posterior and likelihood distributions using neural networks:

Approximate posterior. The **encoder** neural network transforms each input \mathbf{x} into parameters for the posterior distribution. Specifically, it outputs both a mean vector and a variance vector: $\text{enc}(\mathbf{x}; \phi) = \lambda(\mathbf{x}) \equiv (\mu(\mathbf{x}), \sigma^2(\mathbf{x}))$. These parameters fully specify the approximate posterior: $q_\phi(\mathbf{z}|\mathbf{x}) = \mathcal{N}(\mathbf{z}; \mu(\mathbf{x}), \sigma^2(\mathbf{x}))$. Typically, neural networks are made to output $\log \sigma$, which is exponentiated to obtain the variance. This choice ensures the variance always remains positive.

Likelihood. The **decoder** neural network maps sampled latent variables back to reconstructions in the input space, producing the mean of the likelihood distribution: $\mu(\mathbf{z}) = \text{dec}(\mathbf{z}; \theta)$.

Likelihood variance. There are several approaches for handling the variance of the likelihood:

- Fixed variance: Setting a constant variance for all dimensions (this is bad practice: [159]).
- Input-dependent variance: Using a separate neural net to predict variance as a function of \mathbf{z} .
- Learned global variance: Learning a set of global variance parameters σ^2 for the entire dataset [69].

In our implementation, we use learned global variance parameters for the decoder, meaning: $p_\theta(\mathbf{x}|\mathbf{z}) = \mathcal{N}(\mathbf{x}; \text{dec}(\mathbf{z}; \theta), \sigma^2)$.

Training. A critical component enabling end-to-end training of VAEs is the reparameterization trick [18]. This technique allows gradients to flow through the sampling operation by expressing a sample \mathbf{z} from $q_\phi(\mathbf{z}|\mathbf{x})$ as a deterministic function of \mathbf{x} and a noise variable $\epsilon \sim \mathcal{N}(\mathbf{0}, \mathbf{I})$:

$$\mathbf{z} = \boldsymbol{\mu}(\mathbf{x}) + \boldsymbol{\sigma}(\mathbf{x}) \odot \epsilon,$$

With this formulation, both encoder and decoder parameters can be jointly optimized by maximizing the ELBO objective shown in eq. (12).

Extensions and modifications. Since the advent of VAEs [18, 19], numerous proposals have extended or modified the standard Gaussian framework. These efforts can be broadly categorized into three main directions: (i) developing more expressive or learnable priors, (ii) replacing the likelihood function with non-Gaussian alternatives, and (iii) altering the latent distribution.

In terms of priors $p_\theta(\mathbf{z})$, researchers have introduced hierarchical variants [115, 160, 161], structured priors such as VampPrior [162], and nonparametric approaches like the stick-breaking process [163].

For the likelihood function $p_\theta(\mathbf{x}|\mathbf{z})$, alternatives to the standard Gaussian have been proposed to better accommodate binary, count, or highly structured data. Examples include the Bernoulli distribution for binary data [18, 164], Poisson [165] and negative binomial [166] for count data, and mixtures of discretized Logistic distributions for natural images [161, 167].

Finally, for inference, many have enhanced the expressiveness of the variational posterior $q_\phi(\mathbf{z}|\mathbf{x})$ by applying normalizing flows [168] or inverse autoregressive flows [169], thereby relaxing the mean-field assumption. Others have replaced the Gaussian latents altogether, exploring alternative distributions such as categorical [170, 171], Bernoulli [172, 173], Laplace [174], Dirichlet [175], hyperbolic normal [176], von Mises-Fisher [177], Student’s t [178], and negative binomial [179].

A.7 Poisson Variational Autoencoder (\mathcal{P} -VAE)

A particularly relevant departure from Gaussian latent variables is the Poisson VAE (\mathcal{P} -VAE; [50]). Motivated by findings in neuroscience that neural spike counts follow Poisson statistics over short temporal windows [51, 180], Vafaii et al. [50] introduced a VAE variant in which posterior inference is performed over discrete spike counts. In \mathcal{P} -VAE, both the prior and approximate posterior distributions of the standard Gaussian VAE are replaced with Poisson distributions. The authors also developed a novel Poisson reparameterization trick and derived a corresponding ELBO for Poisson-distributed VAEs.

An important theoretical insight arises from the \mathcal{P} -VAE ELBO: the KL divergence term induces a firing rate penalty that resembles *sparse coding* [54], a fundamental and widely documented property of biological neural representations [151]. When trained on natural image patches, \mathcal{P} -VAE learns sparse latent representations with Gabor-like basis vectors [107–110], much like classic sparse coding [54]. \mathcal{P} -VAE has also been extended to model psychophysical response times [181].

Despite these advances, \mathcal{P} -VAE underperformed the *locally competitive algorithm* (LCA; [39])—a classic iterative sparse coding algorithm from 2008—in both reconstruction accuracy and sparsity. The authors attributed this performance gap to a key difference in inference mechanisms: VAEs rely on *amortized* inference; whereas, sparse coding uses *iterative* optimization at test time.

A.8 Amortized versus iterative variational inference

Once we select our approximate posterior distribution—such as a Gaussian (\mathcal{G} -VAE) or Poisson (\mathcal{P} -VAE)—we must decide how to parameterize and optimize it. Let $\boldsymbol{\lambda}$ denote the distributional parameters of the approximate posterior (distinct from neural network weights). For example, a Gaussian posterior requires both a mean $\boldsymbol{\mu}$ and variance $\boldsymbol{\sigma}^2$, i.e., $\boldsymbol{\lambda} \equiv (\boldsymbol{\mu}, \boldsymbol{\sigma}^2)$; whereas, a Poisson posterior is specified by a vector of rates, $\boldsymbol{\lambda} \equiv \mathbf{r}$. We now describe three strategies for optimizing $\boldsymbol{\lambda}$: amortized, iterative, and hybrid iterative-amortized inference.

Amortized inference. In *amortized variational inference*, an encoder neural network $\text{enc}(\mathbf{x}; \boldsymbol{\phi})$, parameterized by weights $\boldsymbol{\phi}$, maps each observation \mathbf{x} to its corresponding posterior parameters in a single forward pass: $\boldsymbol{\lambda}(\mathbf{x}) = \text{enc}(\mathbf{x}; \boldsymbol{\phi})$. This approach, central to VAEs, is efficient at test time, as the cost of inference is “amortized” over training, much like spreading out a fixed expense over time in accounting [36].

The amortized approach is partially motivated by the universal approximation capability of neural networks [182]: if there exists a mapping from samples to their optimal posterior parameters, $\mathbf{x} \rightarrow \boldsymbol{\lambda}^*(\mathbf{x})$, then a sufficiently large and deep neural network should theoretically be able to learn it.

However, despite this theoretical promise, amortized inference often suffers from an *amortization gap*—a systematic mismatch between the inferred posterior parameters, $\boldsymbol{\lambda}(\mathbf{x}) = \text{enc}(\mathbf{x}; \phi)$, and the optimal variational parameters, $\boldsymbol{\lambda}^*(\mathbf{x})$. This gap can significantly degrade model performance [183, 184] and can be conceptualized in two equivalent ways.

First, within a given family of distributions, the optimal variational parameters $\boldsymbol{\lambda}^*(\mathbf{x})$ are by definition those that minimize the KL divergence from the approximate posterior to the true posterior (the last term in eq. (1)). Second, due to the equality in eq. (1), this KL divergence is mathematically equivalent to the difference between the ELBO and the model evidence, $\log p_{\theta}(\mathbf{x})$. The closer the variational approximation is to the true posterior distribution in terms of KL, the smaller the gap between ELBO and $\log p_{\theta}(\mathbf{x})$ becomes, thereby increasing the “tightness” of the lower bound.

In summary, the amortization gap reveals that despite the promise of the universal approximation theorem [182], even highly parameterized deep neural networks often fail to find the optimal variational parameters [183]. This results in both poor inference quality, as well as substantial discrepancy between the ELBO and the model evidence.

Iterative inference. In contrast to amortized inference, *iterative variational inference* optimizes the posterior parameters $\boldsymbol{\lambda}$ separately for each data point by directly maximizing the ELBO, typically via gradient-based optimization. Although more computationally intensive at test time, this approach often achieves tighter variational bounds and more accurate posterior approximations [183, 185].

A canonical example is stochastic variational inference (SVI; [186]), which updates local variational parameters via stochastic gradient ascent. Iterative optimization is also central to classical Bayesian approaches such as expectation maximization (EM; [13, 187]), coordinate ascent variational inference [188], mean-field variational inference [17, 189], and expectation propagation [190], all of which refine posterior estimates through successive updates.

In neuroscience-inspired models, iterative inference emerges naturally in biologically plausible frameworks such as the *locally competitive algorithm* (LCA; [39]) for sparse coding (SC), and in predictive coding models (PC; [22, 23]). Both SC and PC implement inference through local, recurrent dynamics. While these models are not always formulated explicitly in terms of ELBO maximization, as reviewed in the main text, appendix A.9, and illustrated in Fig. 2, both SC and PC can be interpreted as performing variational inference via iterative refinement of latent variables in response to sensory input.

In summary, iterative inference methods can substantially reduce the amortization gap by producing more accurate posterior approximations. But they incur increased computational cost at test time, often requiring multiple optimization steps per observation.

Hybrid iterative-amortized inference. Several hybrid approaches have been proposed to bridge the gap between amortized and iterative inference, aiming to combine the speed and scalability of amortized methods with the accuracy and flexibility of iterative refinement. The *Helmholtz machine* [4] is an early example, using a recognition network for approximate inference (similar to amortization) but trained through the *wake-sleep* algorithm. This approach alternates between updating the generative model in the “wake” phase and the recognition model in the “sleep” phase, combining aspects of both amortized and iterative approaches in an EM-like fashion.

More recent examples include *iterative amortized inference* [91], which trains a neural network to predict parameter updates rather than the posterior parameters themselves. This approach draws inspiration from meta-learning [191], where the inference procedure is learned as a dynamical process conditioned on data. By learning to iteratively improve posterior estimates, such models can adapt inference trajectories to individual data points while still leveraging amortization during training.

Another example is the *semi-amortized variational autoencoder* [92], which uses a standard encoder network to produce an initial guess for the approximate posterior, and then performs a small number of gradient-based updates, as in stochastic variational inference (SVI; [186]), to refine the estimate. This two-stage approach retains the test-time efficiency of amortization while reducing the amortization gap via local adaptation.

Our models are fully iterative, in the spirit of LCA, but remain conceptually related to these hybrid strategies. We compare to them thoroughly in our extended results below.

Iterative versus amortized inference: which approach is more brain-like? Unlike one-shot amortized inference, neural dynamics unfold over time [75], allowing for progressive refinement of perceptual representations [42, 44]. This temporal unfolding is consistent with recurrent processing and resonance phenomena observed in neural circuits [40, 41, 43], suggesting that the brain engages in a form of iterative inference. This idea is reflected in biologically inspired algorithms such as sparse coding [39] and predictive coding [22, 33], where inference is implemented through ongoing dynamical interactions that minimize error over time.

A counterpoint comes from Gershman and Goodman [36], who argues that the brain may instead employ amortized inference, using fast, feedforward mappings (e.g., learned neural networks) that approximate posterior beliefs without requiring iterative updates. This view emphasizes the efficiency of inference through learned function approximation, contrasting with the flexibility and adaptivity of iterative approaches.

However, this efficiency comes at the cost of adaptability and biological realism. Given the strong evidence for recurrent, time-evolving neural dynamics, we view iterative inference as the more plausible default. Though in practice, the brain may implement a hybrid of both strategies.

The jury is still out.

A.9 Predictive coding as variational inference

Having established the variational framework for perception, we now demonstrate how the classic predictive coding model of Rao and Ballard [22] can also be understood as a form of variational inference with specific distributional choices. Here, we focus on a single-layer predictive coding network (PCN) with a linear decoder. See Millidge et al. [33] for a comprehensive review, covering more general cases including hierarchical PCNs.

The key insight is that predictive coding is mathematically identical to free energy minimization (or ELBO maximization), with three specific distributional choices: (1) factorized Gaussian prior, (2) factorized Gaussian likelihood, and (3) a Dirac-delta distribution for the approximate posterior, combined with iterative inference.

Consider images $\mathbf{x} \in \mathbb{R}^M$ and latent variables $\mathbf{z} \in \mathbb{R}^K$. Starting from the free energy formulation in eq. (13), we substitute $q_\phi(\mathbf{z}|\mathbf{x}) = \delta(\mathbf{z} - \boldsymbol{\mu})$, where $\phi \equiv \boldsymbol{\mu}$ are the encoding parameters. With this delta distribution, the entropy term vanishes, simplifying the free energy to:

$$\mathcal{F}(\mathbf{x}; \boldsymbol{\theta}, \boldsymbol{\mu}) = \mathbb{E}_{\mathbf{z} \sim \delta(\mathbf{z} - \boldsymbol{\mu})} \left[-\log p_\theta(\mathbf{x}, \mathbf{z}) \right] = -\log p_\theta(\mathbf{x}, \boldsymbol{\mu}). \quad (14)$$

For the generative model, we adopt factorized Gaussians:

$$\begin{aligned} \text{Gaussian prior: } p_\theta(\boldsymbol{\mu}) &= \mathcal{N}(\boldsymbol{\mu}; \boldsymbol{\mu}_0, \mathbf{I}), \\ \text{Gaussian likelihood: } p_\theta(\mathbf{x}|\boldsymbol{\mu}) &= \mathcal{N}(\mathbf{x}; \Phi\boldsymbol{\mu}, \mathbf{I}), \end{aligned}$$

where $\boldsymbol{\mu}_0 \in \mathbb{R}^K$ are learnable prior parameters, and $\Phi \in \mathbb{R}^{M \times K}$ is a linear decoder (i.e., the dictionary in sparse coding). Therefore, the generative model parameters are $\boldsymbol{\theta} \equiv (\boldsymbol{\mu}_0, \Phi)$.

Substituting these Gaussians into eq. (14) yields:

$$\begin{aligned} \mathcal{F}(\mathbf{x}; \boldsymbol{\theta}, \boldsymbol{\mu}) &= -\log p_\theta(\mathbf{x}|\boldsymbol{\mu}) - \log p_\theta(\boldsymbol{\mu}) \\ &= \frac{1}{2} [(\mathbf{x} - \Phi\boldsymbol{\mu})^2 + (\boldsymbol{\mu} - \boldsymbol{\mu}_0)^2] + \dots, \end{aligned} \quad (15)$$

where the dots represent constant terms irrelevant to optimization. The two squared terms capture prediction errors at different levels of the hierarchy.

In predictive coding, the neural dynamics emerge directly from gradient descent on \mathcal{F} . Specifically, predictive coding assumes neural activity $\boldsymbol{\mu}$ evolves according to $\dot{\boldsymbol{\mu}} = -\nabla_{\boldsymbol{\mu}} \mathcal{F}$, which gives:

$$\dot{\boldsymbol{\mu}} = \underbrace{\Phi^T \mathbf{x}}_{\text{feedforward drive}} - \underbrace{\Phi^T \Phi \boldsymbol{\mu}}_{\text{lateral connections}} - \underbrace{(\boldsymbol{\mu} - \boldsymbol{\mu}_0)}_{\text{leak term}}. \quad (16)$$

Table 1: Models considered in this paper. Variational autoencoders (VAEs), sparse coding (SC), and predictive coding networks (PCNs) are different instantiations of variational inference with specific “prescriptive” choices. Our theoretical synthesis explicitly identifies these critical choices—including distribution families for priors and approximate posteriors, as well as the inference optimization method (amortized versus iterative)—that define and distinguish each model. Iterative VAEs, SC, and PCNs optimize encoding parameters λ through iteration, while amortized VAEs perform one-shot inference using neural networks with parameters ϕ . The main paper (sections 4 and 5, Fig. 5) focuses on linear decoders (dictionary Φ), with the general nonlinear decoder case explored in appendices B.6 and C.8 to C.10, Figs. 6 and 13 to 17, and tables 4 and 5. For an illustration of this table as a model tree, see Fig. 2. $\varphi(\cdot)$: nonlinear activation function (e.g., relu), Nat. GD: natural gradient descent.

Model family	Model	Posterior	Prior	Likelihood	Architecture		Reference
		$q_{\lambda}(z x)$	$p_{\theta}(z)$	$p_{\theta}(x z)$	Encoder	Decoder	
iterative VAE	iP-VAE	Poisson	Poisson			Φz	This paper
	iG-VAE	Gaussian	Gaussian	Gaussian	Nat. GD	Φz	
	iG $_{\varphi}$ -VAE	Gaussian	Gaussian			$\Phi\varphi(z)$	
amortized VAE	P-VAE	Poisson	Poisson			$\text{dec}(z; \theta)$	Vafaii et al. [50]
	G-VAE	Gaussian	Gaussian	Gaussian	$\text{enc}(x; \phi)$	$\text{dec}(z; \theta)$	Kingma and Welling [18]
	G $_{\varphi}$ -VAE	Gaussian	Gaussian			$\text{dec}(\varphi(z); \theta)$	Whittington et al. [89]
PCN	PC	Dirac-delta					Rao and Ballard [22]
	iPC		Gaussian	Gaussian	GD	$\varphi(\Phi z)$	Salvatori et al. [90]
Sparse coding	LCA	Dirac-delta	Laplace	Gaussian	GD	Φz	Olshausen and Field [54] Rozell et al. [39]

A.10 Variational free energy minimization unifies machine learning and neuroscience

Throughout this extended background, we reviewed how variational free energy (\mathcal{F}) minimization serves as a unifying theoretical framework that connects seemingly disparate approaches across machine learning and theoretical neuroscience. This synthesis reveals that models as diverse as variational autoencoders (VAEs), predictive coding, and sparse coding can all be derived from the same fundamental principle of \mathcal{F} minimization, differing only in their specific prescriptive choices.

Our synthesis emphasizes two critical dimensions of choice that determine a model’s characteristics:

1. Distributional choices: The selection of three distributions

- *approximate posterior* : $q_{\lambda}(z|x)$,
- *prior* : $p_{\theta}(z)$,
- *likelihood* : $p_{\theta}(x|z)$.

2. Inference optimization strategy: The decision between

- *amortized inference*: training a neural network to compute posterior parameters in a single forward pass, versus
- *iterative inference*: optimizing parameters through iterative (e.g., gradient-based) refinement.

These choices define a rich taxonomy of models, illustrated in Fig. 2. For example, combining amortized inference with factorized Gaussian distributions yields the standard VAE (G-VAE; [18]). Replacing the Gaussian prior and posterior with Poisson distributions leads to the Poisson VAE (P-VAE; [50]).

On the neuroscience side, models based on iterative inference with Dirac-delta posteriors and Gaussian likelihoods give rise to predictive coding [22] and sparse coding [54]. Predictive coding typically assumes a Gaussian prior, while sparse coding often uses a Laplace prior to encourage sparsity (Fig. 2). See Friston [23] and Millidge et al. [33] for derivations of predictive coding as variational inference, and Olshausen [55] and Chapter 10 of Dayan and Abbott [56] for sparse coding.

Overall, this systematic mapping clarifies how models originally developed in separate domains and described with different terminology can be understood through a common theoretical lens.

Building on this synthesis, our contribution is introducing the FOND framework (*Free energy Online Natural-gradient Dynamics*), which derives brain-like inference dynamics as natural gradient descent on free energy with specific distributional and structural assumptions. Unlike post-hoc theoretical interpretations, FOND starts with principles and derives algorithms in a top-down manner. We apply FOND to derive a new family of iterative VAE architectures: the iterative Poisson VAE ($i\mathcal{P}$ -VAE), the iterative Gaussian VAE ($i\mathcal{G}$ -VAE), and the iterative Gaussian-relu VAE ($i\mathcal{G}_{\text{relu}}$ -VAE).

These models exemplify FOND’s prescriptive power, while combining the strengths of two theoretical traditions: the probabilistic foundation of machine learning and the recurrent, adaptive processing characteristic of neuroscience models. By making our prescriptive choices explicit and theoretically grounded, FOND provides not just a synthesis of existing approaches, but a principled framework for developing new algorithms that address limitations in both fields. See Table 1 for a summary of models considered in this work.

B Extended Theory: Motivations, Derivations, and Discussions

In this appendix, we present additional motivations for our modeling choices, detailed derivations, and occasional commentary on key outcomes, complementing the theoretical exposition in the main paper (sections 3 and 4).

We begin by clarifying what we mean by “prescriptive” using an analogy from fundamental physics. We then motivate the Poisson assumptions, which led us to the $i\mathcal{P}$ -VAE architecture. In the remainder of this appendix, we further develop the theoretical foundations and present generalizations of our framework beyond what is covered in the main paper, along with interpretive insights that clarify its connection to principles of neural computation.

B.1 What do we mean by “prescriptive”?

In physics, prescriptive theories derive dynamics from first principles rather than hand-tuning to fit data. Notably, the *Principle of Least Action* [61] states that physical systems follow trajectories minimizing the *Action* (time integral of the Lagrangian). However, this principle alone is insufficient without addressing two fundamental questions:

Deriving dynamics from first principles

(Q1) Dynamical Objects: What are the mathematical objects of interest which exhibit the dynamics we seek to understand?

(Q2) Dynamical Equations: What differential equations govern these objects’ time evolution?

For instance, effective field theory [62] addresses these questions most elegantly, where symmetry principles alone resolve both questions (e.g, see Chapter 17 in Schwichtenberg [63]). Thus, in prescriptive theories, the arrow goes from *principles* \rightarrow *dynamics*, and not the other way around.

While the elegant derivations of physics (where everything follows from symmetry alone [64]) may not be fully achievable in the messy world of NeuroAI, we can still apply this prescriptive philosophy.

In this work, we follow the same arrow—from *principles to dynamics*—to derive brain-like inference dynamics from first principles. Specifically: (1) we choose real-valued neural membrane potentials as our dynamical objects (Fig. 1a). This is because membrane potentials are the source of information processing in the brain and they directly generate spiking activity [70, 84], which in turn causally drive perception and behavior [192], and (2) we derive inference dynamics as natural gradient descent on variational free energy with Poisson assumptions in an online inference setting (Fig. 1b, FOND).

B.2 Why Poisson?

To fully specify the variational free energy objective, one must make concrete decisions about distributional assumptions. Our choice of Poisson distributions for both the approximate posterior and prior is motivated by both theoretical principles and empirical observations from neuroscience.

From a theoretical perspective, Poisson is a natural choice for neural coding because spike counts are, by definition, discrete, non-negative integers. When implementing variational inference, distributional choices should reflect the natural constraints of the variables being modeled, and the Poisson distribution inherently respects these constraints for neural spike counts.

Empirically, the Poisson assumption aligns with extensive neurophysiological observations. Neurons exhibit variable responses across repeated presentations of identical stimuli, with spike-count variance proportional to the mean [51–53]. For brief time windows, this proportionality approaches unity [193–195], approximately matching Poisson statistics. While longer windows and higher cortical areas often show super-Poisson variability, this can be attributed to modulation of an underlying inhomogeneous Poisson process [180].

In other words, neurons can be modeled as conditionally Poisson, even if not marginally so [196].

The apparent precision observed in certain neuronal responses [197] is not inconsistent with Poisson processes. Modern models demonstrate that inhomogeneous Poisson rate codes can capture precise spike timing [198], and the high-precision examples often cited against rate coding are effectively captured by Poisson-process Generalized Linear Models [199].

Overall, the Poisson assumption offers mathematical convenience, and it is not too biologically implausible. Neurons are not literally Poisson in all contexts, but this distributional choice provides a reasonable approximation that respects the discrete nature of spike counts while capturing key statistical properties of neural activity. By grounding our theory in these biologically realistic assumptions, we derive dynamics that naturally reproduce important features of cortical computation.

B.3 Poisson Kullback–Leibler (KL) divergence

We provide a closed-form derivation of the KL divergence between two Poisson distributions. Recall that the Poisson distribution for a single spike count variable z , with rate $r \in \mathbb{R}_{>0}$, is given by:

$$\mathcal{Pois}(z; r) = \frac{r^z}{z!} e^{-r}. \quad (17)$$

Now suppose $p = \mathcal{Pois}(z; r_0)$ is the prior distribution for this single neuron, and $q = \mathcal{Pois}(z; r)$ is the approximate posterior. The KL divergence is given by:

$$\begin{aligned} \mathcal{D}_{\text{KL}}(q \parallel p) &= \mathbb{E}_{z \sim q} \left[\log \frac{q}{p} \right] \\ &= \mathbb{E}_{z \sim q} \left[\log \frac{r^z e^{-r} / z!}{r_0^z e^{-r_0} / z!} \right] \\ &= \mathbb{E}_{z \sim q} \left[\log \left(\left(\frac{r}{r_0} \right)^z e^{-(r-r_0)} \right) \right] \\ &= \mathbb{E}_{z \sim q} \left[z \log \left(\frac{r}{r_0} \right) - (r - r_0) \right] \\ &= \mathbb{E}_{z \sim q} \left[z \log \left(\frac{r}{r_0} \right) \right] - r + r_0 \\ &= r \log \left(\frac{r}{r_0} \right) - r + r_0 \\ &= r_0 + r \left(\log \left(\frac{r}{r_0} \right) - 1 \right). \end{aligned} \quad (18)$$

We now express the final result in terms of the membrane potentials, $u := \log r$, to get:

$$\mathcal{D}_{\text{KL}}\left(\text{Pois}(z; \exp(u)) \parallel \text{Pois}(z; \exp(u_0))\right) = e^{u_0} + e^u (u - u_0 - 1). \quad (19)$$

This concludes our derivation of KL divergence for a single Poisson variable. It's easy to see how this result would generalize to K latents, which is what we show in eq. (2).

B.4 Fisher information matrix

To derive inference dynamics as natural gradient descent on free energy, we must account for the geometry of distributional parameter space. The Fisher information matrix defines this geometry by acting as a Riemannian metric over the space of probability distributions, measuring how sensitively a distribution changes with its parameters.

When small parameter changes produce large shifts in the distribution, the Fisher information is high, meaning those parameters are farther apart in distribution space. Natural gradient descent leverages this structure, adjusting updates to reflect the true curvature of the space; whereas, standard gradient descent implicitly assumes a flat, Euclidean geometry. These geometry-aware updates lead to more efficient and stable optimization, especially in ill-conditioned settings [35, 57, 76, 200].

In what follows, we formalize this idea and derive explicit Fisher information matrices for Poisson and Gaussian distributions.

B.4.1 Fisher information matrix as a second-order approximation of the KL divergence

To derive the Fisher information matrix, we begin with a local approximation of the KL divergence between two nearby distributions. Consider a distribution $p_{\lambda}(x)$ parameterized by λ , and the same distribution with slightly perturbed parameters, $p_{\lambda+\Delta\lambda}(x)$. The KL divergence between these distributions can be expanded using a second-order Taylor approximation:

$$\begin{aligned} \mathcal{D}_{\text{KL}}(p_{\lambda} \parallel p_{\lambda+\Delta\lambda}) &= \int p_{\lambda}(x) \log \frac{p_{\lambda}(x)}{p_{\lambda+\Delta\lambda}(x)} dx \\ &\approx \frac{1}{2} \Delta\lambda^T \mathbf{G}(\lambda) \Delta\lambda + \mathcal{O}(\|\Delta\lambda\|^3), \end{aligned} \quad (20)$$

where $\mathbf{G}(\lambda)$ is the Fisher information matrix defined as:

$$\mathbf{G}(\lambda) = \mathbb{E}_{x \sim p_{\lambda}(x)} \left[\nabla_{\lambda} \log p_{\lambda}(x) \nabla_{\lambda} \log p_{\lambda}(x)^T \right] \quad (21)$$

This matrix appears as the Hessian in the second-order approximation of the KL divergence, revealing its role as the natural metric for measuring distances between nearby probability distributions.

From this perspective, natural gradient descent updates take the form:

$$\lambda_{t+1} = \lambda_t - \eta \mathbf{G}^{-1}(\lambda_t) \nabla_{\lambda} \mathcal{L}(\lambda_t) \quad (22)$$

where $\mathcal{L}(\lambda)$ is the loss function (in our case, variational free energy), and η is the learning rate. By incorporating the inverse Fisher information matrix, the update accounts for the curvature of distribution space, leading to more effective optimization.

B.4.2 Poisson Fisher information matrix

In this paper, we considered the canonical parameterization of the Poisson distribution in terms of log rate, $u := \log r$, interpreted as membrane potentials. We now derive the Fisher information matrix for a single Poisson variable in this log rate parameterization, where the probability mass function is:

$$\text{Pois}(z; e^u) = \frac{e^{uz}}{z!} e^{-e^u} \quad (23)$$

The log-likelihood as a function of u is:

$$\log \text{Pois}(z; e^u) = uz - e^u - \log z! \quad (24)$$

Taking the derivative with respect to u :

$$\frac{\partial}{\partial u} \log \mathcal{Pois}(z; e^u) = z - e^u \quad (25)$$

Plug this expression in eq. (21) to get:

$$\begin{aligned} \mathbf{G}(u) &= \mathbb{E}_{z \sim \mathcal{Pois}(z; e^u)} \left[\left(\frac{\partial}{\partial u} \log \mathcal{Pois}(z; e^u) \right)^2 \right] \\ &= \mathbb{E}_{z \sim \mathcal{Pois}(z; e^u)} \left[(z - e^u)^2 \right] \\ &= \mathbb{E}_{z \sim \mathcal{Pois}(z; e^u)} \left[z^2 - 2ze^u + e^{2u} \right] \\ &= \mathbb{E}_{z \sim \mathcal{Pois}(z; e^u)} \left[z^2 \right] - 2e^u \mathbb{E}_{z \sim \mathcal{Pois}(z; e^u)} [z] + e^{2u}. \end{aligned} \quad (26)$$

For a Poisson distribution with rate e^u , we know $\mathbb{E}[z] = e^u$ and $\text{Var}[z] = e^u$, which means $\mathbb{E}[z^2] = \text{Var}[z] + \mathbb{E}[z]^2 = e^u + e^{2u}$. Substituting, we get:

$$\begin{aligned} \mathbf{G}(u) &= (e^u + e^{2u}) - 2e^u \cdot e^u + e^{2u} \\ &= e^u + e^{2u} - 2e^{2u} + e^{2u} \\ &= e^u. \end{aligned} \quad (27)$$

The final result reveals a remarkably simple form for the Fisher information matrix in the membrane potential parameterization:

Poisson: $\mathbf{G}(u) = e^u$

(28)

For the multivariate case with independent Poisson components, the Fisher information matrix becomes diagonal with entries $\mathbf{G}_{ii}(\mathbf{u}) = e^{u_i}$, or in vector notation, $\mathbf{G}(\mathbf{u}) = \text{diag}(e^{\mathbf{u}})$.

The natural gradient update for the membrane potentials thus takes the form:

$$\dot{\mathbf{u}} = -\mathbf{G}^{-1}(\mathbf{u}) \nabla_{\mathbf{u}} \mathcal{F} = -e^{-\mathbf{u}} \odot \nabla_{\mathbf{u}} \mathcal{F}. \quad (29)$$

This derivation leads directly to the dynamic equations shown in eq. (6), providing a principled foundation for our spiking neural inference model.

B.4.3 Gaussian Fisher information matrix

For the Gaussian distribution, we define the log standard deviation, $\xi := \log \sigma$, and derive the Fisher information matrix using the (μ, ξ) parameterization. The probability density function is:

$$\mathcal{N}(x; \mu, e^{2\xi}) = \frac{1}{\sqrt{2\pi}e^{2\xi}} \exp\left(-\frac{(x - \mu)^2}{2e^{2\xi}}\right) \quad (30)$$

And the log-likelihood is:

$$\log \mathcal{N}(x; \mu, e^{2\xi}) = -\frac{1}{2} \log(2\pi) - \xi - \frac{(x - \mu)^2}{2e^{2\xi}} \quad (31)$$

We compute the partial derivatives with respect to the parameters:

$$\begin{aligned} \frac{\partial}{\partial \mu} \log \mathcal{N}(x; \mu, e^{2\xi}) &= \frac{x - \mu}{e^{2\xi}}, \\ \frac{\partial}{\partial \xi} \log \mathcal{N}(x; \mu, e^{2\xi}) &= -1 + \left(\frac{x - \mu}{e^\xi} \right)^2. \end{aligned} \quad (32)$$

The Fisher information matrix components are:

$$\begin{aligned}
\mathbf{G}_{\mu\mu} &= \mathbb{E}_{x \sim \mathcal{N}(x; \mu, e^{2\xi})} \left[\left(\frac{\partial}{\partial \mu} \log \mathcal{N}(x; \mu, e^{2\xi}) \right)^2 \right] \\
&= \mathbb{E}_{x \sim \mathcal{N}(x; \mu, e^{2\xi})} \left[\frac{(x - \mu)^2}{e^{4\xi}} \right] \\
&= \frac{1}{e^{4\xi}} \mathbb{E}_{x \sim \mathcal{N}(x; \mu, e^{2\xi})} [(x - \mu)^2] \\
&= \frac{1}{e^{4\xi}} \cdot e^{2\xi} \\
&= e^{-2\xi}.
\end{aligned} \tag{33}$$

And for the ξ component:

$$\begin{aligned}
\mathbf{G}_{\xi\xi} &= \mathbb{E}_{x \sim \mathcal{N}(x; \mu, e^{2\xi})} \left[\left(\frac{\partial}{\partial \xi} \log \mathcal{N}(x; \mu, e^{2\xi}) \right)^2 \right] \\
&= \mathbb{E}_{x \sim \mathcal{N}(x; \mu, e^{2\xi})} \left[\left(-1 + \left(\frac{x - \mu}{e^\xi} \right)^2 \right)^2 \right] \\
&= \mathbb{E}_{x \sim \mathcal{N}(x; \mu, e^{2\xi})} \left[1 - 2 \left(\frac{x - \mu}{e^\xi} \right)^2 + \left(\frac{x - \mu}{e^\xi} \right)^4 \right].
\end{aligned} \tag{34}$$

For a Gaussian, we have $\mathbb{E}[(x - \mu)^2] = e^{2\xi}$ and $\mathbb{E}[(x - \mu)^4] = 3e^{4\xi}$. After expansion and computing the expectations, we get the final result:

$$\mathbf{G}_{\xi\xi} = 2. \tag{35}$$

Remarkably, when using the log standard deviation parameterization, the corresponding Fisher information metric becomes constant.

Finally, for the cross-terms we have:

$$\begin{aligned}
\mathbf{G}_{\mu\xi} &= \mathbb{E}_{x \sim \mathcal{N}(x; \mu, e^{2\xi})} \left[\frac{\partial}{\partial \mu} \log \mathcal{N}(x; \mu, e^{2\xi}) \cdot \frac{\partial}{\partial \xi} \log \mathcal{N}(x; \mu, e^{2\xi}) \right] \\
&= \mathbb{E}_{x \sim \mathcal{N}(x; \mu, e^{2\xi})} \left[\frac{x - \mu}{e^{2\xi}} \cdot \left(-1 + \left(\frac{x - \mu}{e^\xi} \right)^2 \right) \right].
\end{aligned} \tag{36}$$

Since $\mathbb{E}[x - \mu] = \mathbb{E}[(x - \mu)^3] = 0$ for a Gaussian, this cross-term vanishes:

$$\mathbf{G}_{\mu\xi} = 0. \tag{37}$$

Therefore, the Fisher information matrix for a univariate Gaussian with (μ, ξ) parameterization is:

Gaussian: $\mathbf{G}(\mu, \xi) = \begin{pmatrix} e^{-2\xi} & 0 \\ 0 & 2 \end{pmatrix} = \begin{pmatrix} \frac{1}{\sigma^2} & 0 \\ 0 & 2 \end{pmatrix}$

(38)

For the multivariate case with a diagonal covariance matrix, the Fisher information becomes block-diagonal with entries corresponding to each dimension's parameters. This structure leads to separate natural gradient updates for means and log standard deviations.

Equation (38) shows that natural gradient descent in Gaussian parameter space involves scaling the mean gradients by the variance, while the log standard deviation updates require a simple constant scaling factor. In appendix B.7, we will use this result to derive the inference dynamics for the case of Gaussian posterior distributions.

B.5 Interpreting the terms in Poisson dynamics equations

In this section, we interpret each term in the neural dynamics, eq. (6). We explain their biological significance and draw connections to canonical models in computational neuroscience.

B.5.1 Feedforward drive

The first term, $\Phi^T \mathbf{x}$, represents the feedforward excitatory input to neurons (i.e., “feedforward drive”). It projects the incoming stimulus \mathbf{x} into the linear subspace spanned by each neuron’s receptive field (the columns of Φ). This operation loosely corresponds to the selective tuning of synaptic weights, with each neuron responding strongly to stimuli matching its preferred feature. In sensory cortices, for example, this feedforward drive could correspond to thalamocortical projections that relay sensory information to cortical neurons [201, 202].

B.5.2 Recurrent explaining away

The second term, $\Phi^T \Phi \mathbf{z}(\mathbf{u})$, with spikes sampled from the posterior $\mathbf{z}(\mathbf{u}) \sim q_{\mathbf{u}}(\mathbf{z}|\mathbf{x})$, captures recurrent interactions within the neural population. Crucially, this interaction occurs through spiking activity $\mathbf{z}(\mathbf{u})$, not membrane potentials, thereby preserving the biological principle that neurons communicate via discrete spikes rather than continuous voltages [82, 84].

The recurrent connectivity matrix, $\Phi^T \Phi$, allows lateral interactions among latent dimensions. This is known as “explaining away” in probabilistic inference contexts [7]; or as “lateral competition” or “lateral inhibition” in neural circuit models [81, 86, 203–207].

Two distinct suppressive mechanisms emerge: (1) self-suppression via diagonal terms ($[\Phi^T \Phi]_{ii} > 0$), where neurons with high activity suppress their own future responses, acting as a form of spike-frequency adaptation [208]; and (2) lateral inhibition through off-diagonal terms ($[\Phi^T \Phi]_{ij} \neq 0$), where neurons with similar feature preferences compete [85–87]. While most interactions are inhibitory when features are positively correlated ($[\Phi^T \Phi]_{ij} > 0$), excitatory effects can also arise when features are anti-correlated ($[\Phi^T \Phi]_{ij} < 0$).

B.5.3 Homeostatic leak

The final term, $\beta(\mathbf{u} - \mathbf{u}_0)$, effectively functions as a homeostatic “leak” that pulls membrane potentials back toward their prior values. This establishes a direct formal connection between a fundamental biophysical property of neurons—their leaky integrator dynamics [81]—and the Kullback-Leibler divergence in variational inference, which measures the *relative information* [209] between posterior and prior distributions.

From a biological perspective, this leak term reflects passive membrane properties that restore neural excitability to baseline in the absence of input, preventing hyperactivity and ensuring metabolic efficiency [210]. From an information-theoretic standpoint, it implements a regularization pressure that penalizes deviations from the prior, balancing the reconstruction objective against representational complexity [77, 78].

The strength of our framework lies in unifying these perspectives: the biophysical constraint of “*don’t deviate too much from your baseline state*” aligns nicely with the information-theoretic principle that “*encoding more stimulus-specific information incurs a coding cost*.” This duality offers a principled explanation for why neural systems operate in sparse regimes: they naturally minimize free energy by balancing reconstruction fidelity against metabolic constraints [50].

Overall, the derived iP-VAE dynamics, eq. (6), reveals how neural circuits can implement Bayesian inference through local computations and spiking communication, in a way that mimics established principles of neural physiology. The emergence of these biologically plausible mechanisms directly from variational principles suggests that evolution may have indeed optimized neural systems to perform approximate Bayesian inference [6, 74, 148].

B.6 Extension to nonlinear decoders

In the main derivation (section 4), we made two simplifying assumptions to enhance clarity: (1) we assumed a linear decoder, and (2) we ignored the variance of the decoder. In this section, we relax these assumptions and provide a full derivation that reduces to those in the main text.

Throughout this work, we assume a Gaussian likelihood function for all models considered. The mean is produced by a decoder neural network, $\mu(\mathbf{z}) = \text{dec}(\mathbf{z}; \theta) \equiv f_\theta(\mathbf{z})$, with parameters θ . For the main derivation, we assumed a unit covariance. But in fact, in the code we have a set of global learnable parameters, σ^2 , that we learn end-to-end alongside other parameters [69]. Given these assumptions, the likelihood is given by:

$$p_\theta(\mathbf{x}|\mathbf{z}) = \mathcal{N}(\mathbf{x}; f_\theta(\mathbf{z}), \sigma^2).$$

And the negative log-likelihood is:

$$-\log p_\theta(\mathbf{x}|\mathbf{z}) = \frac{1}{2} \left\| \frac{\mathbf{x} - f_\theta(\mathbf{z})}{\sigma} \right\|^2 + \dots,$$

where the dots represent terms that are going to vanish after differentiating with respect to the variational parameters, so we didn't bother writing them out.

Similar to the main text, we approximate the reconstruction term using a single Monte Carlo sample:

$$\mathcal{L}_{\text{recon.}}(\mathbf{x}; \theta, \lambda) \approx \frac{1}{2} \left\| \frac{\mathbf{x} - f_\theta(\mathbf{z}); \theta}{\sigma} \right\|^2,$$

where $\mathbf{z}(\lambda) \sim q_\lambda(\mathbf{z}|\mathbf{x})$. We see that to compute the gradient of the reconstruction term, we only need to compute the gradient of the sample and simply use chain rule $\partial/\partial \lambda_i = (\partial z_i / \partial \lambda_i) (\partial / \partial z_i)$:

$$\frac{\partial}{\partial \lambda_i} \mathcal{L}_{\text{recon.}}(\mathbf{x}; \theta, \lambda) = -\frac{\partial z_i}{\partial \lambda_i} \sum_{j=1}^M [\mathbf{J}_\theta]_{ij} \frac{x_j - [f_\theta]_j}{\sigma_j},$$

where we defined the decoder Jacobian as follows:

$$[\mathbf{J}_\theta(\mathbf{z})]_{ij} := \frac{\partial}{\partial z_i} [f_\theta(\mathbf{z})]_j. \quad (39)$$

In matrix form, the gradient of the reconstruction term reads:

$$\nabla_\lambda \mathcal{L}_{\text{recon.}}(\mathbf{x}; \theta, \lambda) = -\frac{\partial \mathbf{z}}{\partial \lambda} \odot \left(\mathbf{J}_\theta(\mathbf{z}) \left[\frac{\mathbf{x} - f_\theta(\mathbf{z})}{\sigma^2} \right] \right), \quad (40)$$

where $\partial \mathbf{z} / \partial \lambda$ is a vector of length K , the decoder Jacobian \mathbf{J}_θ is a $K \times M$ matrix, the expression inside the bracket is a vector of length M , and \odot is the Hadamard (element-wise) product. During inference, we evaluate eq. (40) at the particular sample drawn from the posterior, $\mathbf{z} = \mathbf{z}(\lambda)$.

This concludes our extension of the results to the case of nonlinear decoders with a learned global variance. If the decoder is a neural network with relu activations, then the Jacobian can be interpreted as a dynamic feedforward receptive field. In the case of a linear decoder, $f_\theta(\mathbf{z}) = \Phi \mathbf{z}$, we get a fixed Jacobian: $\mathbf{J}_\theta = \Phi^T$, producing the main paper result: $\nabla_\lambda \mathcal{L}_{\text{recon.}} \propto -(\Phi^T \mathbf{x} - \Phi^T \Phi \mathbf{z})$.

Finally, compare Fig. 5 and Fig. 6 for a ResNet-style view of the unrolled encoding algorithms, contrasting linear and nonlinear decoders.

B.7 Extension to Gaussian posteriors

In the main text, we derived dynamics for the case of Poisson latent variables, resulting in the spiking inference dynamics shown in eq. (6). This led to the corresponding iterative Poisson VAE (iP-VAE) architecture.

Here, we extend these results to Gaussian latents, with an optional nonlinearity, $\varphi(\cdot)$, applied after sampling, corresponding to the iG-VAE and iG $_\varphi$ -VAE architectures, respectively.

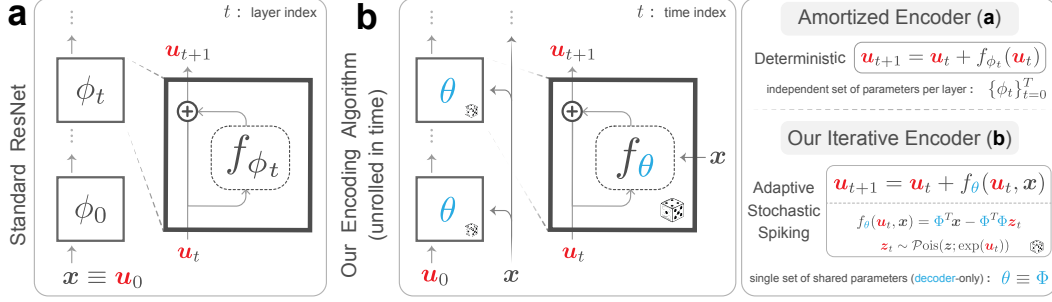


Figure 5: Comparison between standard deep residual neural networks (ResNet; [211]) and our inference algorithm. **(a)** Standard ResNets process information through a series of deterministic layers, each with independent parameters ϕ_t , where t is the layer index. **(b)** The iP-VAE encoding algorithm (eq. (7)) unrolled in time resembles a ResNet with shared parameters, but incorporates adaptive, stochastic, and spiking dynamics. This recurrent architecture is conceptually similar to *Looped Transformers* [212–214], which use “input injection”—conditioning on the input x at each step—as an effective heuristic to improve stability and performance. In our framework, this mechanism is not a heuristic choice, but emerges directly from the first principles of online variational inference. Finally, unlike conventional networks [95], the iP-VAE uses only decoder parameters θ , enabling online Bayesian inference through iterative sampling and recurrent updates conditioned on both current state u_t and input x . This figure illustrates the linear decoder implementation used in the main paper. For the general nonlinear decoder case, see Fig. 6.

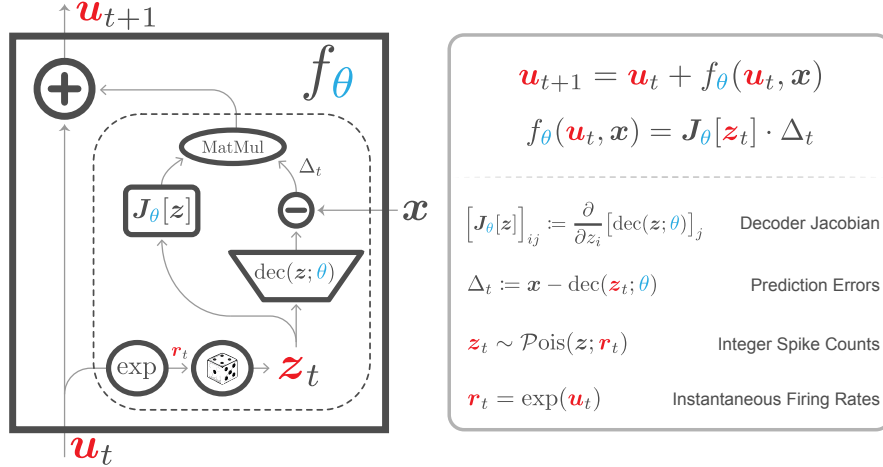


Figure 6: Detailed view of the iP-VAE iterative inference algorithm with a nonlinear decoder. The left panel illustrates the computational flow: membrane potentials (u_t) are transformed into firing rates (r_t) through an exponential nonlinearity, then sampled to produce integer spike counts (z_t). These spikes are passed through a decoder to generate predictions, with errors propagated back through the decoder Jacobian. The right panel shows the corresponding mathematical formulation derived in appendix B.6. For the simpler case of linear decoders used in the main paper, see Fig. 5.

Let’s revisit the prescriptive choices needed for deriving dynamics from first principles (appendix B.1). For the Gaussian case, we select the mean, μ , and log standard deviation, $\xi := \log \sigma$, as our dynamical variables. This parameterization avoids constrained optimization that would be necessary with σ directly, since σ must remain strictly positive while ξ can take any real value. Additionally, as shown in appendix B.4.3, the log standard deviation parameterization yields a constant Fisher scaling, which simplifies our derivations.

Next, we derive Gaussian inference dynamics from natural gradient on free energy. Since we use Gaussian likelihoods across all models in this paper, we’ve already addressed this component in the main text for linear decoders (eq. (4)) and extended it to general nonlinear decoders in the appendix (eq. (40)). We now need to derive the KL component.

B.7.1 Gaussian KL divergence

Suppose the posterior and prior parameters for a single latent variable are given by (μ, σ^2) and (μ_0, σ_0^2) , respectively. The Gaussian KL term reads:

$$\mathcal{D}_{\text{KL}}(q_{\mu, \sigma^2}(z|x) \| p_{\mu_0, \sigma_0^2}(z)) = \frac{1}{2} \left[\left(\frac{\mu - \mu_0}{\sigma_0} \right)^2 + \left(\frac{\sigma}{\sigma_0} \right)^2 - \log \left(\frac{\sigma}{\sigma_0} \right)^2 - 1 \right].$$

With our log standard deviation parameterization, $\xi = \log \sigma$, this becomes:

$$\mathcal{D}_{\text{KL}}(q_{\mu, \xi}(z|x) \| p_{\mu_0, \xi_0}(z)) = \frac{1}{2} \left[\left(\frac{\mu - \mu_0}{e^{\xi_0}} \right)^2 + e^{2(\xi - \xi_0)} - 2(\xi - \xi_0) - 1 \right].$$

B.7.2 Gradient of the Gaussian KL term

For the general factorized K -variate Gaussian, we compute derivatives with respect to the variational parameters to find:

$$\begin{aligned} \nabla_{\mu} \mathcal{D}_{\text{KL}}(q \| p) &= \frac{\mu - \mu_0}{e^{2\xi_0}}, \\ \nabla_{\xi} \mathcal{D}_{\text{KL}}(q \| p) &= e^{2(\xi - \xi_0)} - 1. \end{aligned} \quad (41)$$

The next step is to estimate the reconstruction gradient from eq. (40). This requires computing the partial derivative of the sample with respect to each parameter. Using the Gaussian reparameterization trick [20], we have:

$$z = \mu + \exp(\xi) \odot \epsilon, \quad (42)$$

with $\epsilon \sim \mathcal{N}(\mathbf{0}, \mathbf{1})$. Therefore, the sample derivatives are:

$$\frac{\partial z}{\partial \mu} = 1, \quad \frac{\partial z}{\partial \xi} = \exp(\xi) \odot \epsilon. \quad (43)$$

B.7.3 The Gaussian inference dynamics

Following our prescriptive approach:

$$\begin{aligned} \dot{\lambda} &= -\mathbf{G}^{-1}(\lambda) \nabla_{\lambda} \mathcal{F} \\ &= -\mathbf{G}^{-1}(\lambda) [\nabla_{\lambda} \mathcal{L}_{\text{recon.}} + \beta \nabla_{\lambda} \mathcal{L}_{\text{KL}}]. \end{aligned} \quad (44)$$

Combining eqs. (38), (40), (41), (43) and (44) yields the final dynamics for the Gaussian case:

$$\begin{aligned} \dot{\mu} &= e^{2\xi} \odot \left(\mathbf{J}_{\theta}(z) \left[\frac{\mathbf{x} - f_{\theta}(z)}{\sigma^2} \right] \right) - \beta e^{2(\xi - \xi_0)} \odot (\mu - \mu_0) \\ \dot{\xi} &= \frac{1}{2} e^{\xi} \odot \epsilon \odot \left(\mathbf{J}_{\theta}(z) \left[\frac{\mathbf{x} - f_{\theta}(z)}{\sigma^2} \right] \right) - \frac{1}{2} \beta \left(e^{2(\xi - \xi_0)} - 1 \right) \end{aligned} \quad (45)$$

Remember that we had $z = \mu + \exp(\xi) \odot \epsilon$, and $\epsilon \sim \mathcal{N}(\mathbf{0}, \mathbf{1})$.

This completes our derivation of the full Gaussian inference dynamics. Next, we examine how this general equation simplifies for linear decoders and when applying nonlinearities after sampling.

B.7.4 The iterative Gaussian VAE (iG-VAE)

In the main paper, we focus on linear decoders, defining the iterative Gaussian VAE (iG-VAE) model. For a linear decoder, we have $f_{\theta}(z) = \Phi z$ and $\mathbf{J}_{\theta} = \Phi^T$. Substituting these into eq. (45) gives us the iG-VAE dynamics:

$$\begin{aligned} \dot{\mu} &= e^{2\xi} \odot \left[\frac{\Phi^T \mathbf{x} - \Phi^T \Phi z}{\sigma^2} \right] - \beta e^{2(\xi - \xi_0)} \odot (\mu - \mu_0), \\ \dot{\xi} &= \frac{1}{2} e^{\xi} \odot \epsilon \odot \left[\frac{\Phi^T \mathbf{x} - \Phi^T \Phi z}{\sigma^2} \right] - \frac{1}{2} \beta \left(e^{2(\xi - \xi_0)} - 1 \right). \end{aligned} \quad (46)$$

B.7.5 The iterative Gaussian- φ VAE (i \mathcal{G}_φ -VAE)

We can further extend our framework by applying a nonlinearity, $\varphi(\cdot)$, immediately after sampling:

$$\tilde{z} := \varphi(z) = \varphi(\mu + \exp(\xi) \odot \epsilon). \quad (47)$$

This modification affects the dynamics equations in two ways. First, we decode from $\tilde{z} = \varphi(z)$ rather than z directly: $f_\theta(z) \rightarrow f_\theta(\varphi(z))$. In the linear decoder case, this simplifies to: $\Phi z \rightarrow \Phi \varphi(z)$ (see Table 1). Second, we now have to apply the element-wise product of the derivative of the nonlinearity, evaluated at the sample point. This stems from the sample derivative term from eq. (40).

With these two changes applied, the i \mathcal{G}_φ -VAE dynamics becomes:

$$\begin{aligned} \dot{\mu} &= e^{2\xi} \odot \varphi'(z) \odot \left(J_\theta(\varphi(z)) \left[\frac{x - f_\theta(\varphi(z))}{\sigma^2} \right] \right) - \beta e^{2(\xi - \xi_0)} \odot (\mu - \mu_0), \\ \dot{\xi} &= \frac{1}{2} e^\xi \odot \epsilon \odot \varphi'(z) \odot \left(J_\theta(\varphi(z)) \left[\frac{x - f_\theta(\varphi(z))}{\sigma^2} \right] \right) - \frac{1}{2} \beta (e^{2(\xi - \xi_0)} - 1). \end{aligned} \quad (48)$$

This approach provides a general recipe that works with any differentiable function. In this paper, we specifically use $\varphi(\cdot) = \text{relu}(\cdot)$ for two key reasons. First, Whittington et al. [89] demonstrated that applying relu to amortized Gaussian VAEs, combined with activity penalties, produces disentangled representations that can even outperform beta-VAEs [78]. Second, Bricken et al. [215] showed that combining a relu activation with noisy inputs is sufficient to approximate sparse coding.

In our implementation, we use the exact derivative of the relu function:

$$\text{relu}'(z) = \Theta(z),$$

where $\Theta(\cdot)$ is the Heaviside step function.

Finally, the i $\mathcal{G}_{\text{relu}}$ -VAE dynamics under a linear decoder are given by:

$$\begin{aligned} \dot{\mu} &= e^{2\xi} \odot \Theta(z) \odot \left[\frac{\Phi^T x - \Phi^T \Phi \text{relu}(z)}{\sigma^2} \right] - \beta e^{2(\xi - \xi_0)} \odot (\mu - \mu_0), \\ \dot{\xi} &= \frac{1}{2} e^\xi \odot \epsilon \odot \Theta(z) \odot \left[\frac{\Phi^T x - \Phi^T \Phi \text{relu}(z)}{\sigma^2} \right] - \frac{1}{2} \beta (e^{2(\xi - \xi_0)} - 1). \end{aligned} \quad (49)$$

B.8 Biological interpretation of the standard predictive coding dynamics

Due to Gaussian assumptions, the predictive coding inference dynamics (eq. (16), appendix A.9) reveal a rate model where the variables μ are real-valued and only loosely interpretable as neural activity. In contrast, biological neurons communicate through discrete spikes, not continuous values. One possible interpretation is that μ represents membrane potentials resulting from the summation of many stochastic synaptic inputs. By the central limit theorem, these could plausibly follow a Gaussian distribution.

Additionally, the dynamics include a recurrent term of the form $\Phi^T \Phi \mu$, which can be interpreted as each neuron being directly influenced by the membrane potentials of other neurons, which is unrealistic. Membrane potentials of real neurons are typically thought to be internal to each neuron and not accessible to others. Communication between neurons occurs primarily through spikes [84]. One solution to this is to stay in the space of rate models, but apply a nonlinearity to map from the membrane potentials to rates. In canonical circuit models—starting with Amari [80] (1972), and developed further in biologically inspired frameworks [81–83]—it is standard to apply nonlinearities to neuronal activity before it influences other neurons, thereby maintaining biological plausibility.

While some predictive coding formulations incorporate nonlinearities, they typically apply them after the decoder weights [33]: $\Phi \mu \rightarrow \varphi(\Phi \mu)$. This yields recurrent terms like $\Phi^T \varphi(\Phi \mu)$, which are still at odds with principles of local computation and communication. A more biologically plausible formulation would instead apply nonlinearities before lateral communication: $\Phi^T \Phi \varphi(\mu)$.

Our framework addresses these limitations in two distinct ways. In the Poisson case, communication occurs through sampled spike counts, so each neuron only transmits spikes to its neighbors, preserving the privacy of membrane potentials (eq. (6)). In the Gaussian case, we apply a nonlinearity such as

relu after sampling from the posterior, allowing only rectified activity to propagate laterally (eq. (49)). Unlike predictive coding dynamics (eq. (16)), in both of these formulations, membrane potentials remain local to each neuron, in line with biological constraints.

B.9 Free energy for sequences

Consider a sequence of input data, $\{\mathbf{x}_t\}_{t=0}^T$, where $\mathbf{x}_t \in \mathbb{R}^M$ (e.g., frames of a video). For such sequential data, we must account for the temporal dependencies in our inference process. After observing the first t frames, we form a prior belief:

$$p_\theta(\mathbf{z}|\mathbf{x}_{<t}), \quad (50)$$

where $\mathbf{x}_{<t} = \{\mathbf{x}_0, \mathbf{x}_1, \dots, \mathbf{x}_{t-1}\}$ represents all previously observed frames. Upon receiving the next observation \mathbf{x}_t , we update our beliefs by computing the posterior distribution $q(\mathbf{z}_t|\mathbf{u})$.

This posterior update can be formulated through the minimization of a local-in-time free energy:

$$\mathcal{F}_t(\mathbf{u}) = \underbrace{\mathbb{E}_{\mathbf{z}_t \sim q(\mathbf{z}_t|\mathbf{u})} \left[-\log p_\theta(\mathbf{x}_t|\mathbf{z}) \right]}_{\text{reconstruction term}} + \underbrace{\mathcal{D}_{\text{KL}} \left(q(\mathbf{z}_t|\mathbf{u}) \parallel p_\theta(\mathbf{z}_t|\mathbf{x}_{<t}) \right)}_{\text{KL divergence from prior}}. \quad (51)$$

This formulation captures the essence of Bayesian belief updating: the posterior balances fidelity to the current observation (reconstruction term) against deviation from prior beliefs shaped by all the previous observations (KL term).

Applying natural gradient descent on this time-dependent free energy, we derive the general update equation for sequential inference:

$$\mathbf{u}_{t+1} = \mathbf{u}_t + \Phi^T \mathbf{x}_t - \Phi^T \Phi \mathbf{z}_t, \quad (52)$$

where $\mathbf{z}_t \sim q(\mathbf{z}_t|\mathbf{u}_t)$. This equation reflects a rolling update scheme in which the posterior at time t serves as the prior at time $t+1$. We examine this update rule in more detail in the next section.

For stationary sequences (i.e., repeated presentations of the same image, $\mathbf{x}_t \rightarrow \mathbf{x}$), this general update equation reduces to the simplified form presented in the main text (eq. (7)). In this paper, we focus exclusively on such stationary sequences, leaving richer non-stationary dynamics for future work. Future extensions could incorporate more sophisticated predictive dynamics beyond the simple rolling update scheme, potentially allowing the model to *anticipate* future frames rather than just adapt to current ones.

The overall free energy for the entire sequence is the sum of local-in-time free energies:

$$\mathcal{F} = \sum_{t=0}^T \mathcal{F}_t. \quad (53)$$

During model training (i.e., learning the generative model parameters θ), we perform iterative inference updates, computing \mathcal{F}_t at each time point while accumulating gradients. After processing the entire sequence, a single gradient update is then applied to θ to minimize the overall \mathcal{F} , similar to meta-learning approaches [191].

This sequential formulation reveals how our encoding algorithms can be interpreted as unrolled residual networks (ResNets), where each time step corresponds to a network layer with shared parameters (Figs. 5 and 6).

B.10 Static versus online inference

Traditional variational inference operates on static datasets, assuming samples are drawn independently from a fixed distribution. In sharp contrast, biological perception involves continuous belief updating from streaming observations. This fundamental difference motivates our preference for online inference approaches with an evolving prior.

This section contrasts static and online approaches to inference and their mathematical implications. A key distinction is that online inference features an evolving prior, as opposed to a fixed prior in

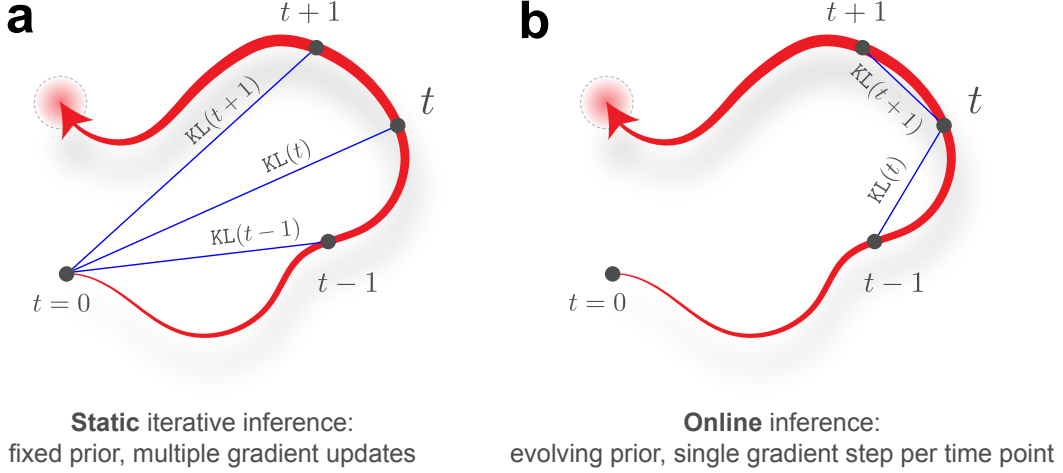


Figure 7: Comparison of static and online inference frameworks. **(a)** In static iterative inference, all posterior distributions (points along the red curve) are regularized toward a fixed prior at $t = 0$. Each blue line represents a KL divergence term computed relative to this same unchanging reference point. **(b)** In online inference, the prior evolves over time, with each posterior becoming the prior for the next time step. KL divergence is computed only between adjacent time points (consecutive points on the red curve), representing a rolling update scheme. This fundamentally different regularization structure leads to the vanishing KL term phenomenon when performing single gradient updates at each time step (e.g., compare eq. (6) with eq. (7)).

static inference. This evolving prior means the KL term (eq. (12)) is always computed relative to the previous time step (Fig. 7b). We show how this observation explains why a single gradient update in online settings naturally leads to dropping the KL contribution to free energy, providing intuition for why BONG [60] advocates using only the expected log-likelihood term in gradient updates.

In static inference (Fig. 7a), the time index t reflects gradient iterations, with each posterior being regularized toward the same fixed prior. As optimization progresses, the KL term consistently pulls the distribution back toward this initial prior point, preventing excessive drift regardless of how many iterations are performed.

In online inference (Fig. 7b), the time index represents sequential data points rather than optimization iterations. The crucial difference is that prior beliefs themselves get updated as new data arrives. When we follow the BONG approach [60] and perform a single gradient update per time step, we only compute the KL divergence between adjacent time points, rather than regularizing all the way back to an initial prior.

Why does the KL regularization term effectively vanish in our discrete-time online setting with single gradient updates? To understand this, we revisit the continuous differential equation from eq. (6):

$$\dot{\mathbf{u}} \propto \Phi^T \mathbf{x} - \Phi^T \Phi \mathbf{z}(\mathbf{u}) - \beta(\mathbf{u} - \mathbf{u}_0)$$

When we discretize this equation for a single update step, we get the following general update rule:

$$\mathbf{u}_{t+\delta t} = \mathbf{u}_{\text{init}} + \delta t [\Phi^T \mathbf{x} - \Phi^T \Phi \mathbf{z}(\mathbf{u}_{\text{init}}) - \beta(\mathbf{u}_{\text{init}} - \mathbf{u}_0)],$$

where δt is some small time interval. We choose to initialize at the prior from the previous time point, $\mathbf{u}_{\text{init}} \leftarrow \mathbf{u}_0$. Consequently, the third term, $\beta(\mathbf{u}_{\text{init}} - \mathbf{u}_0)$, vanishes for this first gradient step:

$$\mathbf{u}_{t+\delta t} = \mathbf{u}_0 + \delta t [\Phi^T \mathbf{x} - \Phi^T \Phi \mathbf{z}(\mathbf{u}_0) - \beta(\mathbf{u}_0 - \mathbf{u}_0)],$$

Because of the rolling update scheme, we know the prior at time t is the same as the posterior from time $t - 1$, denoted by \mathbf{u}_t . In other words, we have $\mathbf{u}_0 \equiv \mathbf{u}_t$, resulting in:

$$\mathbf{u}_{t+\delta t} = \mathbf{u}_t + \delta t [\Phi^T \mathbf{x} - \Phi^T \Phi \mathbf{z}(\mathbf{u}_t)].$$

Assuming $\delta t = 1$, we recover the update rule shown in the main text (eq. (7)). This explains why the leak term is absent in eq. (7). It also explains why BONG [60] advocates dropping the KL term entirely when performing single-step online inference: it has no effect on the first gradient step.

More generally, this analysis reveals a fundamental difference between static and online inference paradigms: static approaches maintain stability through persistent regularization to a fixed prior; whereas, online methods continually update the reference point for regularization and are more adaptive as a result. This distinction is particularly relevant for modeling biological perception, which must balance the preservation of accumulated knowledge with flexibility to new observations.

C Extended Experiments: Methodological Details and Additional Results

This appendix complements the main experimental results from section 5. We provide detailed information about model architectures, hyperparameters, and training protocols in appendix C.1, along with additional methods, analyses, and findings as we summarize below.

We describe our convergence detection methodology (appendix C.2), demonstrate that $i\mathcal{P}$ -VAE exhibits cortex-like properties such as contrast-dependent response latency (appendix C.3), extend our reconstruction-sparsity analysis with MAP decoding experiments (appendix C.4), present MNIST results comparing iterative VAEs with predictive coding networks (appendix C.6), and provide evidence for $i\mathcal{P}$ -VAE’s strong out-of-distribution (OOD) generalization capabilities for both within-dataset perturbations and cross-dataset settings (appendix C.8).

C.1 Architecture, Hyperparameter, and Training details

This appendix describes the implementation details of the iterative VAE models introduced in this paper. We cover architecture design, hyperparameter selection, and training procedures. We also provide details about all the other models we compare to, including amortized VAEs, predictive coding variants (PC, iPC), and LCA.

C.1.1 Architecture details

Our iterative VAE architectures consist of three key components:

Encoding mechanism. The encoding algorithm implements natural gradient descent on variational free energy (eq. (7)), visualized in Figs. 5 and 6. Different distributional choices yield distinct dynamics: Poisson encoding (eq. (7)) for $i\mathcal{P}$ -VAE versus Gaussian encoding (eq. (46)) for $i\mathcal{G}$ -VAE. The encoder is fundamentally coupled to the decoder, performing *analysis-by-synthesis* [68]. We derive results for linear decoders in the main paper and extend to nonlinear decoders in appendix B.6.

Key implementation details include: (1) learned priors (one parameter per latent dimension), and (2) a learned global step size, δt , interpretable as a time constant: $\mathbf{u}_{t+1} = \mathbf{u}_t + \delta t \dot{\mathbf{u}}_t$, with $\dot{\mathbf{u}}$ given by eq. (6). These parameters are learned end-to-end alongside decoder parameters θ .

Sampling mechanism. To approximate the reconstruction loss (eqs. (4) and (40)), we use differentiable sampling from the posterior distribution. For Gaussian models, we employ the standard reparameterization trick [18] (eq. (42)), while for $i\mathcal{P}$ -VAE we use the Poisson reparameterization algorithm [50]. In $i\mathcal{G}_\varphi$ -VAE models, we apply a nonlinearity $\varphi(\cdot)$ post-sampling, which effectively modifies the latent distribution. For example, applying relu to Gaussian samples creates a truncated Gaussian distribution, corresponding to the $i\mathcal{G}_{\text{relu}}$ -VAE architecture.

Decoding mechanism. Our main results use linear decoders (Φ) that map from latent to stimulus space. This enables closed-form theoretical derivations (eqs. (6), (46) and (49)). In appendix B.6 extend our theory to cover nonlinear decoders; and, in appendix C.8, we extend our empirical analysis to MLP and convolutional decoders. Throughout this paper, all models use Gaussian likelihoods (yielding MSE reconstruction loss) with learned global variance parameters [69].

Implementation details for other models. For amortized VAEs, we utilized the implementation from [50], including their five-layer ResNet encoders. For LCA, we used the LCA-PyTorch library [216] (BSD-3 license). For PC and iPC models, we employed the PCX library [113] (Apache-2.0 license) with their default MNIST-optimized MLP architectures. But we matched the latent dimensionality to the other models, using a consistent value of $K = 512$ throughout.

C.1.2 Hyperparameter details

For the reconstruction-sparsity analysis (Fig. 4), we swept across $T_{\text{train}} \in \{8, 16, 32\}$ and β values proportional to each T_{train} , with factors $\in \{0.5, 0.75, 1.0, 1.25, 1.5, 2.0, 3.0, 4.0\}$. This can be seen in the x-axis of Fig. 10. For amortized models, we used the same proportional β values but with $T_{\text{train}} = 1$. For MNIST experiments, we used $\beta = T_{\text{train}}$.

For the convergence experiment (Fig. 3), we used $T_{\text{train}} = 16$ with $\beta = 24.0$ for $i\mathcal{P}$ -VAE and $\beta = 8.0$ for $i\mathcal{G}$ -VAE and $i\mathcal{G}_{\text{relu}}$ -VAE, based on optimal values identified in our hyperparameter sweep (Fig. 4). The contrast experiments (Fig. 8) used the same $i\mathcal{P}$ -VAE configuration.

For LCA, we used a time constant $\tau = 100$ with 1000 inference iterations and a learning rate of 0.01. We optimized the sparsity parameter λ through an extensive sweep on the van Hateren dataset, finding $\lambda = 0.5$ performed best.

C.1.3 Training details

We trained iterative VAEs using PyTorch with the Adamax optimizer [217] and cosine learning rate scheduling [218], but without warm restarts. We implemented KL term annealing during the first 10% of training following standard VAE practices [219, 220], though we observed minimal impact since our models use a single layer.

For $i\mathcal{P}$ -VAE, we adopted the Poisson reparameterization algorithm from [50], annealing the temperature from $\text{temp}_{\text{start}} = 1.0$ to $\text{temp}_{\text{stop}} = 0.01$ during the first half of training.

For the van Hateren dataset, we used a learning rate of 0.002, a batch size of 200, and trained for 300 epochs. MNIST [221] models used identical hyperparameters but were trained for 400 epochs. These settings were consistent across both iterative and amortized VAEs.

For LCA, we adapted the training approach from [50], gradually increasing λ from 0 to the target value over 100 epochs. For PC and $i\mathcal{P}$ models, we followed the PCX library examples [113], doubling the default epoch count to ensure convergence.

C.1.4 Training compute details

The computational requirements for iterative VAEs scale with the number of inference iterations (T_{train}). For example, training the models presented in Fig. 3 with $T_{\text{train}} = 16$ requires approximately three hours per model on an NVIDIA A6000 GPU. Memory usage and training time both scale approximately linearly with T_{train} , as each additional inference iteration requires maintaining the computational graph for backpropagation.

Our complete set of experiments, including all hyperparameter sweeps and model variants, was conducted over the course of approximately one week using six NVIDIA A6000 GPUs (48GB VRAM each). To maximize GPU utilization, we often ran multiple smaller experiments concurrently on a single GPU. Linear decoder models were the most memory-efficient, while experiments with nonlinear decoders for the OOD generalization tasks required more resources due to their additional parameters and the need to backpropagate through relatively more complex architectures.

C.2 Convergence detection procedure

In section 5 and Fig. 3, we determined convergence by finding the first time point where the R^2 trace flattens out and stays flat. Here, we provide more details about this convergence detection algorithm.

The main intuition. We consider inference to be complete once the R^2 trace becomes essentially flat. This is because R^2 is monotonically related to the log-likelihood, and when the curve levels off, further improvements in log-likelihood are negligible.

To obtain a robust estimate of the local trend, we fit a straight line to every 60-step segment (a sliding window) of the trace and measure its slope. We call a window *flat* when the absolute slope falls below a fixed tolerance of 10^{-5} . To protect against short pauses in learning, we require at least five successive windows to be flat before declaring convergence.

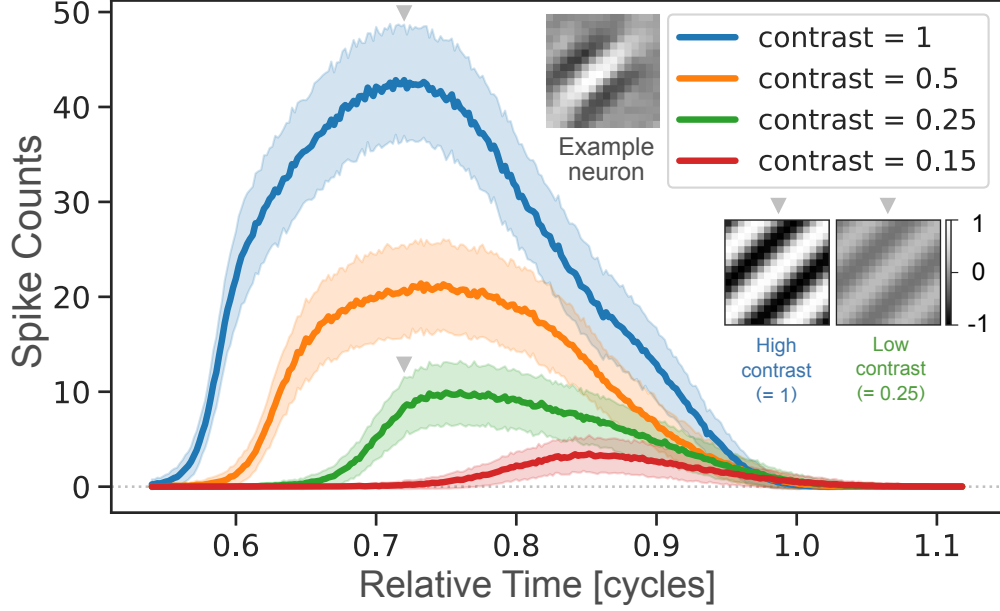


Figure 8: *iP*-VAE neurons exhibit contrast-dependent response latency, mimicking a well-documented property of V1 neurons. The figure shows trial-averaged firing rates (PSTHs) from a representative model neuron in response to drifting gratings of varying contrast levels. Higher contrast stimuli (blue and orange) elicit responses with shorter onset latencies, earlier peak times, and larger firing rates compared to lower contrast stimuli (green and red). Insets show the learned feature of the selected neuron (top) and the appearance of high contrast (left) versus low contrast (right) grating stimuli. The x-axis represents time in units of grating cycles, while the y-axis shows mean spike counts across $N = 500$ trials. Shaded regions indicate standard deviation. This behavior likely emerges from the divisive normalization in our model dynamics (eq. (8)), even though the model was trained only on static images, suggesting that our theoretical framework captures key aspects of visual cortical computation [111, 112].

Details of the convergence detection algorithm. Given $s = (s_1, \dots, s_{T_{\text{test}}})$, a one-dimensional array of R^2 scores in $[0, 1]$, let `window` = 60, `tol` = 10^{-5} , and `consecutive` = 5.

1. **Compute local slopes.** For each start index $i = 0, \dots, T_{\text{test}} - \text{window}$, define

$$\tau = (0, 1, \dots, \text{window} - 1), \quad y = (s_i, \dots, s_{i+\text{window}-1}),$$

and compute the least-squares slope

$$\beta_i = \frac{\sum_j (\tau_j - \bar{\tau})(y_j - \bar{y})}{\sum_j (\tau_j - \bar{\tau})^2}.$$

Store $|\beta_i|$ in an array `slopes`.

2. **Mark flat windows.** Set `flat` = (`slopes` < `tol`).
3. **Require persistence.** Find the smallest index k at which `flat` is true for `consecutive` = 5 windows in a row. If no such run exists, define $t_{\text{converge}} = T_{\text{test}}$.
4. **Report the convergence index.** Otherwise return

$$t_{\text{converge}} = k + \text{window},$$

the first sample that follows the verified flat period (at least $5 \times 60 = 300$ uninterrupted steps).

Please see our code for more info.

C.3 iP-VAE exhibits cortex-like dynamics: contrast-dependent response latency

The iP-VAE learns spatially localized, oriented, and bandpass (i.e., Gabor-like [107–110]) features (Fig. 11), similar to those learned by classic sparse coding models [54] and LCA [39]. Previous studies have shown that LCA exhibits cortex-like properties, including contrast invariance of orientation tuning, cross-orientation suppression, and so on [222]. Given the theoretical (section 4) and empirical (Fig. 4) similarities between iP-VAE and LCA, we investigated whether iP-VAE also exhibits cortex-like dynamics. We focused on two key neural phenomena with strong experimental support: temporal sparsification dynamics and contrast-dependent response latency.

V1-like sparsification dynamics. Recent electrophysiological findings in mouse primary visual cortex (V1) by Moosavi et al. [106] demonstrate that V1 neurons become progressively sparser over time, even after initial response convergence, while maintaining high mutual information with the input stimuli. Remarkably, both iP-VAE and $i\mathcal{G}_{\text{relu}}$ -VAE exhibit analogous dynamics in our experiments, continuing to sparsify their representations by an additional $\sim 10\%$ after functional convergence as measured by reconstruction quality (Fig. 3). For iP-VAE, this post-convergence sparsification coincides with a distinctive dip in the gradient norm $\|\dot{\mathbf{u}}\|$ (Fig. 3), suggesting a transition to a new phase of representational refinement. The emergence of this biological property across both models provides evidence that our normative framework captures fundamental principles of neural computation, without being explicitly designed to do so.

V1-like contrast-dependent response latency. A significant theoretical outcome of our approach is that a multiplicative form of divisive normalization naturally emerges from the derivations (eq. (8)). The resulting equation differs from canonical normalization that was developed to describe cortical circuits in that there is a product instead of a sum [223]. However, in practice, it captures features of normalization in the cortex. In particular, Carandini et al. [111] demonstrated that V1 neurons exhibit contrast-dependent response latency when presented with drifting gratings of varying contrast. Higher contrast stimuli consistently elicit faster responses, as measured by both onset time and time-to-peak [111, 112].

To investigate whether our model reproduces this phenomenon, we conducted an analogous experiment on the spiking “neurons” of the iP-VAE. We first characterized the tuning properties of individual model neurons to identify their preferred orientation and spatial frequency. We then presented drifting gratings matching these preferred parameters while systematically varying contrast levels $\in \{15\%, 25\%, 50\%, 100\%\}$ (a contrast level of 100% corresponds to a maximum amplitude of 1 in the simulated gratings). We measured iP-VAE neuron responses across $N = 500$ trials, and computed trial-averaged firing rates (i.e., *peristimulus time histograms*, PSTHs) as shown in Fig. 8.

The results reveal response dynamics that are similar to those observed in biological V1 neurons (Fig. 8). At high contrasts (50%, 100%), responses exhibit shorter onset latencies and higher peak firing rates compared to lower contrasts (15%, 25%). Response peaks also occur earlier in time at higher contrasts, with peak timing progressively delayed as contrast decreases. Quantitatively, we observe a mean latency difference of approximately 0.15 (in units of relative grating cycles) between the highest (100%) and lowest (15%) contrast stimuli, with intermediate contrasts showing progressively longer delays as contrast decreases.

This contrast-dependent latency shift arises naturally from iP-VAE’s recurrent dynamics and is likely a direct consequence of the divisive normalization mechanism in eq. (8). Notably, the model was trained solely on static natural images, with no exposure to time-varying stimuli or explicit temporal structure.

C.4 Reconstruction-sparsity with deterministic MAP decoding, and dependence on β

In the main text (section 5), we explored the reconstruction-sparsity trade-off, shown in Fig. 4. We found that all iterative VAEs outperformed their amortized counterparts, and that both LCA and iP-VAE achieved the best overall performance (Fig. 4b).

Here we note an important distinction in inference methods: LCA performs *maximum a posteriori* (MAP) estimation [39], while the VAE models maintain uncertainty in their posteriors by sampling. For a more direct comparison, we also evaluated all VAE models using MAP decoding instead of sampling. Specifically, for the Poisson family, we used firing rates directly for reconstruction (instead

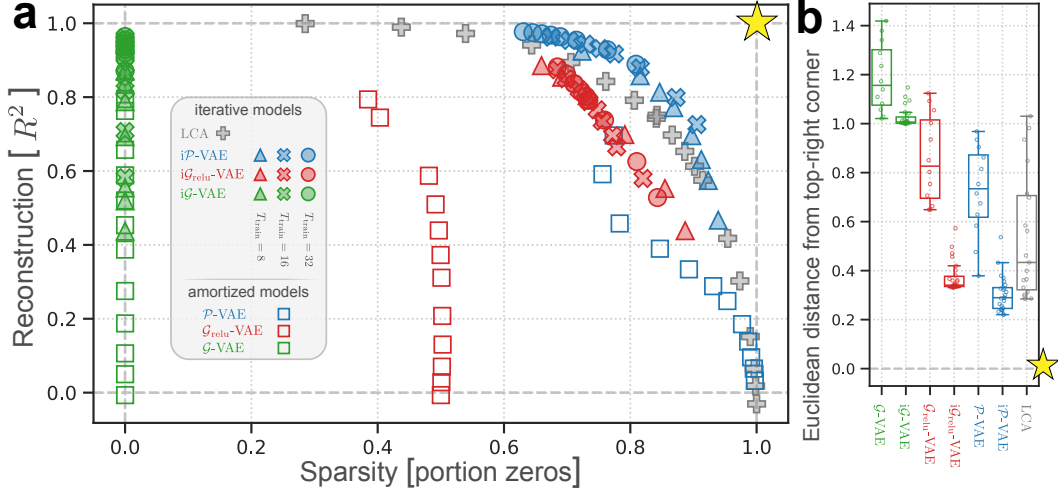


Figure 9: Related to Fig. 4, but using *maximum a posteriori* (MAP) decoding instead of sampling for all VAE-based models. For Poisson models, this means using firing rates directly for reconstruction, while for Gaussian models, we use the posterior means. This approach provides a more direct comparison to LCA, which performs MAP estimation by design [39]. Under these conditions, iP-VAE slightly outperforms LCA while maintaining the benefits of a probabilistic representation.

of spike-count samples), while for the Gaussian family, we used the posterior mean parameters. Note that for iterative VAEs, the inference dynamics was still fully stochastic (eqs. (6), (46) and (49)). The difference here was that for MAP decoding, we simply used the final posterior parameters (instead of samples drawn from it) for the reconstruction.

MAP decoding. The results are presented in Fig. 9. As expected, all VAE models improve their reconstruction R^2 performance under MAP decoding. The best overall reconstruction is achieved by iG-VAE and iP-VAE with a large $T_{\text{train}} = 32$, approaching $R^2 \approx 1.0$. Notably, iP-VAE achieves this high reconstruction quality while maintaining considerable sparsity levels exceeding 60%, and slightly outperforms LCA in this MAP decoding setting. This result demonstrates that our probabilistic framework can match or exceed the performance of established sparse coding algorithms while maintaining the additional benefits of a fully probabilistic, integer spike-count representation.

The effects of varying β . We also analyze the relationship between the β hyperparameter and iP-VAE performance in Fig. 10. The results confirm the theoretical prediction that for Poisson models, the KL divergence term effectively functions as a metabolic cost penalty [50], with higher β values inducing greater sparsity. This relationship establishes a direct link between information rate (KL divergence) and our heuristic “proportion zeros” measure of sparsity, partially justifying the interpretation of the reconstruction-sparsity landscape of Fig. 4 as a rate-distortion map [77].

Interestingly, the relationship between β and model performance is significantly influenced by the training duration T_{train} . As shown in Fig. 10, models trained with longer inference trajectories ($T_{\text{train}} = 32$) achieve better reconstruction across all β values compared to those with shorter training iterations ($T_{\text{train}} = 8$), which tend to be sparser. The overall performance metric (distance from the optimal point, marked by a gold star) reveals different patterns: $T_{\text{train}} = 32$ models show steady improvement that plateaus at higher β values, while models with shorter training durations ($T_{\text{train}} = 8, 16$) exhibit a U-shaped curve, initially improving but then degrading as β increases beyond an optimal point.

These results suggest that extended inference during training enhances the model’s ability to find optimal representations, even when evaluated at a fixed inference length during testing. Our approach bears similarities to meta-learning [191], where the inner loop of optimization affects the outer loop performance. Future work should further explore this dependency on inner-loop iterations to better understand the mechanisms behind these performance differences across training regimes.

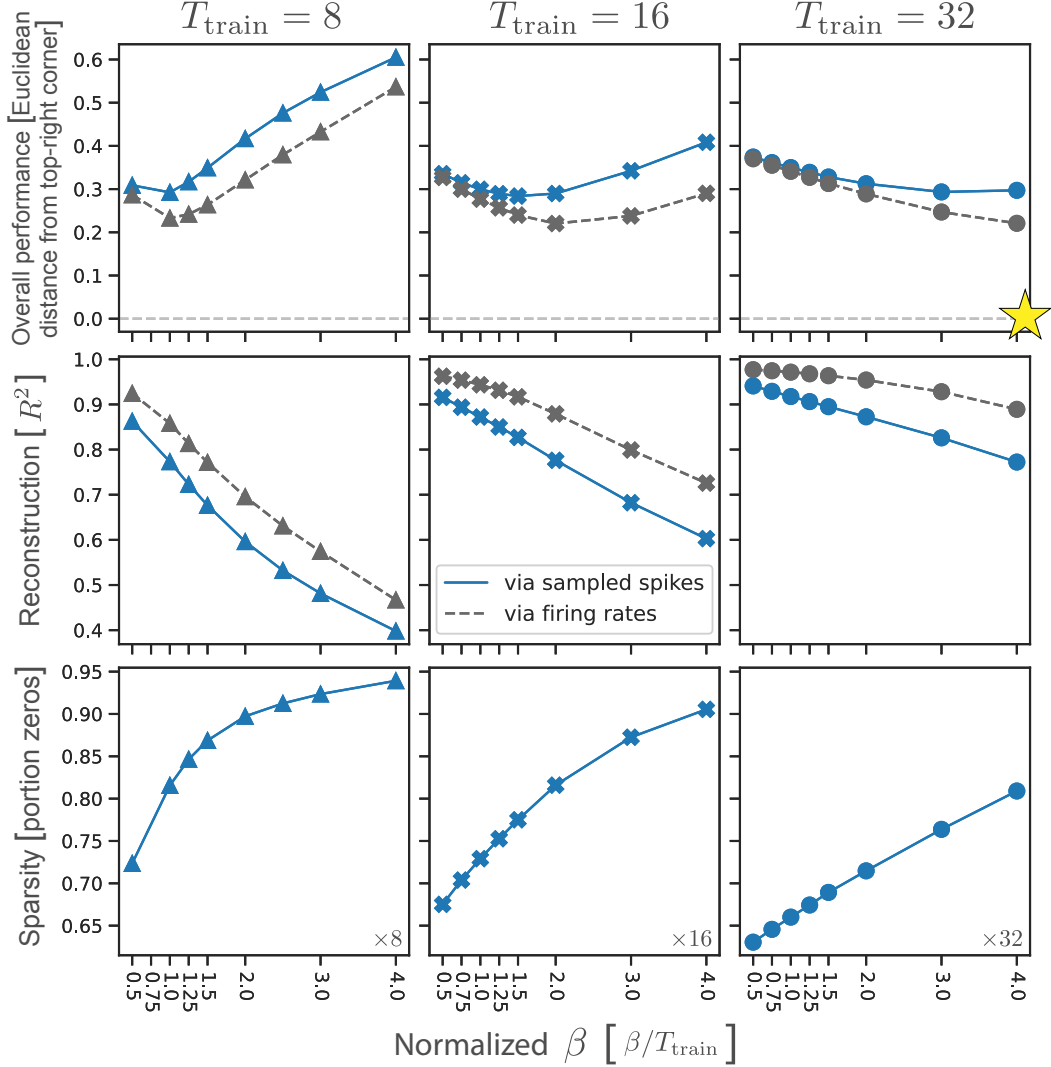


Figure 10: Effect of β on iP-VAE performance metrics across different training durations. Each column represents a different training duration ($T_{\text{train}} \in \{8, 16, 32\}$), with performance metrics shown as a function of normalized β (scaled by T_{train}). **Top row:** Overall performance improves with higher T_{train} , with longer training allowing higher β values before performance degrades. **Middle row:** Reconstruction quality (R^2) decreases with higher β across all training durations, but MAP decoding (using firing rates, gray dashed line) consistently outperforms sampling-based decoding (blue solid line). **Bottom row:** Sparsity monotonically increases with β for all T_{train} values, confirming the direct relationship between the KL penalty and representational sparsity for Poisson latents [50]. The gold star (defined in Fig. 4) indicates the theoretical optimum: perfect reconstruction ($R^2 = 1.0$) with maximum sparsity (portion zeros = 1.0). See Figs. 4 and 9 for a comparison with LCA and other iterative and amortized VAEs, embedded in a shared sparsity-reconstruction landscape.

C.5 Reconstruction-sparsity performance across latent dimensionalities

In addition to β (Fig. 10), latent dimensionality K also influences the reconstruction-sparsity trade-off. To systematically evaluate this effect, we trained iP-VAE models on 16×16 natural image patches (van Hateren dataset) with linear decoders, varying $K \in \{32, 64, 128, 256, 512, 768, 1024, 2048\}$. All models used $T_{\text{train}} = 16$ and $\beta = 24$, matching the configuration from the model shown in Fig. 3.

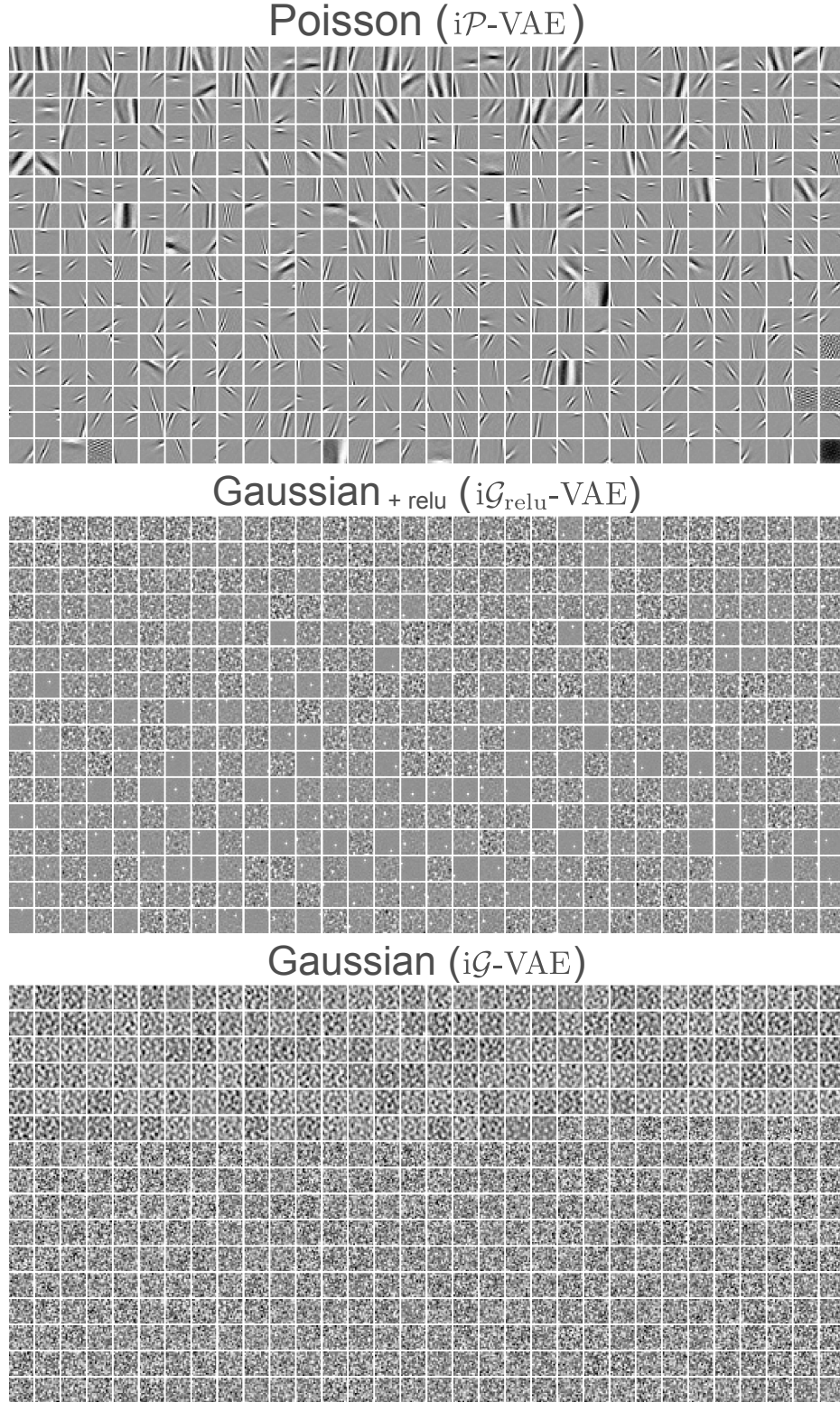


Figure 11: The full set of $K = 512$ dictionary elements, corresponding to the models from Fig. 3. Features are ordered in ascending order of their aggregate posterior membrane potentials (i.e., the final $\mathbf{u}_{t=1000}$ for $i\mathcal{P}$ -VAE, and $\boldsymbol{\mu}_{t=1000}$ for Gaussian models, averaged over the entire test set).

Table 2: Effect of latent dimensionality (K) on reconstruction and sparsity. The iP-VAE model from the main paper used $K = 512$ (highlighted), which balances performance and sparsity.

K	$R^2 \uparrow$	Sparsity \uparrow	Overall perf. \downarrow	Active neurons
32	0.24	0.28	1.05	23
64	0.42	0.28	0.93	46
128	0.64	0.32	0.77	87
256	0.77	0.55	0.51	116
512	0.83	0.77	0.28	116
768	0.83	0.86	0.22	110
1024	0.83	0.90	0.20	107
2048	0.84	0.95	0.17	103

We report reconstruction quality (R^2), sparsity (portion zeros), overall performance—Euclidean distance from the ideal point: $R^2 = 1$, sparsity = 1, golden star in Fig. 4—and the average number of active neurons, defined as $K \times (1 - \text{portion_zeros})$. Results are shown in Table 2.

We observe several key patterns:

1. **Overcompleteness improves performance:** Overall performance consistently improves as K increases, with most gains occurring between $K = 32$ and $K = 512$. Performance saturates around $K = 1024$, with diminishing returns beyond this point.
2. **Efficient coding emerges:** The total number of active neurons plateaus around ~ 110 , even as latent dimensionality grows to 2048. This suggests the model learns an efficient sparse code that maintains a consistent activity budget regardless of available capacity.
3. **Reconstruction-sparsity trade-off:** Beyond $K = 512$, further increases in dimensionality primarily improve sparsity (from 77% to 95% zeros) while reconstruction quality remains stable ($R^2 \approx 0.83$ – 0.84). This validates our choice of $K = 512$ for the main experiments as a reasonable balance point.

These results demonstrate that iP-VAE exhibits the expected overcomplete sparse coding behavior while maintaining computational efficiency through consistent use of approximately 100 active neurons across the natural image patch dataset.

C.6 Reconstruction performance and downstream classification accuracy on MNIST

In this appendix, we explore the reconstruction fidelity and downstream classification accuracy of iterative and amortized VAEs on MNIST, comparing them to predictive coding networks (PCNs). Specifically, we compare to the original PC model of Rao and Ballard [22], and a recent enhanced version, incremental PC (iPC; Salvatori et al. [90]). See Table 1 for a summary of model details.

C.6.1 Temporal scalability: iP-VAE scales consistently with training depth on MNIST

As we saw in the main text (section 5, Fig. 4), iterative VAE performance strongly depends on T_{train} . Therefore, we first performed a systematic search to select an appropriate T_{train} for different iterative VAE models on MNIST, exploring $T_{\text{train}} \in \{4, 8, 16, 32, 64, 128\}$.

We evaluated these models using a consistent $T_{\text{test}} = 1,000$ and examined reconstruction performance. We observed markedly different behavior across variants. iG-VAE showed continuous improvement up until $T_{\text{train}} = 64$, but plateaued thereafter with negligible gains from doubling to $T_{\text{train}} = 128$. iG_{relu}-VAE initially improved but began to deteriorate and diverge beyond $T_{\text{train}} = 32$. We suspect this instability stems from the absence of the divisive normalization mechanism that naturally emerges in iP-VAE theory (eq. (8)).

Notably, iP-VAE was the only model that exhibited consistent improvements as we increased T_{train} . It likely would continue improving with even longer training sequences, but the computational cost becomes prohibitive beyond what we tested (T_{train} can be conceptualized roughly as the number of layers in a deep ResNet, see Fig. 5).

In conclusion, $i\mathcal{P}$ -VAE demonstrated the most promising scalability characteristics (at least on MNIST). Based on these results, we selected $T_{\text{train}} = 128, 64, 32$ for $i\mathcal{P}$ -VAE, $i\mathcal{G}$ -VAE, $i\mathcal{G}_{\text{relu}}$ -VAE, respectively, for the MNIST experiments reported below.

C.6.2 Iterative VAEs with an overcomplete latent space outperform PCNs on MNIST

We trained unsupervised models on MNIST and evaluated reconstruction quality using normalized per-dimension MSE, following prior work [113]. Additionally, as in the main text, we report R^2 , a dimensionality-independent metric bounded between 0 and 1. To evaluate downstream classification performance, we extracted latent representations and trained a logistic regression classifier. Results are shown in Table 3.

Iterative VAEs substantially outperform both PCNs and amortized VAEs in reconstruction fidelity. $i\mathcal{P}$ -VAE achieves the lowest per-dim MSE (4.39×10^{-3}) and highest R^2 (0.951) among all models, significantly surpassing both PC (MSE: 9.24×10^{-3} , R^2 : 0.896) and $i\mathcal{P}$ C (MSE: 9.08×10^{-3} , R^2 : 0.898). Remarkably, $i\mathcal{P}$ -VAE accomplishes this favorable reconstruction while maintaining high sparsity (84% zeros), whereas PCNs produce entirely dense representations.

For classification, \mathcal{P} -VAE achieved the highest accuracy of 97.89% on downstream unsupervised classification, approaching the performance of supervised PCNs reported in ref. [113]. $i\mathcal{P}$ -VAE achieves the second-best classification performance at 96.46%, substantially outperforming both PC (90.74%) and $i\mathcal{P}$ C (91.60%).

Limitations of the PCN comparisons. We acknowledge several important limitations in our comparative analysis. All iterative and amortized VAE models in this experiment used a single linear decoder, while amortized models employed convolutional encoders. In contrast, PCNs utilize hierarchical architectures with fundamentally different design principles. Rather than conducting a comprehensive architectural optimization for PCNs, we used default settings from the official implementations released by Pinchetti et al. [113], with only minor adjustments (e.g., doubling the number of epochs to ensure convergence, or matching latent dimensionality to other models – see appendix C.1 for more details).

These substantial architectural differences limit the conclusiveness of our PCN versus iterative VAE comparisons presented in Table 3. A more rigorous comparison would require carefully controlling for network capacity and depth. Additionally, our evaluation metrics may inherently favor certain architectural choices. For instance, reconstruction metrics advantage models with overcomplete latent representations with direct pathways between the latents and reconstruction spaces.

Despite these methodological limitations, our results provide valuable initial evidence that iterative VAEs can achieve comparable or superior performance to PCNs in both reconstruction quality and downstream classification tasks. Particularly noteworthy is that $i\mathcal{P}$ -VAE accomplishes this while maintaining high sparsity (84% zeros) and using integer-valued spike count representations that better align with biological neural computation. Future work should explore more controlled comparisons across these model families, including matching parameter counts, architectural depth, and computation budgets to establish more definitive performance relationships.

C.7 Runtime comparison: iterative versus amortized inference

A primary motivation for amortized inference is computational efficiency: a single forward pass through an encoder network should be faster than iterative optimization. However, as we saw in Fig. 4, this potential speed advantage comes at the cost of inferior reconstruction-sparsity performance. Here we quantify the actual runtime trade-off to determine whether iterative models’ performance gains justify their computational costs—and whether they are even slower at all.

Experimental setup. We compared the iterative VAE models from Fig. 3 ($T_{\text{train}} = 16$) against amortized counterparts trained with standard ELBO ($\beta = 1$). All models used linear decoders trained on 16×16 natural image patches (van Hateren dataset), with amortized models employing 6-layer convolutional encoders.

We measured inference time using CUDA events for accurate GPU synchronization:

Table 3: Comparison of reconstruction performance, representational sparsity, and downstream classification accuracy on MNIST across model families. Iterative VAEs consistently outperform both PCNs and amortized VAEs in reconstruction metrics while using significantly fewer parameters than their amortized counterparts. Bold values indicate best performance in each category. Amortized VAE models used deep ResNet convolutional encoders, and all VAE models (both iterative and amortized) used a single linear decoder for a consistent comparison with the main text results. Iterative VAE models were trained with optimized iteration counts: $T_{\text{train}} = 128$ for $i\mathcal{P}$ -VAE, $T_{\text{train}} = 64$ for $i\mathcal{G}$ -VAE, and $T_{\text{train}} = 32$ for $i\mathcal{G}_{\text{relu}}$ -VAE, based on convergence properties. Mean squared error (MSE) values are normalized per dimension for consistent comparison with previous benchmarks [113]. Classification accuracy is reported using a linear classifier trained on unsupervised features. Values are mean \pm 99% confidence interval, estimated from 5 random initializations. See appendix C.6.1 for analysis of how T_{train} affects performance, and appendix C.6.2 for detailed interpretation.

Model family	Model	Reconstruction		Portion Zeros \uparrow	Classification Accuracy \uparrow	Num Params \downarrow
		MSE $\times 10^{-3}$ \downarrow	R^2 \uparrow			
iterative VAE	$i\mathcal{P}$ -VAE	4.39 $\pm .04$.951 $\pm .000$.84 $\pm .00$	96.46 $\pm .11$	0.40 <i>M</i>
	$i\mathcal{G}$ -VAE	7.63 $\pm .02$.914 $\pm .000$.00 $\pm .00$	92.73 $\pm .14$	0.40 <i>M</i>
	$i\mathcal{G}_{\text{relu}}$ -VAE	8.45 $\pm .92$.906 $\pm .011$.78 $\pm .05$	95.74 $\pm .43$	0.40 <i>M</i>
amortized VAE	\mathcal{P} -VAE	25.48 $\pm .24$.713 $\pm .002$.84 $\pm .00$	97.89 ± 0.34	6.79 <i>M</i>
	\mathcal{G} -VAE	14.40 $\pm .19$.841 $\pm .002$.00 $\pm .00$	95.75 ± 2.19	6.93 <i>M</i>
	$\mathcal{G}_{\text{relu}}$ -VAE	17.13 $\pm .20$.809 $\pm .002$.50 $\pm .00$	95.41 ± 1.51	6.93 <i>M</i>
PCN	PC [22]	9.24 $\pm .03$.896 $\pm .000$.00 $\pm .00$	90.74 $\pm .26$	0.13 <i>M</i>
	iPC [90]	9.08 $\pm .00$.898 $\pm .000$.00 $\pm .00$	91.60 $\pm .10$	0.13 <i>M</i>

```

start = torch.cuda.Event(enable_timing=True)
end = torch.cuda.Event(enable_timing=True)

start.record()
output = model(x)
end.record()

torch.cuda.synchronize()
duration = start.elapsed_time(end)

```

Since iterative methods distribute computation across many timesteps, they may underutilize available parallelism for small batches but benefit substantially from large-batch parallelization. We therefore evaluated two extreme scenarios: single-sample inference (batch size = 1) and large-batch inference (batch size = 10,000).

C.7.1 Inference runtime results: iterative models match or exceed amortized speed.

Figure 12 shows reconstruction quality, sparsity, and overall performance as functions of wall-clock time. The key question is: how long does it take iterative models to reach the same overall performance as amortized models? The answer challenges conventional assumptions:

Small batches (batch size = 1): Amortized models complete inference in $\sim 3\text{ms}$ (marked by X’s). Iterative models reach equivalent performance (distance from optimal point) within 3–15ms. Iterative models then continue improving, converging to superior final performance by $\sim 400\text{ms}$.

Large batches (batch size = 10,000): Parallel computation reveals an unexpected advantage for iterative inference. Amortized models complete inference in $\sim 50\text{ms}$, but iterative models achieve the same performance (distance from optimal point) in approximately the same duration. After matching amortized performance, iterative models continue refining their representations, converging to substantially better reconstruction-sparsity trade-offs by $\sim 2000\text{ms}$.

This pattern holds across all three iterative variants: $i\mathcal{P}$ -VAE, $i\mathcal{G}$ -VAE, and $i\mathcal{G}_{\text{relu}}$ -VAE all reach amortized-level performance within comparable speed to their amortized counterparts when batch size

is large. The iterative models then leverage additional compute to achieve superior final performance that amortized models cannot match.

Training time considerations. While inference speed is competitive between the two VAE types, training iterative models requires more time. As noted in appendix C.1.4, training iterative VAEs with $T_{\text{train}} = 16$ takes ~ 3 hours—approximately twice as long as amortized models with 6-layer encoders. This reflects the effective depth of iterative models: backpropagation through time across T_{train} steps creates computational graphs comparable to deep ResNets (Fig. 5). Training costs scale with both T_{train} and dataset size, though inference remains efficient.

Implications. These results challenge the assumption that iterative inference is prohibitively slow. For small batches, iterative models match amortized performance at slightly slower speeds. For large batches, iterative models are actually *comparable* at reaching equivalent performance levels, then continue improving to achieve superior reconstruction-sparsity trade-offs. Combined with their better out-of-distribution generalization (appendix C.8) and $25\times$ parameter efficiency, iterative models offer a compelling alternative to amortized inference. The increased training time appears to be the only meaningful trade-off, making iterative models particularly attractive for applications where inference performance matters more than training speed.

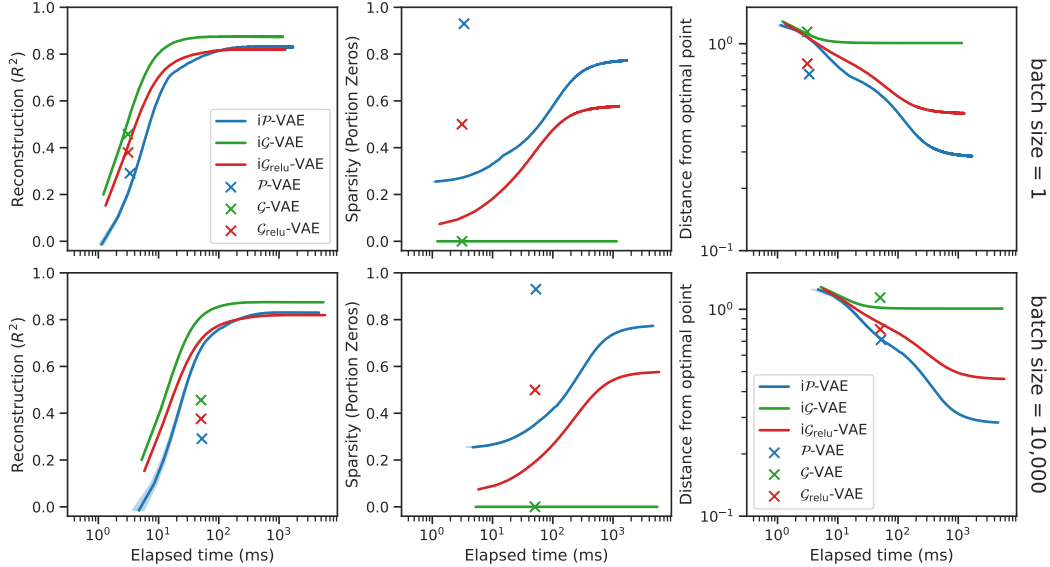


Figure 12: Runtime comparison between iterative and amortized VAEs for batch sizes of 1 (top) and 10,000 (bottom). Iterative models (solid lines) progressively improve over time, while amortized models (X markers) produce immediate but inferior results. **Left:** Reconstruction quality (R^2). **Middle:** Sparsity (portion zeros). **Right:** Overall performance (distance from optimal point, lower is better; see Fig. 4). For large batches, iterative models reach amortized-level performance at comparable speeds to amortized models. Iterative models then continue improving to achieve superior final performance across all metrics by ~ 200 – 300 ms.

C.8 iP -VAE exhibits strong out-of-distribution (OOD) generalization

In the main paper, we compared our novel iterative VAE architectures, including the iP -VAE, to their amortized counterparts, as well as neuroscience models such as sparse coding [39] and predictive coding networks (PCNs; [22, 90]). With the exception of PCNs, all other models we tested in the main paper employed a single linear layer decoder ($\hat{x} = \Phi z$, Fig. 5). In appendix B.6, we extended our theoretical framework to nonlinear decoders by deriving inference algorithms that incorporate the decoder’s Jacobian (eq. (40), Fig. 6).

This appendix presents experiments with nonlinear decoders, where we replace the linear Φ with a deep neural network: $\hat{x} = \text{dec}(z; \theta)$, parameterized by θ . We compare $i\mathcal{P}$ -VAE to \mathcal{P} -VAE and hybrid iterative-amortized VAEs across various generalization tasks.

Tasks and Datasets. We evaluate performance primarily based on out-of-distribution (OOD; [98, 99]) generalization, measured through both reconstruction fidelity and downstream classification accuracy. We use MNIST as our primary training dataset, and test generalization on rotated MNIST, extended MNIST (EMNIST; [224]), Omniglot [225], and ImageNet32 [226], with the latter two resized to 28×28 for consistent comparisons.

Architecture notation. We experimented with both convolutional and multi-layer perceptron (MLP) architectures, denoted using the $\langle \text{enc} | \text{dec} \rangle$ convention. For example, $\langle \text{mlp} | \text{mlp} \rangle$ indicates both **encoder** and **decoder** networks are MLPs. We use $\langle \text{grad} | \text{mlp} \rangle$ to denote our fully iterative (non-amortized) $i\mathcal{P}$ -VAE, which replaces the encoder neural network with natural gradient descent on variational free energy (section 4 and appendix B.6). We designed symmetrical architectures, ensuring that $\langle \text{mlp} | \text{mlp} \rangle$ has exactly twice as many parameters as $\langle \text{grad} | \text{mlp} \rangle$.

Alternative models. To isolate the impact of inference method in OOD settings, we compare $i\mathcal{P}$ -VAE to the amortized \mathcal{P} -VAE and state-of-the-art hybrid methods that combine iterative with amortized inference: iterative amortized VAE (ia-VAE; [91]) in both hierarchical (h) and single-level (s) variants, and semi-amortized VAE (sa-VAE; [92]).

Inference iterations. For $i\mathcal{P}$ -VAE, we explored different training iteration counts, $T_{\text{train}} \in \{4, 16, 32, 64\}$. Recall that during training, we differentiate through the entire sequence of iterations (**learning** to **infer**), which can lead to qualitatively different dynamics. For most OOD experiments, we use a $\langle \text{grad} | \text{mlp} \rangle$ $i\mathcal{P}$ -VAE with $T_{\text{train}} = 64$. At test time, we evaluate with $T_{\text{test}} = 1,000$ iterations. For the hybrid models, we use their default iteration counts unless otherwise specified (sa-VAE: $T_{\text{train}} = T_{\text{test}} = 20$, ia-VAE: $T_{\text{train}} = T_{\text{test}} = 5$).

C.8.1 Stability beyond the training regime and convergence for nonlinear decoders

An algorithm with strong generalization potential should learn inference dynamics that extend beyond the training regime. In the main paper (section 5), we found that all iterative VAEs converge when trained on natural image patches with linear decoders (Fig. 3). Here, we investigate whether this convergence holds for the more challenging case of nonlinear decoders.

We trained models on MNIST using different numbers of training iterations ($T_{\text{train}} \in \{4, 16, 32, 64\}$) with both $\langle \text{grad} | \text{mlp} \rangle$ and $\langle \text{grad} | \text{conv} \rangle$ architectures, then tested whether they continue to improve beyond T_{train} . As shown in Fig. 13a, even $i\mathcal{P}$ -VAE models trained with as few as $T_{\text{train}} = 4$ iterations learn to keep improving during test time, eventually converging to stable solutions. Interestingly, models trained with more iterations initially show worse performance but ultimately converge to better solutions, suggesting that $i\mathcal{P}$ -VAE learns temporally-extended inference dynamics that depend on the training sequence length but generalize well beyond it.

In contrast, hybrid models (sa-VAE and ia-VAE) begin with strong amortized initial guesses but plateau rapidly (Fig. 13a, right), converging to substantially higher MSE than $i\mathcal{P}$ -VAE models despite having more parameters. We note that sa-VAE’s authors acknowledged issues with the dominance of the iterative component on Omniglot and reported using techniques like gradient clipping to mitigate this (see footnote 6 in [92]), which may explain our observations on MNIST. More concerning, ia-VAE (single-level) begins to diverge outside its training regime and frequently resulted in numerical instabilities at test time when exceeding T_{train} .

Overall, $i\mathcal{P}$ -VAE demonstrates better reconstruction performance and continues to improve outside the training regime, unlike other models. This extends our convergence results from linear decoders (Fig. 3) to the more general nonlinear case and reveals $i\mathcal{P}$ -VAE’s first form of OOD generalization: temporal generalization beyond the training horizon. Next, we examine whether $i\mathcal{P}$ -VAE can generalize across visual domains.

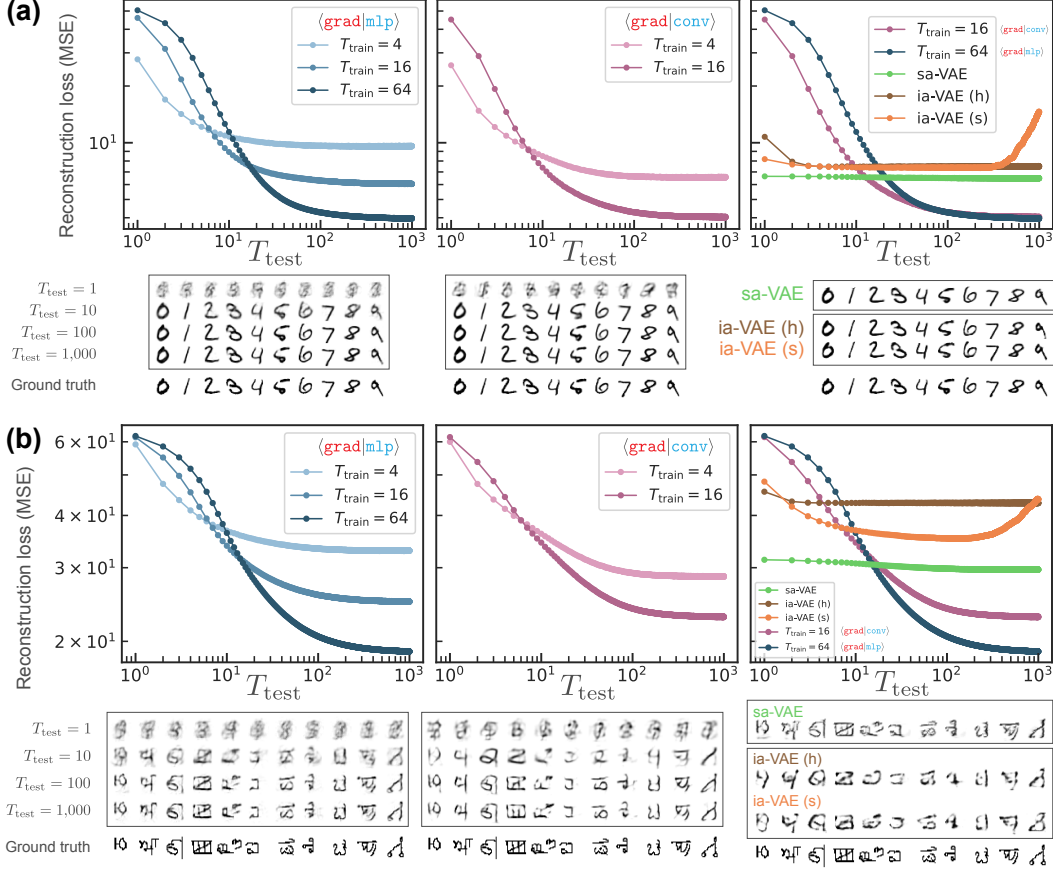


Figure 13: iP -VAE generalizes beyond its training regime and across datasets. All models shown here are trained on MNIST and tested either on MNIST (panel a) or Omniglot (panel b). (a) iP -VAE models trained with as few as $T_{\text{train}} = 4$ inference steps continue to improve well beyond the training regime ($T_{\text{test}} > T_{\text{train}}$). This temporal generalization holds across architectures: $\langle \text{grad}|\text{mlp} \rangle$ (left) and $\langle \text{grad}|\text{conv} \rangle$ (middle). In contrast, hybrid iterative-amortized models either plateau or diverge outside their training regime (right). (b) iP -VAE trained exclusively on MNIST successfully generalizes to the structurally different Omniglot dataset, showing substantial improvement in reconstruction quality as inference iterations increase. With higher T_{train} , iP -VAE models show initially worse but ultimately better performance, suggesting they learn more complex but effective inference dynamics.

C.8.2 Out-of-distribution generalization

We evaluate two levels of generalization for MNIST-trained models: (1) within-dataset perturbations, and (2) transfer across related datasets.

OOD generalization to within-dataset perturbation. We tested whether models trained on standard MNIST could generalize to rotated MNIST digits [98, 227]. At test time, we rotate digits between 0° and 180° in increments of 15° . We evaluated (a) reconstruction quality of the rotated digits, and (b) whether the resulting latent representations support downstream classification (Fig. 14).

iP -VAE and sa-VAE maintained relatively consistent performance across rotation angles, though iP -VAE demonstrated superior performance in both reconstruction and classification. The amortized P -VAE showed substantially worse reconstruction than iterative models, but its classification accuracy remained remarkably stable across angles, outperforming all models except iP -VAE.

In contrast, both ia-VAE variants showed significant degradation in performance as the rotation angle increased, with substantial drops in both reconstruction fidelity and classification accuracy. Overall, iP -VAE maintained the most stable and superior performance across all rotation angles, suggesting it learns rotation-invariant features that generalize effectively to unseen transformations.

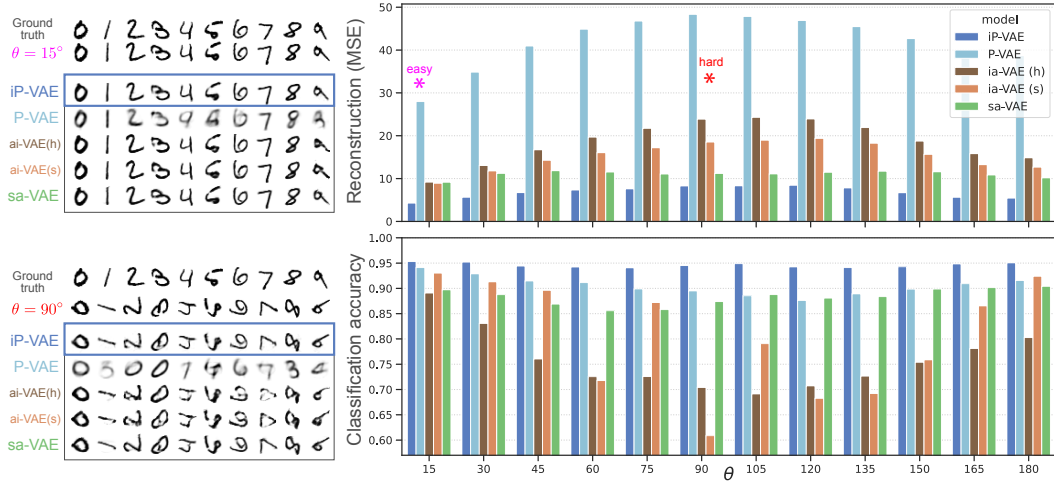


Figure 14: Robustness to rotational transformations of MNIST digits. **Left:** Visual comparison of reconstructions for moderately rotated ($\theta = 15^\circ$) and severely rotated ($\theta = 90^\circ$) digits across models. iP-VAE maintains high reconstruction fidelity across rotation angles, while other models show progressive degradation. **Right:** Quantitative evaluation of reconstruction MSE (top) and downstream classification accuracy (bottom) across rotation angles from 0° to 180° . iP-VAE demonstrates remarkable stability in both metrics, with minimal performance degradation even at extreme angles. The solid lines represent means, while shaded regions show standard deviations across test samples. All models were trained only on standard (unrotated) MNIST, making this a challenging test of generalization to unseen transformations.



Figure 15: Cross-dataset generalization from MNIST to novel character datasets. **Left panels:** Visual comparison of original samples and their reconstructions for EMNIST (left) and Omniglot (center-left) across different models. All models were trained exclusively on MNIST. **Center-right panel:** Reconstruction MSE for EMNIST and Omniglot. Lower is better. iP-VAE consistently achieves the lowest error on both datasets despite never seeing them during training. **Right panel:** Classification accuracy on EMNIST using a linear classifier trained on latent representations. iP-VAE representations support significantly higher accuracy, suggesting they capture more discriminative features that transfer well to new character classes.

OOD generalization across similar datasets. A model that learns compositional features with an effective inference algorithm should generalize to datasets structurally related to, but distinct from, the training distribution. To test this, we evaluated MNIST-trained models on EMNIST (Fig. 15) and Omniglot (Fig. 13b, Fig. 15), reporting both reconstruction MSE and classification accuracy (except for Omniglot, which has over 1,000 classes, making classification challenging).

iP-VAE consistently demonstrated superior generalization, achieving lower reconstruction error and higher classification accuracy than all other models. The visual quality of its reconstructions on both EMNIST and Omniglot was noticeably better, preserving key structural elements of characters it had never seen during training. This suggests that iP-VAE learns a more general and compositional latent space that captures fundamental structural elements shared across different character datasets.

Extreme cross-domain generalization with iP-VAE: from MNIST to natural images. Most remarkably, a `<grad,mlp>` iP-VAE trained exclusively on MNIST still performs well when tested on cropped, grayscale natural images from tiny ImageNet (Fig. 16), a domain vastly different

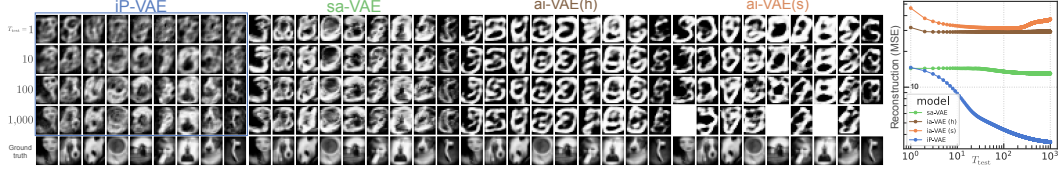


Figure 16: Extreme cross-domain generalization: MNIST-trained models tested on cropped, grayscale natural images. **Left panels:** Ground truth grayscale ImageNet32 samples (resized to 28×28) alongside their reconstructions from various models. Despite being trained exclusively on MNIST digits, $i\mathcal{P}$ -VAE captures significant semantic information and structural details of natural images. **Right panel:** Reconstruction MSE over inference iterations. $i\mathcal{P}$ -VAE continues to improve with more iterations, while hybrid models plateau quickly. The ia-VAE variants fail to adapt to the new domain, while sa-VAE shows moderate adaptation. This challenging generalization task demonstrates $i\mathcal{P}$ -VAE’s ability to represent visual concepts far outside its training distribution. This capability is likely enabled by its Gabor-like primitive features that can be recombined to represent novel visual structures (Fig. 17).

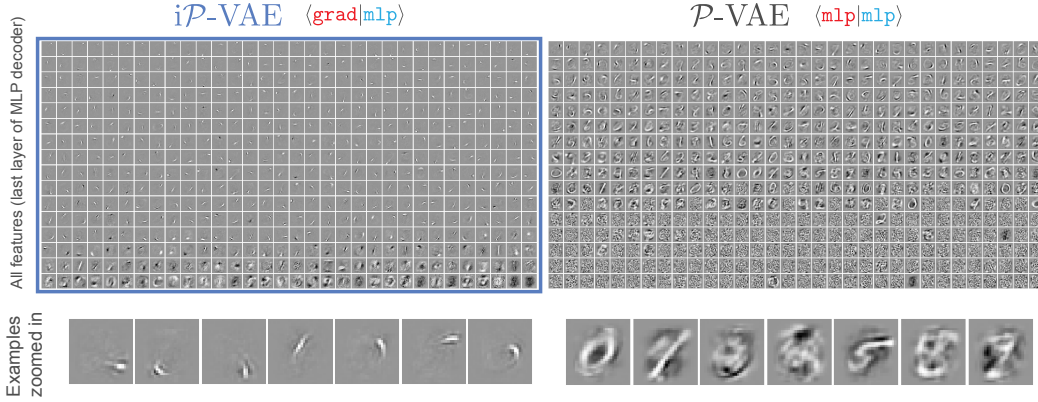


Figure 17: Visualization of learned features in the final decoder layer for $i\mathcal{P}$ -VAE with a $\langle \text{grad} | \text{mlp} \rangle$ architecture (left), versus an $\langle \text{mlp} | \text{mlp} \rangle$ \mathcal{P} -VAE (right), both trained on MNIST. $i\mathcal{P}$ -VAE learns Gabor-like features (fundamental visual primitives found in primate early visual cortex [107–110]) rather than digit-specific features. In contrast, \mathcal{P} -VAE learns more class-specific features resembling complete digits or digit fragments. Features are ordered by increasing kurtosis of their weight distributions to highlight the sparse nature of $i\mathcal{P}$ -VAE’s representations. The more general, primitive features learned by $i\mathcal{P}$ -VAE likely contribute to its superior generalization capability across datasets, as these features can be recombined to represent novel visual structures not seen during training.

from handwritten digits. Despite never seeing natural images during training, $i\mathcal{P}$ -VAE continues to improve its reconstruction quality with increasing inference iterations, capturing significant structural details; whereas, hybrid models like $\langle \text{conv} | \text{conv} \rangle$ sa-VAE and $\langle \text{mlp} | \text{mlp} \rangle$ ia-VAE plateau quickly or even diverge (Fig. 16, right panel). This extreme cross-domain transfer challenges common assumptions about generalization boundaries in representation learning and suggests that $i\mathcal{P}$ -VAE captures something fundamental about visual structure that transcends specific datasets.

Primitive visual codes enable generalization. How does $i\mathcal{P}$ -VAE achieve this unexpected generalization capability? We visualized the 512 learned features from the final layer of the $\langle \text{grad} | \text{mlp} \rangle$ $i\mathcal{P}$ -VAE’s decoder and compared them to those learned by an amortized $\langle \text{mlp} | \text{mlp} \rangle$ \mathcal{P} -VAE (Fig. 17). The contrast is striking: $i\mathcal{P}$ -VAE learns Gabor-like features—fundamental visual primitives similar to those found in primary visual cortex—while \mathcal{P} -VAE learns features that resemble entire digits or digit fragments. Previous work has identified strokes as compositional sub-components of digits [228], but $i\mathcal{P}$ -VAE learns an even more general and primitive visual code. These elementary Gabor-like features, combined with $i\mathcal{P}$ -VAE’s adaptive inference process, create a powerful compositional system that can flexibly recombine primitives to represent novel visual structures far outside the training distribution.

C.8.3 A discussion of the out-of-distribution (OOD) generalization experiments

Empirically, $i\mathcal{P}$ -VAE demonstrates promising adaptability and robustness to OOD samples while dynamically balancing computational cost and performance. It consistently outperforms both amortized models and hybrid iterative-amortized VAEs on the tasks we evaluated, despite using substantially fewer parameters.

These results are especially promising given the growing emphasis on OOD generalization in machine learning [98, 99, 227]. $i\mathcal{P}$ -VAE’s ability to learn primitive, compositional features that transfer across domains suggests its potential value for representation learning, whether as a pretraining method for downstream tasks or as a backbone for diffusion models [229, 230].

That said, we acknowledge that more systematic evaluation is needed to fully characterize the compositional capacity of iterative VAEs. While our experiments focus primarily on reconstruction and classification, future work should explore more diverse tasks and evaluation metrics. The strong performance demonstrated here motivates a deeper investigation into the generalization capabilities of $i\mathcal{P}$ -VAE and its potential applications across a broader range of domains.

C.8.4 Methodological details for the OOD experiments

For our comparisons, we utilized the official implementations of sa-VAE [92], ia-VAE [91], and \mathcal{P} -VAE [50]. Across models, we maintained consistent train/validation splits and hyperparameters unless otherwise specified.

Since sa-VAE’s original code used a Bernoulli observation model, we adapted it for Gaussian compatibility by removing the sigmoid in the decoder and replacing its reconstruction loss with MSE. For sa-VAE, we used the default configurations provided for Omniglot (batch size 50, 100 epochs), and adjusted appropriately for other datasets: MNIST (batch size 50, 32 epochs), and EMNIST (batch size 50, 16 epochs).

For ia-VAE, we used the authors’ provided configurations for both Bernoulli and Gaussian observation models, as appropriate. The MNIST configuration was applied across our MNIST, EMNIST, and Omniglot experiments. Although the codebase hard-codes training to 2000 epochs, we halted training earlier, once the loss had converged (between 780 and 2000 epochs). In some runs, we encountered numerical instabilities that required restarting training from checkpoints.

Overall, the consistently strong performance of $i\mathcal{P}$ -VAE across these generalization tasks suggests significant potential for applications in representation learning and transfer learning. We hope these results motivate further exploration of iterative inference models for representation learning.

C.9 $i\mathcal{P}$ -VAE scales up to complex, high-dimensional color image datasets

Theoretical neuroscience has produced many normative models, including predictive coding [22], sparse coding [39, 54], efficient coding [231], and the free-energy principle [24]. However, from a machine learning standpoint, existing implementations rarely meet modern data complexity requirements. Sparse coding, despite decades of development and widespread recognition of its advantages, still predominantly uses linear decoders and operates on small, grayscale image patches. While we previously demonstrated that $i\mathcal{P}$ -VAE can perform *nonlinear* deep sparse coding (appendices B.6, C.8 and C.10), a critical question remains: can it scale to realistic, high-dimensional datasets?

Here we show that $i\mathcal{P}$ -VAE successfully scales to modern color image datasets, including CIFAR-10 ($3 \times 32 \times 32$), tiny ImageNet ($3 \times 32 \times 32$), and CelebA ($3 \times 128 \times 128$).

CelebA (cropped to 128×128). We trained four models on CelebA to systematically compare iterative versus amortized inference and deep versus linear decoders:

1. $i\mathcal{P}$ -VAE, $\langle \text{grad} | \text{conv} \rangle$: iterative encoding + 8-layer convolutional decoder
2. $i\mathcal{P}$ -VAE, $\langle \text{grad} | \text{lin} \rangle$: iterative encoding + single-layer convolutional layer decoder
3. \mathcal{P} -VAE, $\langle \text{conv} | \text{conv} \rangle$: convolutional encoder + 8-layer convolutional decoder (amortized counterpart of #1)
4. \mathcal{P} -VAE, $\langle \text{conv} | \text{lin} \rangle$: convolutional encoder + single-layer convolutional decoder (amortized counterpart of #2)

All models used latent dimensionality $256 \times 16 \times 16$, with linear decoders using kernel size 38. We trained with $\beta = 1$ and evaluated reconstruction-sparsity performance. Overall performance is measured as Euclidean distance from the ideal point ($R^2 = 1$, sparsity = 1, marked by the gold star in Fig. 4); lower is better. Results are shown in Table 4.

Table 4: Reconstruction-sparsity performance on CelebA (cropped to 128×128). The $\langle \text{grad} | \text{conv} \rangle$ i \mathcal{P} -VAE with deep decoder (model #1) achieves the best overall performance while using 63% fewer parameters than its amortized counterpart (model #3).

Model	Encoder	Decoder	$R^2 \uparrow$	Sparsity \uparrow	Performance \downarrow	Params \downarrow
(1) i \mathcal{P} -VAE	iterative	8-layer conv	0.95	0.93	0.09	0.7 M
(2) i \mathcal{P} -VAE	iterative	linear conv	0.90	0.91	0.13	1.1 M
(3) \mathcal{P} -VAE	conv	8-layer conv	0.86	0.96	0.15	1.9 M
(4) \mathcal{P} -VAE	conv	linear conv	0.74	0.99	0.26	2.3 M

CIFAR-10 and Tiny ImageNet (32×32). To verify scalability across datasets, we trained a $\langle \text{grad} | \text{conv} \rangle$ i \mathcal{P} -VAE with 6 convolutional layers and latent dimensionality $256 \times 8 \times 8$ on both CIFAR-10 and tiny ImageNet ($\beta = 1$). Results are shown in Table 5.

Table 5: Reconstruction-sparsity performance on CIFAR-10 and tiny ImageNet (32×32). The i \mathcal{P} -VAE consistently achieves strong performance across diverse natural image datasets.

Dataset	$R^2 \uparrow$	Sparsity \uparrow	Performance \downarrow
CIFAR-10	0.93	0.97	0.08
Tiny ImageNet	0.95	0.94	0.08

Across all three datasets, i \mathcal{P} -VAE achieves overall performance scores of 0.08–0.09, demonstrating consistent scalability to complex, high-dimensional color images. These results provide strong evidence that normative, brain-inspired models need not be limited to toy datasets: i \mathcal{P} -VAE bridges theoretical neuroscience and modern machine learning, achieving superior reconstruction–sparsity trade-offs with fewer parameters than amortized alternatives.

C.10 i \mathcal{P} -VAE generates novel samples through an iterative procedure

The primary focus of this work (and of FOND more broadly) is on brain-like *inference* dynamics, where generation serves as a means to this end (i.e., “analysis-by-synthesis” [68]). Nevertheless, assessing the model’s generative behavior provides useful insights into its learned representations.

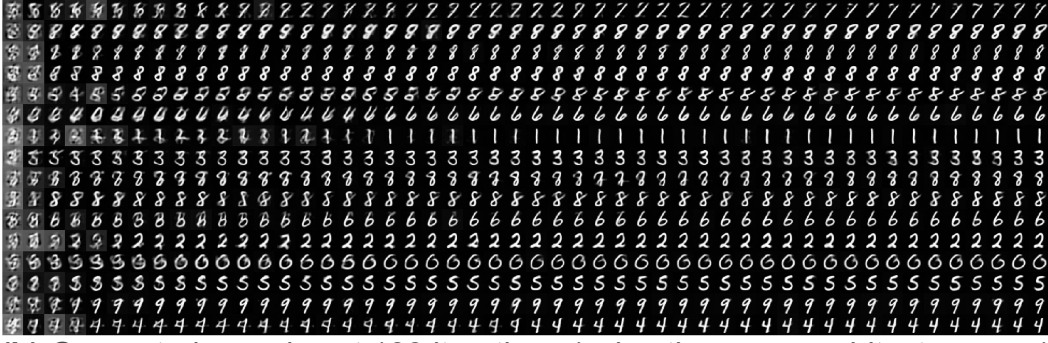
To this end, we performed a qualitative evaluation of a $\langle \text{grad} | \text{conv} \rangle$ i \mathcal{P} -VAE trained on the MNIST dataset with $T_{\text{train}} = 16$. The generation procedure is as follows:

Algorithm 1 Iterative Generation Procedure for i \mathcal{P} -VAE

- 1: Sample from initial prior: $z_0 \sim \mathcal{P}_{\text{ois}}(z_0; \exp(\mathbf{u}_0))$
 - 2: **for** $t = 1$ to T **do**
 - 3: Generate image: $\hat{x}_{t-1} \leftarrow f_{\theta}(z_{t-1})$ \triangleright decoder output
 - 4: Treat generated image as input: $\mathbf{x}_t \leftarrow \hat{x}_{t-1}$
 - 5: Run one inference step: update \mathbf{u}_t via eq. (7), where $\mathbf{x} \equiv \mathbf{x}_t$
 - 6: Sample new latent: $z_t \sim \mathcal{P}_{\text{ois}}(z_t; \exp(\mathbf{u}_t))$
 - 7: **end for**
-

The model successfully produced coherent and recognizable digits (Fig. 18). Notably, during the iterative generation process, some initially ambiguous samples (e.g., resembling both ‘3’ and ‘6’) would converge to well-defined digits after several refinement steps. This progressive clarification mirrors the convergence behavior observed during inference (Fig. 3), suggesting a unified dynamical principle underlying both processes.

(a) Sample generation process across time (using a $\langle \text{grad}|\text{conv} \rangle$ iP-VAE)



(b) Generated samples at 100 iterations (using the same architecture as a)



Figure 18: Generation results from a $\langle \text{grad}|\text{conv} \rangle$ iP-VAE trained on MNIST, sampled using Algorithm 1. (a) Temporal dynamics of generation: horizontal axis shows iteration steps, vertical axis shows different sampled trajectories. (b) Final generated samples after 100 iterations.

However, we observed modest class imbalance in generated samples: certain digits (e.g., ‘8’) appeared more frequently than their $\sim 10\%$ training prevalence. This bias likely reflects the learned prior distribution $\exp(\mathbf{u}_0)$ and could be mitigated through more expressive hierarchical priors.

D Extended Discussion

This appendix expands on key topics introduced in the main paper’s discussion (section 6). We begin by summarizing FOND and discuss how it relates to existing literature (appendix D.1). We then analyze possible factors underlying iP-VAE’s effectiveness (appendix D.2), assess its potential for hardware implementation (appendix D.3), and explore relationships to sampling-based inference methods (appendix D.4).

We conclude with a discussion of limitations and future directions (appendix D.5). These include: accelerating iterative inference (appendix D.5.1), biologically plausible learning (appendix D.5.2), predictive dynamics (appendix D.5.3), hierarchical extensions (appendix D.5.4), and applications to explain neural data variance, thereby bringing theory and experiment closer together (appendix D.5.5).

D.1 A summary of our prescriptive framework, and how it relates to BLR and BONG

In this work, we started by reviewing and synthesizing existing models—from VAEs in machine learning to sparse coding and predictive coding in neuroscience—as instances of variational free energy (\mathcal{F}) minimization. Drawing on this unification potential, we introduced FOND (*Free energy Online Natural-gradient Dynamics*): a framework that prescribes a clear sequence of choices to derive brain-like inference algorithms and architectures from first principles.

FOND establishes a three-step guideline for developing inference models:

1. Select the distributions that fully specify the variational free energy, \mathcal{F}
2. Identify the dynamic variables that parameterize the approximate posterior
3. Apply online natural gradient descent on \mathcal{F} to derive the dynamics

The first two steps are flexible design choices, while the third is fixed: it is an algorithmic prescription that determines the equations governing the temporal evolution of the dynamic variables. Equivalently, this also fully determines the dynamics of the posterior distribution.

To fulfill the “online” component (the O in FOND), we require that inference is performed through continual belief updates, reflecting the adaptive [45–49] and recurrent [40–44] nature of neural processing. This iterative, sequential approach departs from the one-shot amortized inference typical in VAEs [37, 38, 217]. The “natural gradient” component [34, 35, 57] (the N in FOND) ensures that optimization respects the intrinsic geometry of probability distribution space [65, 76, 200].

Situating FOND within existing literature: FOND vs. BONG vs. BLR. Both FOND and BONG [60] are specialized applications of the Bayesian Learning Rule (BLR; [34]) in sequential settings, but they address fundamentally different problems through distinct technical approaches. We clarify these relationships here.

Bayesian Learning Rule (BLR, [34]) — BLR provides a general mathematical framework for deriving learning algorithms as natural gradient descent on variational objectives. It unifies diverse optimization methods—from SGD to Adam—under a single principled lens. Both FOND and BONG instantiate this framework but diverge in their goals, scope, and technical implementation.

BONG (Bayesian Online Natural Gradient, [60]) — BONG focuses on *learning* the parameters θ of Bayesian neural networks in supervised settings. Given labeled data (x, y) , BONG updates network weights online to improve predictive performance. Technically, BONG restricts itself to Gaussian approximate posteriors, which enables the use of analytical results—specifically Price’s [232] and Bonnet’s [233] theorems—to compute gradients of expectations (their Eq. 3). This Gaussian-specific approach yields closed-form update rules (their Eqs. 9-10) that BONG then approximates in various ways to achieve computational efficiency.

FOND (Free energy Online Natural-gradient Dynamics) — FOND, by contrast, focuses on *deriving inference dynamics* for variational parameters (e.g., membrane potentials u) in unsupervised settings. FOND’s goal is to specify how neural activity evolves over time to perform posterior inference, not to learn network weights.

This fundamental difference in goals necessitates a different technical approach: FOND must be distribution-agnostic to derive models like $i\mathcal{P}$ -VAE (Poisson) alongside $i\mathcal{G}$ -VAE (Gaussian). Because Price’s and Bonnet’s theorems do not apply beyond Gaussians, FOND follows the standard VAE approach: approximate expectations via Monte Carlo sampling, then compute gradients of the resulting stochastic objective. This generality allows FOND to derive the spiking dynamics of $i\mathcal{P}$ -VAE, which is impossible within BONG’s Gaussian-restricted framework.

BONG vs. FOND: Key Differences

Goal: BONG learns network parameters (θ); FOND derives neural dynamics (\dot{u})

Setting: BONG primarily targets supervised learning (though applicable to unsupervised settings via likelihood choice); FOND targets unsupervised inference

Scope: BONG is Gaussian-specific; FOND is distribution-agnostic

Technical approach: BONG uses analytical gradient computation via Price’s and Bonnet’s theorems; FOND uses Monte Carlo sampling then differentiation

These are not merely different “flavors” of the same algorithm but distinct mathematical procedures addressing complementary problems. BONG focuses on online supervised learning with Gaussian uncertainty, while FOND derives brain-inspired inference dynamics across diverse distributional assumptions. Both enrich the BLR framework by demonstrating its versatility in different domains.

FOND’s utility: application to derive iterative VAEs. To demonstrate the viability and utility of FOND, we developed a novel iterative VAE model family, including a spiking variant, the $i\mathcal{P}$ -VAE.

For this specific implementation, we made two biologically motivated choices:

1. Modeling neural activity as spike counts [180, 192, 193, 195, 234–236] via Poisson distributions [50], departing from the standard Gaussian assumptions in predictive coding [22, 33].
2. Assigning log-rate as the dynamic variable for each neuron. Log-rate is the canonical parameter of the Poisson distribution, and it is interpretable as the membrane potential of the neuron [70, 71].

With these choices fixed, the natural gradient descent on \mathcal{F} unambiguously determined the form of the spiking neural dynamics in $i\mathcal{P}$ -VAE.

The resulting architecture, $i\mathcal{P}$ -VAE, shares theoretical and empirical similarities with LCA [39], effectively functioning as a spiking, stochastic extension of this classic model. Our empirical results showed that all iterative VAEs ($i\mathcal{P}$ -VAE, $i\mathcal{G}$ -VAE, $i\mathcal{G}_{\text{relu}}$ -VAE) consistently outperformed their amortized counterparts in balancing reconstruction and sparsity, with $i\mathcal{P}$ -VAE and LCA achieving the best overall trade-offs. Additionally, when evaluated against hybrid iterative-amortized VAEs in out-of-distribution generalization tasks, $i\mathcal{P}$ -VAE showed strong performance.

Why is $i\mathcal{P}$ -VAE effective? We explore this next by drawing connections to recent advances in sequence modeling and hierarchical VAE theory.

D.2 Three possible explanations for the effectiveness of $i\mathcal{P}$ -VAE

Several complementary factors contribute to $i\mathcal{P}$ -VAE’s effectiveness. First, we note interesting parallels with recent advances in sequence modeling. Recently, Beck et al. [114] introduced extended LSTM (xLSTM) that performs competitively with state-of-the-art transformers and state space models. xLSTM achieves this mainly through two key modifications: (1) replacing sigmoid gates with *exponential* nonlinearities, and (2) implementing a *normalization* scheme that stabilizes training. Similarly, $i\mathcal{P}$ -VAE employs the $\exp(\cdot)$ nonlinearity to map membrane potentials to firing rates, providing a highly expressive activation function (Figs. 5 and 6). Furthermore, the theoretical derivations naturally gave rise to a multiplicative divisive normalization that stabilizes network dynamics and promotes convergence (eq. (8)).

Second, all our iterative VAEs, including $i\mathcal{P}$ -VAE, benefit from effective *stochastic depth*. Child [115] demonstrated both theoretically and empirically that hierarchical VAEs gain their effectiveness from stochastic depth. When we unroll the iterative VAE encoding algorithms in time (e.g., Figs. 5 and 6), they resemble specialized hierarchical VAEs, but without the spatial coarse-graining found in typical hierarchical architectures [115, 125, 161]. Based on the arguments put forth by Child [115], we speculate that this temporal depth in $i\mathcal{P}$ -VAE’s stochastic representations contributes significantly to model performance.

In summary, $i\mathcal{P}$ -VAE’s success likely stems from at least three key elements: (1) the exponential nonlinearity providing expressiveness, (2) emergent normalization ensuring stability and convergence, and (3) effective stochastic depth through temporal unrolling.

A promising direction for future work would be extending $i\mathcal{P}$ -VAE into a full hierarchical architecture with spatial coarse-graining, potentially further enhancing its already strong performance, which we discuss in detail below.

D.3 Hardware-efficient implementation and real-world deployment potential of $i\mathcal{P}$ -VAE

The computational characteristics of $i\mathcal{P}$ -VAE make it particularly well-suited for efficient hardware implementation, especially on specialized accelerators and resource-constrained devices. This efficiency stems from three key properties: (1) sparsity, (2) weight reuse, and (3) integer-valued representations, as detailed below.

First, $i\mathcal{P}$ -VAE generates sparse, integer-valued spike counts as representations. This sparse coding strategy aligns with emerging sparse tensor accelerators and neuromorphic computing architectures, which can achieve substantial improvements in energy efficiency compared to dense matrix operations [116]. The predominance of zeros in these representations (60%-95%, in natural image patch experiments, Fig. 4; and up to 84% in MNIST experiments, Table 3) enables both memory and computation savings through sparse storage formats [102] and compute-skipping optimizations [103].

Second, $i\mathcal{P}$ -VAE’s inference algorithm reuses the same set of weights across all iterations (Fig. 5), potentially reducing memory bandwidth requirements compared to deep neural networks with unique parameters at each layer. This is particularly significant for hardware deployment, as memory transfers often dominate energy consumption in neural network inference [103, 237, 238]. Where traditional deep networks must continuously load new parameters from memory, $i\mathcal{P}$ -VAE’s weight-sharing minimizes costly memory accesses and allows for efficient on-chip caching of the entire model.

Third, the discrete, integer-valued nature of spike counts eliminates the need for high-precision floating-point arithmetic [103–105], enabling deployment on simpler fixed-point hardware with reduced power consumption. Combined with the inherent sparsity, this positions $i\mathcal{P}$ -VAE as a promising candidate for edge computing applications where energy and computational resources are severely constrained.

These properties are particularly valuable for real-world autonomous systems and robotics applications, where power budgets are limited and attaching power-hungry GPUs is impractical [103]. For instance, drones, mobile robots, and wearable devices could leverage $i\mathcal{P}$ -VAE for efficient on-device perception without requiring cloud connectivity or massive batteries.

As noted above, $i\mathcal{P}$ -VAE and LCA share key theoretical, computational, and empirical characteristics. Given that LCA has been successfully implemented both as a spiking neural network [123] and on neuromorphic hardware [239], we expect $i\mathcal{P}$ -VAE to be similarly deployable on such platforms, potentially with even greater efficiency due to its principled stochastic dynamics.

Overall, $i\mathcal{P}$ -VAE’s combination of sparse integer representations, weight reuse, and alignment with neuromorphic computing principles offers a promising path toward deploying sophisticated perception capabilities in resource-constrained environments, bridging the gap between theoretical neuroscience models and practical applications.

D.4 Relationship to sampling-based inference methods

Throughout this work, we focused on variational inference (VI) as our framework for approximating Bayesian posteriors. However, sampling-based methods, particularly Markov Chain Monte Carlo (MCMC; [240–243]), represent an equally important alternative approach. Like VI, sampling-based methods have been extensively explored in theoretical neuroscience [117–122, 244–252]. See Haefner et al. [253] for a balanced review.

Both VI and sampling address a key limitation of *maximum a posteriori* (MAP) inference by providing access to the full posterior distribution rather than just a point estimate. The $i\mathcal{P}$ -VAE extends LCA [39] from a deterministic point estimate to a probabilistic representation with full posterior uncertainty. Similarly, recent sampling-based approaches have enhanced both sparse coding [120] and predictive coding [121, 122] by incorporating stochastic dynamics that explore the full posterior landscape rather than converging to a single point. These parallel developments in both VI and sampling frameworks reveal their complementary roles in addressing the limitations of traditional MAP estimation.

Sampling-based models all perform Bayesian posterior inference, but differ in whether they adopt a “prescriptive” approach, as outlined in appendix B.1. For a non-prescriptive example, Echeveste et al. [247] began with a well-established biophysical circuit—the stochastic *stabilized supralinear network* (SSN; [83, 254, 255])—and adapted it to perform posterior inference. Their optimized network exhibited key biological properties and achieved substantially faster sampling than standard Langevin samplers. These results compellingly demonstrate that biologically realistic circuits can perform Bayesian inference. However, this represents a bottom-up, descriptive strategy—starting from an existing circuit and adapting it for inference; whereas, other sampling-based approaches align more closely with the top-down, principle-driven methodology we advocate.

A particularly relevant example is the work of Masset et al. [119], who demonstrated that incorporating natural gradients into Langevin sampling significantly accelerates convergence. Their approach directly parallels ours: they derive a spiking neural network algorithm prescriptively from first principles, drawing inspiration from Ma et al. [256], who proposed a “complete recipe” for constructing MCMC samplers. This “complete recipe” serves a role analogous to the Bayesian learning rule (BLR; [34]) in our work, as they both provide a unifying framework for their respective domains. While BLR unifies learning algorithms under variational inference with natural gradient updates, the “complete recipe” provides a corresponding unifying framework for sampling-based MCMC methods.

Interestingly, our iterative VAE models, while fundamentally grounded in VI principles, incorporate sampling elements during inference by approximating the reconstruction loss through Monte Carlo sampling. This hybrid character hints at an opportunity for theoretical unification between VI and MCMC. Prior work has explored this direction [257, 258], but further research is needed to clarify the relationships between VI and sampling. This unification potential is particularly interesting in the context of brain-like inference models [23, 117, 253].

D.5 Limitations and future work

In this final appendix, we discuss the limitations of our work and how future work can address them.

D.5.1 Iterative inference: Generalization advantages with manageable computational costs

Our experiments consistently suggest that iterative inference outperforms amortized approaches in reconstruction-sparsity trade-offs (Fig. 4). Additionally, the fully iterative $i\mathcal{P}$ -VAE also outperformed hybrid iterative-amortized VAEs in out-of-distribution (OOD) generalization experiments, including both reconstruction and downstream classification OOD tasks (Figs. 13 to 16).

Furthermore, we observed a clear pattern: the less amortized the inference process, the better the generalization capability. *Semi-amortized VAE* (sa-VAE; [92]), which relies partially on iterative updates, outperformed the more heavily amortized *iterative amortized VAE* (ia-VAE; [91]), suggesting that reducing dependence on learned amortization functions enhances adaptability to novel inputs.

Iterative reasoning in other domains. Similar advantages of iterative inference have been observed in other domains as well. Recent advances in large language models employ iterative reasoning at test time, either explicitly through prompting techniques like *chain-of-thought* [259] and *tree-of-thought* [260], or through more sophisticated inference-time algorithms and architectures. These approaches generally fall into two categories: some focus on the inference algorithm, like the MCMC-based sampler from Karan and Du [261], which elicits latent reasoning from a base model. Others modify the architecture itself to be inherently more iterative. For instance, the brain-inspired *Hierarchical Reasoning Model* (HRM; [262]) introduces a novel recurrent structure for latent reasoning, while Koishekenov et al. [263] train a model to recursively apply its own reasoning-critical layers.

This principle has earlier roots in computer vision, where the brain-inspired *recursive cortical network* (RCN; [264, 265]) showed that a generative model using iterative message-passing, equipped with both feedback and lateral recurrent connections, could achieve remarkable data efficiency and generalization on challenging visual reasoning tasks, such as breaking text-based CAPTCHAs [264].

These diverse approaches—spanning prompting, sampling, and architecture—all converge on a similar principle: dedicating more test-time computational steps to a problem enables superior performance on complex reasoning tasks, despite the additional overhead.

The power of iterative inference is particularly evident on benchmarks designed to test the limits of abstract reasoning. On the challenging ARC-AGI benchmark [266], Liao and Gu [267] achieved strong performance (34.75% on training set, 20% on evaluation set) by replacing encoder networks entirely with expectation-maximization (EM) iterative updates. This is conceptually similar to our approach, where iterative optimization replaces learned encoders. Remarkably, Liao and Gu [267] achieved these strong results without any pretraining, further supporting the idea that iterative inference may offer inherent advantages for generalization on difficult, abstract problems.

The serial scaling hypothesis. These results align with the emerging *serial scaling hypothesis* [268], which posits that many challenging problems in machine learning, particularly those involving reasoning, planning, sequential decision-making, or physical simulation, are “inherently serial.” Such problems possess computational dependencies that resist parallelization, meaning that simply scaling parallel compute (e.g., model width) is insufficient.

Therefore, progress fundamentally requires scaling *serial computation*: increasing the number of sequential processing steps (e.g., recurrent iterations or model depth). This perspective suggests the benefits of iterative methods might stem not just from mimicking biological processes, but from fulfilling a fundamental computational requirement for certain task classes.

Re-evaluating the computational trade-off. Our runtime analysis (appendix C.7) challenges the assumption that iterative inference is prohibitively slow at test time. Iterative models reached amortized-level performance within comparable wall-clock times (especially with large-batch parallelization), then continued refining to achieve substantially better reconstruction-sparsity trade-offs. The primary cost is training time—roughly $2\times$ longer than amortized models (appendix C.1.4)—which is understandable given their increased effective depth, interpretable as training deeper ResNets with shared parameters (Fig. 5). This suggests that iterative models are particularly well-suited for applications where inference quality and generalization are central, and the one-time cost of longer training is acceptable.

Despite these encouraging runtime results, the general efficiency of iterative methods remains an active area of research. The growing adoption of iterative techniques in large-scale commercial models has spurred optimization efforts. Recent advances in hardware acceleration [269, 270], specialized architectures for recurrent computation [114, 271], and algorithmic improvements for iterative processes [272, 273] suggest that the efficiency gap may narrow in the coming years.

The fundamental question remains whether the generalization advantages of iterative inference, increasingly supported by both empirical results and theoretical arguments, will continue to justify any remaining computational costs as both approaches evolve.

D.5.2 Biologically plausible learning rules

In this paper, we presented a prescriptive framework for deriving inference dynamics from first principles, but we did not address this question for learning the generative model. In other words, our work is prescriptive about \mathbf{u} , but not $\hat{\theta}$.

We optimized model parameters through a procedure that can be interpreted as backpropagation through time [93, 94]. This is not biologically plausible, because it still suffers from the weight transport problem [274]. It’s even worse for temporal credit assignment because neurons lack a mechanism to store activation histories needed for precise backward passes through time [275, 276].

Other models, like predictive coding (PC), are prescriptive about both inference and learning aspects. Specifically, PC learning is effectively Hebbian [33, 277]. Biologically plausible synaptic learning rules exist for sparse coding as well. For instance, Zylberberg et al. [123] introduced SAILnet, a spiking network that performs sparse coding using only synaptically local information. Interestingly, the distribution of inhibitory connections learned by SAILnet is lognormal, matching experimental observations in cortex [278].

In general, we consider inference dynamics as more fundamental than learning, for several reasons. First, inference is far more experimentally accessible than synaptic weight dynamics. We can record from large populations of neurons while animals receive sensory stimulation, but we lack complete electron microscopy reconstructions of synapses before, during, and after learning. Second, what we call “learning” in machine learning likely corresponds to a complex mixture of evolution, development, and experience-dependent plasticity in biology [143]. Given this complexity, it is reasonable to achieve learning in neural networks using powerful but biologically implausible methods such as backpropagation [279–281].

With that said, future work should still explore biologically plausible prescriptive frameworks for learning synaptic weights, potentially building on emerging theories like eligibility traces [282], feedback alignment [283, 284], and e-prop [275].

A natural extension: combining BONG and FOND for continual learning. Beyond biological plausibility, an exciting direction is to combine BONG with FOND. As we discussed in appendix D.1, BONG and FOND are complementary specializations of BLR. Using the same framing adopted here, BONG can be viewed as a prescriptive framework for deriving weight dynamics, $\hat{\theta}$, while FOND prescribes inference dynamics, \mathbf{u} . Since both frameworks minimize the same free energy objective, their combination is mathematically natural.

This BONG/FOND fusion would yield a fully Bayesian, principled algorithm that is prescriptive about both learning and inference: a continually learning, online Bayesian system that adapts both its beliefs and its generative model simultaneously—potentially enabling lifelong learning without catastrophic forgetting. We consider this unified framework a promising direction for future work.

D.5.3 Predictive dynamics, with application to non-stationary sequences

Brains are prediction machines [146, 285, 286]. Overwhelming evidence, ranging from retina [287] to cortex [288], suggests that biological circuits are engaged in predictive computations, *anticipating* the future [289], rather than merely adapting to the past. However, our current framework lacks a concrete mechanism for such anticipatory computation. While we emphasized the importance of online inference for modeling biological perception, we left a crucial element unaddressed: online inference is most meaningful in the context of non-stationary inputs. Our work, however, explored only the simplest type of sequence: stationary inputs with the same sample repeated multiple times.

Future extensions should incorporate genuinely predictive updates that *evolve* the current posterior into a predictive prior distribution, rather than relying on the identity mapping we used in this work.

Several promising approaches could guide this development. In machine learning, Duran-Martin et al. [124] introduced *Bayesian online learning in non-stationary environments* (BONE), a unifying framework for probabilistic online learning in changing environments. Within neuroscience, Jiang and Rao [290] introduced *dynamic predictive coding*, in which higher-level neurons modulate the transition dynamics of lower-level ones, which is conceptually similar to *HyperNetworks* [291]. Millidge et al. [292] introduced *temporal predictive coding* networks, where recurrent connections are used to predict the network’s own future activity, allowing it to approximate a Kalman filter with biologically plausible, local learning rules. Another notable contribution is the *polar prediction model* proposed by Fiquet and Simoncelli [293]. Inspired by the temporal “straightening” hypothesis [294], the model performs linear extrapolation of phase in a learned complex-valued latent space, enabling next-frame prediction with strong performance, interpretability, and computational simplicity.

We believe predicting the future and adapting to the past represent two distinct yet complementary computations employed by biological systems. When modeling these processes, both should be clearly motivated and, ideally, derived from first principles. In this work, we addressed adaptation but left prediction largely unexplored. We aim to develop the missing predictive component in future work, while evaluating the resulting architectures on non-stationary datasets such as natural videos.

D.5.4 Hierarchical extensions with realistic synaptic transmission delays

Another dimension of being prescriptive lies in architectural design. In this paper, we focused on single-layer models and did not provide prescriptions for multi-layer, hierarchical architectures [5, 295]. Yet this is an important direction, given growing evidence that hierarchical VAEs exhibit cortex-like organization [125, 126]. Future extensions should address two key components [296]: (1) the structure of the generative model, and (2) information flow during inference.

For the generative model, a fundamental decision concerns the probabilistic dependencies between latent variables across different layers. Should the joint distribution be structured in a Markovian chain, where each layer interacts only with its immediate neighbors? Or might a more flexible *heterarchical* structure [297–299] with an arbitrary graph topology [300] better capture the complex causal structure of natural signals?

For information flow during inference, several questions arise: what information propagates between layers, and in which directions [301]? Each choice leads to different computational trade-offs and makes distinct predictions about neural dynamics. For example, predictive coding typically propagates prediction errors upward in the hierarchy. Crucially, biological systems do not transmit raw signals between hierarchical levels, but instead apply various forms of pooling [302] or coarse-graining [125] operations that transform lower-level representations into increasingly abstract features at higher layers. This pooling serves both computational efficiency and representational purposes, enabling the extraction of invariant features while reducing dimensionality [303]. In the future, our framework could be extended to derive normative pooling operations through free energy minimization under appropriate architectural constraints, potentially explaining why the visual system employs specific receptive field pooling strategies rather than alternatives.

Finally, realistic neural models should account for finite signal propagation delays in biological axons [304–306]. In future work, we plan to incorporate such transmission delays into our framework to enhance biological realism and potentially uncover computational mechanisms uniquely enabled by temporally structured information flow [307].

D.5.5 Applications to explain neural data variance

The ultimate test of a model is its ability to explain empirical data. $i\mathcal{P}$ -VAE demonstrated several emergent behaviors that mimic cortical properties at a phenomenological level (Figs. 3, 8 and 11), but this is only a first step toward rigorous validation against neural data. A comprehensive assessment would require testing our model’s capacity to explain neural response variance [308, 309], for example, in frameworks like Brain-Score [127].

Our philosophical approach differs from purely descriptive models that are directly optimized to fit neural responses [128, 310]. Instead, we advocate for normative models that are *validated* against neural data, rather than trained explicitly to *reproduce* it, in line with critiques of purely descriptive approaches [311]. This approach offers greater interpretability, as the model’s behavior stems from principled objectives (e.g., free energy minimization) rather than parameter fitting [312]. From this point of view, there are two promising paths forward.

First, we can systematically explore different prescriptive choices within our framework to identify which configurations best explain neural data. For instance, comparing how alternative inference dynamics or distributional assumptions affect the model’s ability to predict neural responses to novel stimuli. Second, we might consider a semi-supervised training approach [313], where free energy minimization is augmented with a neural regularization term that encourages alignment between $i\mathcal{P}$ -VAE spike patterns and recorded neural activity in response to identical stimuli.

The spiking nature of $i\mathcal{P}$ -VAE makes it particularly appropriate for comparison with neural recordings, offering closer parallels to biological data than non-spiking alternatives. Beyond explaining variance, $i\mathcal{P}$ -VAE’s spiking representation also enables *in silico* experiments that can potentially inform future *in vivo* studies [128, 314]. Finally, this compatibility with spike train data creates an opportunity for rigorous comparisons between variational inference approaches like ours and sampling-based spiking models [118, 119, 245, 247, 249–252, 305] (appendix D.4), in terms of their ability to account for empirical neural responses.

In the future, we are excited to test a fully predictive, hierarchical version of $i\mathcal{P}$ -VAE against neural data to put our framework to the ultimate test. Such experiments could validate the theory and help identify which aspects of neural computation are most effectively captured by variational principles.

NeurIPS Paper Checklist

1. Claims

Question: Do the main claims made in the abstract and introduction accurately reflect the paper's contributions and scope?

Answer: [\[Yes\]](#)

Justification: In section 4 we show that online natural gradient descent on \mathcal{F} , under Poisson assumptions, leads to a recurrent spiking neural network that performs variational inference via membrane potential dynamics. In the same section we also show its desirable theoretical features. In section 5 and appendix C we present the empirical results.

Guidelines:

- The answer NA means that the abstract and introduction do not include the claims made in the paper.
- The abstract and/or introduction should clearly state the claims made, including the contributions made in the paper and important assumptions and limitations. A No or NA answer to this question will not be perceived well by the reviewers.
- The claims made should match theoretical and experimental results, and reflect how much the results can be expected to generalize to other settings.
- It is fine to include aspirational goals as motivation as long as it is clear that these goals are not attained by the paper.

2. Limitations

Question: Does the paper discuss the limitations of the work performed by the authors?

Answer: [\[Yes\]](#)

Justification: We briefly overview limitations in section 6, and then substantially expand upon them in appendix D.5. Specifically, we discuss limitations concerning iterative inference (appendix D.5.1), learning rules (appendix D.5.2), sequences (appendix D.5.3), architecture (appendix D.5.4), and applications to neural data (appendix D.5.5).

Guidelines:

- The answer NA means that the paper has no limitation while the answer No means that the paper has limitations, but those are not discussed in the paper.
- The authors are encouraged to create a separate "Limitations" section in their paper.
- The paper should point out any strong assumptions and how robust the results are to violations of these assumptions (e.g., independence assumptions, noiseless settings, model well-specification, asymptotic approximations only holding locally). The authors should reflect on how these assumptions might be violated in practice and what the implications would be.
- The authors should reflect on the scope of the claims made, e.g., if the approach was only tested on a few datasets or with a few runs. In general, empirical results often depend on implicit assumptions, which should be articulated.
- The authors should reflect on the factors that influence the performance of the approach. For example, a facial recognition algorithm may perform poorly when image resolution is low or images are taken in low lighting. Or a speech-to-text system might not be used reliably to provide closed captions for online lectures because it fails to handle technical jargon.
- The authors should discuss the computational efficiency of the proposed algorithms and how they scale with dataset size.
- If applicable, the authors should discuss possible limitations of their approach to address problems of privacy and fairness.
- While the authors might fear that complete honesty about limitations might be used by reviewers as grounds for rejection, a worse outcome might be that reviewers discover limitations that aren't acknowledged in the paper. The authors should use their best judgment and recognize that individual actions in favor of transparency play an important role in developing norms that preserve the integrity of the community. Reviewers will be specifically instructed to not penalize honesty concerning limitations.

3. Theory assumptions and proofs

Question: For each theoretical result, does the paper provide the full set of assumptions and a complete (and correct) proof?

Answer: [\[Yes\]](#)

Justification: Our theory includes derivations from first principles, with the full set of assumptions and details provided in section 4 and appendix B.

Guidelines:

- The answer NA means that the paper does not include theoretical results.
- All the theorems, formulas, and proofs in the paper should be numbered and cross-referenced.
- All assumptions should be clearly stated or referenced in the statement of any theorems.
- The proofs can either appear in the main paper or the supplemental material, but if they appear in the supplemental material, the authors are encouraged to provide a short proof sketch to provide intuition.
- Inversely, any informal proof provided in the core of the paper should be complemented by formal proofs provided in appendix or supplemental material.
- Theorems and Lemmas that the proof relies upon should be properly referenced.

4. Experimental result reproducibility

Question: Does the paper fully disclose all the information needed to reproduce the main experimental results of the paper to the extent that it affects the main claims and/or conclusions of the paper (regardless of whether the code and data are provided or not)?

Answer: [\[Yes\]](#)

Justification: Details about architectures, hyperparameters, training, and experiment are provided in section 5 and appendix C (specifically, appendix C.1).

Guidelines:

- The answer NA means that the paper does not include experiments.
- If the paper includes experiments, a No answer to this question will not be perceived well by the reviewers: Making the paper reproducible is important, regardless of whether the code and data are provided or not.
- If the contribution is a dataset and/or model, the authors should describe the steps taken to make their results reproducible or verifiable.
- Depending on the contribution, reproducibility can be accomplished in various ways. For example, if the contribution is a novel architecture, describing the architecture fully might suffice, or if the contribution is a specific model and empirical evaluation, it may be necessary to either make it possible for others to replicate the model with the same dataset, or provide access to the model. In general, releasing code and data is often one good way to accomplish this, but reproducibility can also be provided via detailed instructions for how to replicate the results, access to a hosted model (e.g., in the case of a large language model), releasing of a model checkpoint, or other means that are appropriate to the research performed.
- While NeurIPS does not require releasing code, the conference does require all submissions to provide some reasonable avenue for reproducibility, which may depend on the nature of the contribution. For example
 - (a) If the contribution is primarily a new algorithm, the paper should make it clear how to reproduce that algorithm.
 - (b) If the contribution is primarily a new model architecture, the paper should describe the architecture clearly and fully.
 - (c) If the contribution is a new model (e.g., a large language model), then there should either be a way to access this model for reproducing the results or a way to reproduce the model (e.g., with an open-source dataset or instructions for how to construct the dataset).
 - (d) We recognize that reproducibility may be tricky in some cases, in which case authors are welcome to describe the particular way they provide for reproducibility.

In the case of closed-source models, it may be that access to the model is limited in some way (e.g., to registered users), but it should be possible for other researchers to have some path to reproducing or verifying the results.

5. Open access to data and code

Question: Does the paper provide open access to the data and code, with sufficient instructions to faithfully reproduce the main experimental results, as described in supplemental material?

Answer: [Yes]

Justification: Our code, data, and model checkpoints are available at: <https://github.com/hadivafai/IterativeVAE>

- The answer NA means that paper does not include experiments requiring code.
- Please see the NeurIPS code and data submission guidelines (<https://nips.cc/public/guides/CodeSubmissionPolicy>) for more details.
- While we encourage the release of code and data, we understand that this might not be possible, so “No” is an acceptable answer. Papers cannot be rejected simply for not including code, unless this is central to the contribution (e.g., for a new open-source benchmark).
- The instructions should contain the exact command and environment needed to run to reproduce the results. See the NeurIPS code and data submission guidelines (<https://nips.cc/public/guides/CodeSubmissionPolicy>) for more details.
- The authors should provide instructions on data access and preparation, including how to access the raw data, preprocessed data, intermediate data, and generated data, etc.
- The authors should provide scripts to reproduce all experimental results for the new proposed method and baselines. If only a subset of experiments are reproducible, they should state which ones are omitted from the script and why.
- At submission time, to preserve anonymity, the authors should release anonymized versions (if applicable).
- Providing as much information as possible in supplemental material (appended to the paper) is recommended, but including URLs to data and code is permitted.

6. Experimental setting/details

Question: Does the paper specify all the training and test details (e.g., data splits, hyperparameters, how they were chosen, type of optimizer, etc.) necessary to understand the results?

Answer: [Yes]

Justification: Most details needed for understanding the train and test details are provided in section 5 and appendix C. The code will also be provided for full details.

Guidelines:

- The answer NA means that the paper does not include experiments.
- The experimental setting should be presented in the core of the paper to a level of detail that is necessary to appreciate the results and make sense of them.
- The full details can be provided either with the code, in appendix, or as supplemental material.

7. Experiment statistical significance

Question: Does the paper report error bars suitably and correctly defined or other appropriate information about the statistical significance of the experiments?

Answer: [Yes]

Justification: For the main experiments shown in Fig. 4, we report variability with respect to hyperparameters using box plots (showing median, interquartile range, minimum, and maximum). For our only numerical result in Table 3, we report 99% confidence intervals estimated from 5 random initializations, assuming the sample means follow a t-distribution by the central limit theorem.

Guidelines:

- The answer NA means that the paper does not include experiments.
- The authors should answer "Yes" if the results are accompanied by error bars, confidence intervals, or statistical significance tests, at least for the experiments that support the main claims of the paper.
- The factors of variability that the error bars are capturing should be clearly stated (for example, train/test split, initialization, random drawing of some parameter, or overall run with given experimental conditions).
- The method for calculating the error bars should be explained (closed form formula, call to a library function, bootstrap, etc.)
- The assumptions made should be given (e.g., Normally distributed errors).
- It should be clear whether the error bar is the standard deviation or the standard error of the mean.
- It is OK to report 1-sigma error bars, but one should state it. The authors should preferably report a 2-sigma error bar than state that they have a 96% CI, if the hypothesis of Normality of errors is not verified.
- For asymmetric distributions, the authors should be careful not to show in tables or figures symmetric error bars that would yield results that are out of range (e.g. negative error rates).
- If error bars are reported in tables or plots, The authors should explain in the text how they were calculated and reference the corresponding figures or tables in the text.

8. Experiments compute resources

Question: For each experiment, does the paper provide sufficient information on the computer resources (type of compute workers, memory, time of execution) needed to reproduce the experiments?

Answer: [Yes]

Justification: We specify the hardware and compute usage in appendix C.1.4. Overall our experiments were very light on compute and are accessible to academic research.

Guidelines:

- The answer NA means that the paper does not include experiments.
- The paper should indicate the type of compute workers CPU or GPU, internal cluster, or cloud provider, including relevant memory and storage.
- The paper should provide the amount of compute required for each of the individual experimental runs as well as estimate the total compute.
- The paper should disclose whether the full research project required more compute than the experiments reported in the paper (e.g., preliminary or failed experiments that didn't make it into the paper).

9. Code of ethics

Question: Does the research conducted in the paper conform, in every respect, with the NeurIPS Code of Ethics <https://neurips.cc/public/EthicsGuidelines>?

Answer: [Yes]

Justification: Our research conforms to the NeurIPS code of ethics in every aspect.

Guidelines:

- The answer NA means that the authors have not reviewed the NeurIPS Code of Ethics.
- If the authors answer No, they should explain the special circumstances that require a deviation from the Code of Ethics.
- The authors should make sure to preserve anonymity (e.g., if there is a special consideration due to laws or regulations in their jurisdiction).

10. Broader impacts

Question: Does the paper discuss both potential positive societal impacts and negative societal impacts of the work performed?

Answer: [NA]

Justification: Our work aims to provide a theoretical understanding of how brain-like inference models can be derived from first principles. The experiments are conducted on small-scale, controlled settings without practical deployment. As such, we do not foresee immediate societal impact, either positive or negative, or potential for malicious applications.

Guidelines:

- The answer NA means that there is no societal impact of the work performed.
- If the authors answer NA or No, they should explain why their work has no societal impact or why the paper does not address societal impact.
- Examples of negative societal impacts include potential malicious or unintended uses (e.g., disinformation, generating fake profiles, surveillance), fairness considerations (e.g., deployment of technologies that could make decisions that unfairly impact specific groups), privacy considerations, and security considerations.
- The conference expects that many papers will be foundational research and not tied to particular applications, let alone deployments. However, if there is a direct path to any negative applications, the authors should point it out. For example, it is legitimate to point out that an improvement in the quality of generative models could be used to generate deepfakes for disinformation. On the other hand, it is not needed to point out that a generic algorithm for optimizing neural networks could enable people to train models that generate Deepfakes faster.
- The authors should consider possible harms that could arise when the technology is being used as intended and functioning correctly, harms that could arise when the technology is being used as intended but gives incorrect results, and harms following from (intentional or unintentional) misuse of the technology.
- If there are negative societal impacts, the authors could also discuss possible mitigation strategies (e.g., gated release of models, providing defenses in addition to attacks, mechanisms for monitoring misuse, mechanisms to monitor how a system learns from feedback over time, improving the efficiency and accessibility of ML).

11. Safeguards

Question: Does the paper describe safeguards that have been put in place for responsible release of data or models that have a high risk for misuse (e.g., pretrained language models, image generators, or scraped datasets)?

Answer: [NA]

Justification: Our work is primarily theoretical and involves small-scale experiments using publicly available datasets. It does not involve the release of models or data with high risk of misuse, so this question is not applicable.

Guidelines:

- The answer NA means that the paper poses no such risks.
- Released models that have a high risk for misuse or dual-use should be released with necessary safeguards to allow for controlled use of the model, for example by requiring that users adhere to usage guidelines or restrictions to access the model or implementing safety filters.
- Datasets that have been scraped from the Internet could pose safety risks. The authors should describe how they avoided releasing unsafe images.
- We recognize that providing effective safeguards is challenging, and many papers do not require this, but we encourage authors to take this into account and make a best faith effort.

12. Licenses for existing assets

Question: Are the creators or original owners of assets (e.g., code, data, models), used in the paper, properly credited and are the license and terms of use explicitly mentioned and properly respected?

Answer: [Yes]

Justification: We credit and cite the creators of the code libraries, models, and datasets used in the paper. We specify licenses in appendix C.

Guidelines:

- The answer NA means that the paper does not use existing assets.
- The authors should cite the original paper that produced the code package or dataset.
- The authors should state which version of the asset is used and, if possible, include a URL.
- The name of the license (e.g., CC-BY 4.0) should be included for each asset.
- For scraped data from a particular source (e.g., website), the copyright and terms of service of that source should be provided.
- If assets are released, the license, copyright information, and terms of use in the package should be provided. For popular datasets, paperswithcode.com/datasets has curated licenses for some datasets. Their licensing guide can help determine the license of a dataset.
- For existing datasets that are re-packaged, both the original license and the license of the derived asset (if it has changed) should be provided.
- If this information is not available online, the authors are encouraged to reach out to the asset's creators.

13. **New assets**

Question: Are new assets introduced in the paper well documented and is the documentation provided alongside the assets?

Answer: [\[Yes\]](#)

Justification: We provide code for reproducibility, which contains documentation on how to replicate experiments. We will also release code notebooks with more learning-oriented documentation.

Guidelines:

- The answer NA means that the paper does not release new assets.
- Researchers should communicate the details of the dataset/code/model as part of their submissions via structured templates. This includes details about training, license, limitations, etc.
- The paper should discuss whether and how consent was obtained from people whose asset is used.
- At submission time, remember to anonymize your assets (if applicable). You can either create an anonymized URL or include an anonymized zip file.

14. **Crowdsourcing and research with human subjects**

Question: For crowdsourcing experiments and research with human subjects, does the paper include the full text of instructions given to participants and screenshots, if applicable, as well as details about compensation (if any)?

Answer: [\[NA\]](#)

Justification: This paper does not involve research with human subjects or crowdsourcing.

Guidelines:

- The answer NA means that the paper does not involve crowdsourcing nor research with human subjects.
- Including this information in the supplemental material is fine, but if the main contribution of the paper involves human subjects, then as much detail as possible should be included in the main paper.
- According to the NeurIPS Code of Ethics, workers involved in data collection, curation, or other labor should be paid at least the minimum wage in the country of the data collector.

15. **Institutional review board (IRB) approvals or equivalent for research with human subjects**

Question: Does the paper describe potential risks incurred by study participants, whether such risks were disclosed to the subjects, and whether Institutional Review Board (IRB) approvals (or an equivalent approval/review based on the requirements of your country or institution) were obtained?

Answer: [NA]

Justification: The paper does not involve crowdsourcing nor research with human subjects.

Guidelines:

- The answer NA means that the paper does not involve crowdsourcing nor research with human subjects.
- Depending on the country in which research is conducted, IRB approval (or equivalent) may be required for any human subjects research. If you obtained IRB approval, you should clearly state this in the paper.
- We recognize that the procedures for this may vary significantly between institutions and locations, and we expect authors to adhere to the NeurIPS Code of Ethics and the guidelines for their institution.
- For initial submissions, do not include any information that would break anonymity (if applicable), such as the institution conducting the review.

16. **Declaration of LLM usage**

Question: Does the paper describe the usage of LLMs if it is an important, original, or non-standard component of the core methods in this research? Note that if the LLM is used only for writing, editing, or formatting purposes and does not impact the core methodology, scientific rigorousness, or originality of the research, declaration is not required.

Answer: [NA]

Justification: The core method development in this research does not involve LLMs as any important, original, or non-standard components.

Guidelines:

- The answer NA means that the core method development in this research does not involve LLMs as any important, original, or non-standard components.
- Please refer to our LLM policy (<https://neurips.cc/Conferences/2025/LLM>) for what should or should not be described.