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# A SURVEY ON BRAIN-INSPIRED DEEP LEARNING VIA PREDICTIVE CODING

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**Tommaso Salvatori<sup>1,2</sup>** **Ankur Mali<sup>3</sup>** **Christopher L. Buckley<sup>1,4</sup>** **Thomas Lukasiewicz<sup>2,5</sup>,**  
**Rajesh P. N. Rao<sup>6</sup>** **Karl Friston<sup>1,7</sup>** **Alexander Ororbia<sup>8</sup>**

<sup>1</sup> VERSES AI Research Lab Los Angeles, California, USA

<sup>2</sup> Institute of Logic and Computation, Vienna University of Technology, Austria

<sup>3</sup> University of South Florida Tampa, FL 33620, USA

<sup>4</sup> Sussex AI Group, Department of Informatics, University of Sussex, Brighton, UK

<sup>5</sup> Department of Computer Science, University of Oxford, UK

<sup>6</sup> Paul G. Allen School of Computer Science and Engineering, University of Washington Seattle, Washington, USA

<sup>7</sup> The Wellcome Centre for Human Neuroimaging, Queen Square Institute of Neurology University College London

<sup>8</sup> The Neural Adaptive Computing Laboratory, Rochester Institute of Technology Rochester, NY 14623

tommaso.salvatori@verses.ai, ankurarjunmali@usf.edu

chris.buckley@verses.ai, thomas.lukasiewicz@tuwien.ac.at

rao@cs.washington.edu, karl.friston@verses.ai, ago@cs.rit.edu

## ABSTRACT

Artificial intelligence (AI) is rapidly becoming one of the key technologies of this century. The majority of results in AI thus far have been achieved using deep neural networks trained with the error backpropagation learning algorithm. However, such an algorithm has always been considered biologically implausible. To this end, recent works have studied learning algorithms for deep neural networks inspired by the neurosciences. One such theory, called *predictive coding* (PC), has shown promising properties that make it potentially valuable for the machine learning community: it can model information processing in different areas of the brain, can be used in cognitive control and robotics, has a solid mathematical foundation in variational inference, and performs its computations asynchronously. Inspired by such properties, works that propose novel PC-like algorithms are starting to be present in multiple sub-fields of machine learning and artificial intelligence at large. Here, we survey such efforts by first providing a broad overview of the history of PC to provide a common ground for the understanding of the recent developments, then by surveying current efforts and results, and concluding with a large discussion of possible implications and ways forward.

## 1 Introduction

The machine learning community is developing and producing models that push the boundaries of the field on a weekly basis: we have witnessed considerable breakthroughs in the fields of generative artificial intelligence (AI) [1, 2, 3, 4], game playing [5, 6], and text-generation [7, 8, 9]. These results reflect over a decade of advances in the field, made possible by the joint effort of tens of thousands of researchers and engineers who have built on seminal work [10, 11] in order to improve the performance of deep artificial neural networks trained with the error backpropagation algorithm [12, 13]. It may thus come as a surprise that research on alternative training methods for machine learning is more active than ever, with many works often co-authored by the same scientists who pioneered backpropagation-based schemes [14, 15, 16, 17]. These lines of research, however, are not *contradictory* but *complementary*: the increasingly impressive results of standard deep neural networks have also highlighted several significant limitations, that may be addressed via alternative training methods. There is, in fact, a common belief that, to accelerate progress in AI, we must invest in fundamental research, inspired by the findings and ideas in computational neuroscience [18, 17, 19]. To this end, in this review, we focus on a specific approach, inspired from a theory of learning and perception in the brain called *predictive coding* (PC) [20, 21, 22]. Models of PC exhibit several valuable properties, the main one being the locality of the operations, meaning that every update of the parameters is performed using only the information of adjacent neurons

or synapses in an Hebbian-way [23]. Differently from backprop, that is a sequential algorithm, locality allows for a full parallelization of the operations, making it potentially more suitable for applications in neuromorphic computing. Locality also allows the training of artificial neural networks with any given topology [24, 25]. This facilitates the training of models with arbitrarily entangled structures, similar to the biological networks that constitute our brains and underwrite our level of intelligence [26]. Furthermore, PC networks are naturally more robust in relation to standard models trained with backprop, due to the relaxation process that spreads error signals across the whole network [27]. In supervised learning, this process emulates implicit gradient descent [28], is naturally more stable, and is less reliant on hyperparameter searches. This allows predictive-coding-based models to perform better in tasks that are more likely to be faced by natural agents, while regularizing the underlying energy landscape [29] and avoiding troublesome phenomena, such as vanishing and exploding gradients [27, 30].

**Structure of the Survey.** This article is organized as follows. In Section 2, we present the general theoretical characterization of PC as (the inversion of) a generative model that minimizes variational free energy, provide an historical introduction to the topic, as well as an informal definition of what characterizes a predictive coding algorithm in the literature. Section 3 is quite technical, as we dive into the mathematical formulations to study and dissect three key computational frameworks that have emerged over the past three decades: the classical setup proposed by Rao and Ballard, neural generative coding, and biased competition with divisive modulation. Following this, in Section 4, we review the machine learning problems that PC has been tested on, such as supervised learning, natural language processing, computer vision, temporal and continual learning, and reinforcement learning and control for robotics and cognitive architecture design. In Section 5, we examine key neuroscience studies of PC, and, in Sections 6 and 7, we consider available software tools and libraries that support PC, and discuss how research on hardware could realize the full potential of PC or similar algorithms. To conclude, in Section 8, we discuss important future directions, as well as the grand challenges that lie ahead.

**Notation.** In this paper, the symbol  $\odot$  is employed to represent the Hadamard product, i.e., element-wise multiplication.  $\oslash$  is used to indicate element-wise division. On the other hand, the symbol  $\cdot$  denotes the (dot product) multiplication of matrices or vectors. The transpose of a vector  $\mathbf{v}$  is represented as  $(\mathbf{v})^\top$ . It is important to note that matrices and vectors are distinguished by using boldface type, as in matrix  $\mathbf{M}$  and vector  $\mathbf{v}$ , while scalars are depicted in italicized font, as in scalar  $s$ . In the context of neural networks, an input observation, or a sensory input pattern, is represented as  $\mathbf{o} \in \mathcal{R}^{J_0}$ , where  $J_\ell$  represents the dimension of layer  $\ell$  of the network,  $\ell = 0$  is the input layer and  $\ell = L$  is the output layer; a label is represented by  $\mathbf{y} \in \mathcal{R}^{J_L}$ , and a latent vector (or code) by  $\mathbf{x}^\ell \in \mathcal{R}^{J_\ell}$ .

## 2 Generative Models and Predictive Coding

Given an observation  $\mathbf{o}$ , and a latent variable  $\mathbf{x}$ , a generative model is described by the marginal probability  $p(\mathbf{o}, \mathbf{x}) = p(\mathbf{o} | \mathbf{x})p(\mathbf{x})$ . In the spirit of one of Richard Feynman’s famous, oft-quoted statements, *What I cannot create, I do not understand*, this family of models aims to understand patterns found within a dataset by learning how the dataset can be generated. Making these types of models work for specific tasks entails two steps: (1) building the correct structure of the generative model, that requires making assumptions on the structure of the function that generates plausible datapoints using latent variables as inputs, and (2) inverting the ensuing generative model, that requires understanding what is the best or optimal inference (i.e., belief) updating scheme that enables us to invert such a probabilistic generative model.

To invert a generative model means to map from consequences (i.e., content or data) to causes (i.e., latent states), that is, to identify the posterior  $p(\mathbf{x} | \mathbf{o})$ . After the advent of variational autoencoders (VAEs) [31], the inversion behind most, if not all, modern, successful generative AI models is *amortized*, meaning that the computation of the (approximate) posterior is performed via a forward pass on a specifically trained deep neural network, called the *encoder*, as sketched in Fig. 1 (left). However, statistical models have been around for many decades, and provided many techniques that facilitate the inversion of a generative model that does not rely on an amortized scheme, that is, can be defined as sketched in Fig. 1 (right). We now describe how a generative model based on PC first performs *inference* – that describes how the latent variables are updated – and *learning* – that describes how the parameters of the model are updated.

**Inference.** Given an observation  $\mathbf{o}$ , the goal here is to approximate a posterior distribution  $p(\mathbf{x} | \mathbf{o})$  using the joint distribution of observations and latent variables  $\mathbf{x}$ . As  $\mathbf{x}$  is often of lower dimension than  $\mathbf{o}$ , this can be read as a compression mechanism, where compression can be defined as the process of assigning a lower dimensional code to a particular observation. This *coding* mechanism is what originally gives the name to the PC framework. In fact, the first algorithmic formulation of PC dates back to the 1950’s, and was a compression algorithm for time series data [32, 33, 34]. The first instances of PC in neuroscience also treated it as a pure inference algorithm, with no learning involved, as the goal was to model how spatial information was encoded in the retina [35].

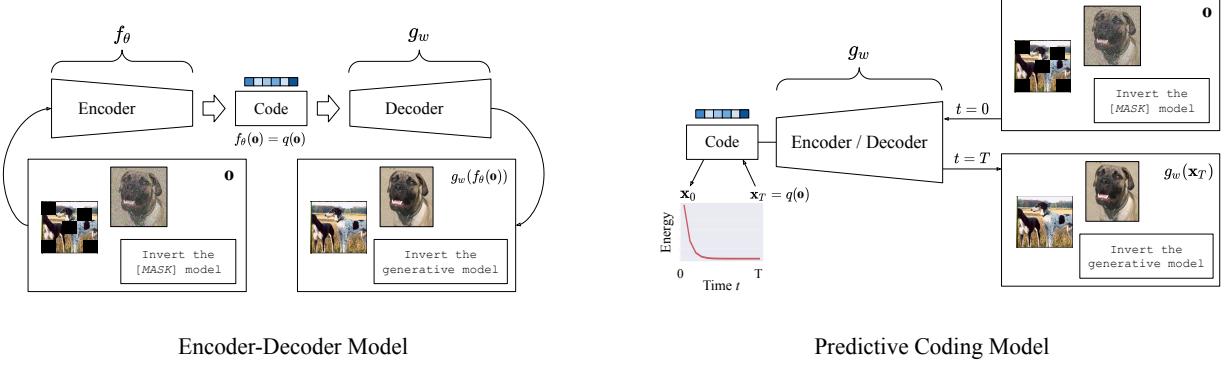


Figure 1: Generative models effectively compress information about a specific data point  $\mathbf{o}$ , with missing information, into a low-dimensional code vector (or latent *embedding*), and use it to generate a (e.g., semantically) similar, complete data point. Left: the standard encoder-decoder model used in machine learning [31]; Right: an equivalent PC model, which iteratively computes and refines the code through a free-energy minimization process. At convergence, the code is then used to generate a data point via the same model used to perform the compression. Typically, PC associates the encoder with ascending (prediction error) messages and the decoder with descending (prediction) messages. Note that the implicit conflation of the encoding and decoding means that there is only one set of parameters in PC. These are the parameters of the generative model that, crucially, can be optimized locally, given the requisite predictions and prediction errors.

**Learning.** A major paradigm shift, however, happened several years later, with the work of Rao and Ballard, which employed PC as a *learning* algorithm, instead of just an inference one to model hierarchical processing in the visual cortex [20]. In this formulation, synaptic weights are updated after inference to minimize the prediction error of the model. The connection with variational inference was discovered a couple of years later, and connected PC to hierarchical Gaussian generative models [36, 37]. As a result of these independent, but deeply related lines of work, a recent general theory has unified these views by showing that these iterative updating schemes can be described as a process of minimizing a *variational free energy* [38], also known in machine learning as an evidence bound [39]. A sketch of a timeline of the main breakthroughs in the history of PC is given in Fig. 2.

The ability to memorize a training set, learn its patterns, and generalize to an unseen test set is the primary goal of any machine learning algorithm. The variational free energy is a function that encodes the two factors that model this behavior, one that encourages the fitting of the training dataset (training *accuracy*), and one that penalizes the *complexity* of the generative model, facilitating a better performance on unseen data. This enforces regularity, as it facilitates convergence towards the minimally complex model that provides an accurate fit of a specific dataset, aligned with Occam’s razor formulations [40]. As an example, let us assume that we have a discrete generative model, expressed as the probability  $p(\mathbf{o}, \mathbf{x}) = p(\mathbf{o} | \mathbf{x})p(\mathbf{x}) = p(\mathbf{x} | \mathbf{o})p(\mathbf{o})$ , where  $\mathbf{x}$  denotes a latent vector, and  $\mathbf{o}$  is an observed data point. Given an observation  $\mathbf{o}$ , and an approximate posterior distribution  $q_\theta(\mathbf{x})$ , parameterized by a vector  $\theta$ , the (negative) variational free energy is defined as follows:

$$E(p, q, \mathbf{o}) = \underbrace{\sum_{\mathbf{x}} q_\theta(\mathbf{x}) \log \left( \frac{q(\mathbf{x})}{p(\mathbf{x})} \right)}_{\text{Complexity}} + \underbrace{\sum_{\mathbf{x}} q_\theta(\mathbf{x}) \log \left( \frac{1}{p(\mathbf{o} | \mathbf{x})} \right)}_{\text{Accuracy}},$$

A typical schema to minimize such a variational free energy is the expectation-maximization (EM) algorithm, where inference is first used to find the latent vector that minimize  $E(p, q, \mathbf{o})$ , and then the parameters  $\theta$  are further updated to follow the same goal.

## 2.1 What Defines Predictive Coding?

In the following section, we will discuss in detail different variations of PC proposed in the recent literature. However, when can an algorithm be defined as PC? Here, we address this question by providing an informal definition of what predictive coding is today. Let  $\mathbf{o} = g(\mathbf{x}, \mathbf{W})$  be a generative model, where a vector of latent variables  $\mathbf{x}$  and a set of parameters  $\mathbf{W}$  are used to generate an observation  $\mathbf{o}$ . In our case, we consider generative models with  $L$  layers, whose

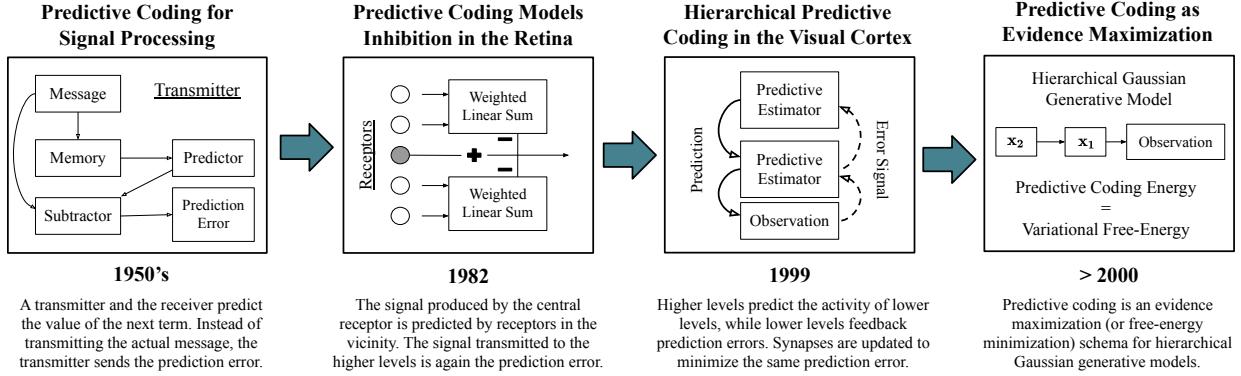


Figure 2: A timeline of how the perception of what PC has changed through the years. Initially, it was developed as a signal compression mechanism [34, 41]; then, it was used to model inhibition in the retina [35]. It then became a more general model of both learning and perception in the visual cortex [20]. Nowadays, it can be abstractly defined as an evidence-maximization scheme for hierarchical Gaussian generative models [42, 21]. For a detailed discussion on different PC algorithms, we also refer to another survey [43]

marginal probability has the following dependencies:

$$p(\mathbf{x}_L, \dots, \mathbf{x}_0) = p(\mathbf{x}_L) \prod_{\ell=0}^{L-1} p(\mathbf{x}_\ell | \mathbf{x}_{\ell+1}). \quad (1)$$

We further consider the probability distribution  $p(\mathbf{x}_\ell | \mathbf{x}_{\ell+1})$  to be a multivariate Gaussian distribution, whose mean is given by a transformation  $g_\ell$  of the latent variables of the level above. In the majority of the literature, the map  $g_\ell$  is a composition of an activation function (such as ReLU), and a transformation matrix  $\mathbf{W}_\ell$  (with bias  $\mathbf{b}_\ell$  possibly folded into this matrix), which results in a linear map. As a result, we then, more formally, arrive at the following:

$$p(\mathbf{x}_L) = \mathcal{N}(\mathbf{x}_L, \Sigma_L), \quad p(\mathbf{x}_\ell | \mathbf{x}_{\ell+1}) = \mathcal{N}(g_{\ell+1}(\mathbf{x}_{\ell+1}), \Sigma_\ell). \quad (2)$$

**Inversion.** Given the above, we now have the structure of the main object of study that centrally characterizes the PC literature, that is, a hierarchical generative model, which lives in a continuous state space and whose probability distributions are Gaussian in nature. However, what also defines PC is the process that is used to invert the generative model, which means estimating  $p(\mathbf{x}_1, \dots, \mathbf{x}_L | \mathbf{o})$  via an approximate posterior  $q(\mathbf{x}_1, \dots, \mathbf{x}_L)$ . To do this, we need to appeal to two different approximation results: first, we leverage a mean-field approximation, which allows us to assume that the variational posterior factorizes into conditionally independent posteriors  $q(\mathbf{x}_\ell)$ ; then, through the Laplace approximation, we approximate posterior distributions as Gaussian forms [44]. At this point, it is now possible to minimize the resulting variational free energy. In essence, what results is an inversion mechanism that has the same dynamics as the original computational model in Rao and Ballard [20], which was notably developed before PC was cast as variational learning and inference. The minimization of variational free energy can either use gradient descent or fixed point iterations [45]. The latter follows from the fact that Gaussian priors are conjugate to Gaussian posteriors. In either case, the gradients of variational free energy are just prediction errors. This means, to evaluate requisite free energy gradients one has to evaluate prediction errors. One might argue that PC is the explicit (or implicit) use of prediction errors for the inversion of generative models (under Gaussian assumptions about random effects).

We have now introduced all of the core concepts needed to provide a definition of PC. This definition could be used as an umbrella for all of the variations on PC in the literature.

**Definition (Informal).** Let us assume that we have a hierarchical generative model  $g(\mathbf{x}, \mathbf{o})$ , inverted using an algorithm  $\mathcal{A}$ . Then,  $\mathcal{A}$  is a predictive coding algorithm if and only if:

1. it maximizes the model evidence  $p(\mathbf{o})$  by minimizing a variational free energy,
2. the posterior distributions of the nodes of the hierarchical structure are factorized via a mean-field approximation, and
3. each posterior distribution is approximated under the Laplace approximation (i.e., random effects are Gaussian).

Note that the above definition does not say anything explicitly about *prediction error* or properties such as *locality*, which, as mentioned earlier, are commonly used to describe PC. This is because they are not foundational to PC but

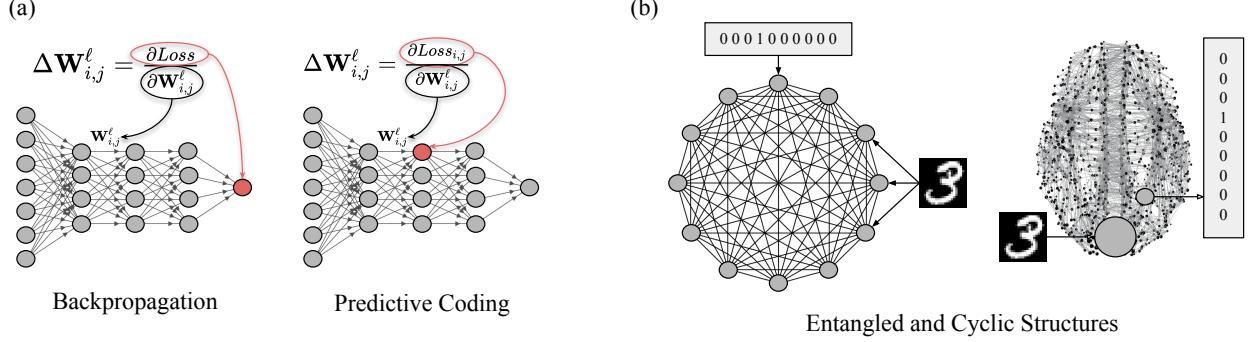


Figure 3: (a) The difference between PC and standard models in terms of locality: backprop updates its synaptic weights  $\mathbf{W}_{i,j}^\ell$  to minimize the output error, even if it is not directly connected to it. PC models, on the other hand, perform their updates to correct the error of their postsynaptic neuron. (b) PC can be used to train models with cycles. An example is the fully connected model on the left, where every pair of neurons is connected via two different synapses, one in each direction. Being able to train models like this facilitates the inversion of models with arbitrarily expressive architectures (such as realistic brain structures) by simply masking specific connections of a fully connected model via an adjacency matrix. For an example of interesting models that operate on realistic brain structures, see right panel, taken from [26].

rather consequences of the commitment to the aforementioned generative model: the mean field approximation enforces independence, and hence, results in locality in the update rules; the Laplace assumption lends the consequent variational free energy a quadratic form, meaning that its gradients are linear prediction errors. It is crucial to note that the above definition of PC does not mean, however, that the algorithms surveyed here are optimal and cannot be improved: the above definition is quite general and does not impose any constraint on the exact computation of the posteriors as well as the optimization technique(s) used to minimize the variational free energy. The goal of this work is to survey existing PC methods and to anticipate future research in the field.

### 3 Popular Implementations of Predictive Coding

Informally, PC claims that there exist two families of neurons that define an internal (i.e., generative) model of the world: the first generates predictions that are passed to lower layers, and the second encodes prediction errors that are passed to higher layers [20, 46]. To discuss this basic PC architecture, in this section, we define three quantities, referred to as the *value node*, the *error node*, and the *prediction* of every neuron. The *value node*  $\mathbf{x}_{i,t}^\ell$  (where the indices  $i$  and  $\ell$  refer to the  $i$ -th neuron of the  $\ell$ -th layer at time  $t$ ) encodes the most likely value of some latent state. The second computational unit is the *prediction*  $\mathbf{u}_{i,t}^\ell$ , which is a function of the value nodes of a higher level in the hierarchy, and is computed as follows:

$$\mathbf{u}_{i,t}^\ell = \sum_{j=1}^{J_\ell} \mathbf{W}_{i,j}^{\ell+1} \phi(\mathbf{x}_{j,t}^{\ell+1}), \quad (3)$$

where  $\phi$  is a nonlinear function (akin to the activation function in deep neural networks), and  $\mathbf{W}^{\ell+1}$  is a matrix containing the predictive synaptic parameters for layer  $\ell + 1$ . The third computational unit is the prediction error  $\mathbf{e}_{i,t}^\ell$ , given by the difference between its value node and its prediction node, i.e.,  $\mathbf{e}_{i,t}^\ell = \mathbf{x}_{i,t}^\ell - \mathbf{u}_{i,t}^\ell$ . This local definition of error, which exists in every network neuron, foregrounds a key difference between PC and models trained with backprop (e.g., the multilayer perceptron), as it enables learning through only local computations. A graphical example depicting the differences in locality between PC and backprop is given in Fig. 3. Taken together, the above three quantities, as well as the set of synaptic weight matrices  $(\mathbf{W}^0, \dots, \mathbf{W}^L)$ , define a generative model where both inference and learning are performed as a means to minimize a single (global) energy function, formally defined as the sum of the squared prediction errors of every neuron:

$$\mathcal{E}_t = \frac{1}{2} \sum_{i,l} (\mathbf{e}_{i,t}^\ell)^2. \quad (4)$$

This energy function is exactly the variational free energy defined in the previous section, and a proper derivation can be found in [47]. Let us assume that our generative model is presented with an observation  $\mathbf{o} \in \mathbb{R}^{J_0}$ . Then, the following process describes the credit assignment and consequent update of the synaptic parameters of the model: first, the neurons of the lowest layer are set equal to the sensory observation, i.e.,  $\mathbf{x}^0 = \mathbf{o}$ . Next, the unconstrained neural

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**Algorithm 1** Updating the value/state dynamics and synaptic weights in a PC model, given a data point  $\mathbf{o}$ .

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**Require:**  $\mathbf{x}^L$  is fixed to  $\mathbf{o}$  for every time step  $t$ .

- 1: **for**  $t = 0$  to  $T$  (included) **do**
- 2:   **for** each neuron  $i$  in each level  $\ell$  **do**
- 3:     Update  $\mathbf{x}_{i,t}^\ell$  to minimize  $\mathcal{E}_t$  via Eq. (5)
- 4:   **if**  $t = T$  **then**
- 5:     Update  $\mathbf{W}^\ell$  to minimize  $\mathcal{E}_t$  via Eq. (6)

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activities are updated until convergence (or, for a fixed number  $T$  of iterations) to minimize the energy of Eq. 4 via gradient descent. In particular, the equation for the update dynamics of the value nodes is the following:

$$\Delta \mathbf{x}_t^\ell = -\gamma \cdot \frac{\partial \mathcal{E}_t}{\partial \mathbf{x}_t^\ell} = \begin{cases} \gamma \cdot (\phi'(\mathbf{x}_t^\ell) \odot (\mathbf{W}^\ell)^\top \cdot \mathbf{e}_t^{\ell-1}) & \text{if } \ell = L \text{ (and unclamped)} \\ \gamma \cdot (-\mathbf{e}_t^\ell + \phi'(\mathbf{x}_t^\ell) \odot (\mathbf{W}^\ell)^\top \cdot \mathbf{e}_t^{\ell-1}) & \text{if } 0 < \ell < L \\ \gamma \cdot (-\mathbf{e}_t^\ell) & \text{if } \ell = 0 \text{ (and unclamped),} \end{cases} \quad (5)$$

where  $\gamma$  is the learning rate of the neural activities (usually read as a precision or inverse variance). This optimization process drives the underlying credit assignment process of PC and computes the best configuration of value nodes needed to perform a synaptic weight update. When this process has converged, the value nodes are then frozen and a single weight update is performed (via gradient descent) to further minimize the same energy function:

$$\Delta \mathbf{W}^{\ell+1} = -\alpha (\partial \mathcal{E}_T / \partial \mathbf{W}^{\ell+1}) = \alpha (\mathbf{e}_T^\ell \cdot \phi(\mathbf{x}_T^{\ell+1})^\top), \quad (6)$$

where  $\alpha$  is the learning rate for the synaptic update. The alternation of these two phases, i.e., the value node update and weight update steps, defines the learning algorithm used to train PC networks [20, 46]. Importantly, although every computation is local, both update rules minimize the same energy function, which is globally defined over the whole network. The difference in locality between a weight update of backprop and the one for PC is given in Fig. 3(a).

**Supervised Learning.** In the above, we have described how to use PC to perform unsupervised learning tasks. However, this algorithm or variations of it have been shown to obtain a performance comparable to deep networks learned with backprop on supervised learning tasks [46, 48, 49]. To extend the above formulation to the domain of labeled data, we have to re-imagine the PC network as *generating the label*  $\mathbf{y}$  and that the data point  $\mathbf{o}$  serves as a prior on the value of the neurons in the first layer of the network. Let us assume that we have a labeled data point  $(\mathbf{o}, \mathbf{y})$ , where, again,  $\mathbf{y}$  is the label<sup>1</sup>. Supervised learning is then realized by fixing the value nodes of the first and last layer to the entries of the data point and its label, respectively, i.e.,  $\mathbf{x}_{0,t} = \mathbf{o}$  and  $\mathbf{x}_{L,t} = \mathbf{y}$  for every time step  $t$ . A graphical depiction of the difference between supervised and unsupervised learning using PC is given in Fig. 4.

**Generalization to Arbitrary Topologies.** It is often remarked that the networks in the brain are not strictly hierarchical [24, 51] but are extremely entangled and full of cyclic connections. Recent work has shown how PC can be utilized to model networks with any kind of structure, making it ideal to digitally perform learning tasks that require brain-like architectures such as parallel cortical columns or sparsely connected brain regions [25]. To do this, the more general concept of a PC graph is required. Let  $G = (V, E)$  be a fully connected directed graph, where  $V$  is a set of  $n$  vertices  $\{1, 2, \dots, n\}$  and  $E \subseteq V \times V$  is a set of directed edges between them, where every edge  $(i, j) \in E$  has a weight parameter encoded in an  $n \times n$  weight matrix  $\mathbf{W}$ . As a result, the predictions come from all of the neurons of the network, and the free energy of the model is again the summation over all of the (squared) prediction errors:

$$\mathbf{u}_{i,t} = \sum_{j=0}^n \mathbf{W}_{j,i} \phi(\mathbf{x}_{j,t}) \quad \text{and} \quad \mathcal{E}_t = \frac{1}{2} \sum_{i=0}^n (\mathbf{e}_{i,t})^2. \quad (7)$$

While defining this generalization on fully connected graphs makes the notation simpler, interesting use-cases can be found in graphs that are not fully connected. To this end, it suffices to note that every graph is a subset of a fully connected one and, hence, we can consider sparse weight matrices  $\mathbf{W}$ , where only the entries of the edges that we need to define our structure are non-zero. This can be done by multiplying  $\mathbf{W}$  by an adjacency matrix. In the original work along these lines, the authors trained a network of multiple, sparsely-connected brain regions and tested the resulting model on image denoising and image completion tasks. The exact structure of this network is that of the *Assembly Calculus*, a Hebbian learning framework/method specifically designed to model brain regions [52]. A graphical sketch of how to derive such a model is given in Fig. 3(b).

<sup>1</sup>In supervised learning, the total energy of the model can also be decomposed as  $\mathcal{E} = \tilde{\mathcal{E}}_t + \mathcal{L}$ , with  $\tilde{\mathcal{E}}_t$  be the total energy of all the internal neurons only, and  $\mathcal{L}$  be the squared error defined on the label, as in standard regression tasks. This allows to define interesting similarities with backprop [50].

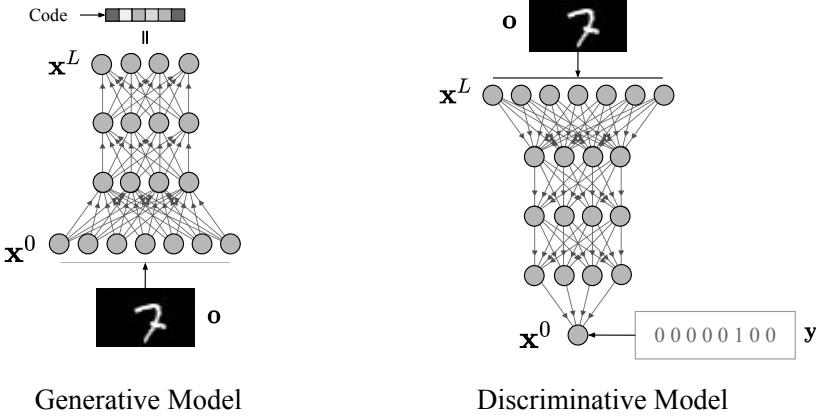


Figure 4: A graphical depiction of PC in an unsupervised generative form (left) and in a supervised discriminative form (right). Note that the generative form of PC entails iteratively inferring a latent code (or embedding)  $\mathbf{x}^L$  for sensory input  $\mathbf{x}^0 = \mathbf{o}$ , while the discriminative form of PC requires iteratively learning a predictive mapping between sensory input  $\mathbf{x}^L = \mathbf{o}$  to target  $\mathbf{x}^0 = \mathbf{y}$ .

**Associative Memories.** A body of literature has investigated the efficacy of PC networks in memory-related tasks. Specifically, this literature studies their capacity to store a dataset and retrieve individual data points when a related cue is presented. In practice, this cue is often an incomplete or corrupted version of a stored memory and the task is successfully completed if and only if the correct data point is retrieved. PC schemes have demonstrated their ability to effectively store and retrieve complex memories, such as images from the COIL and ImageNet datasets [53, 54, 55]. However, while their retrieval capabilities are robust, their capacity is still limited, and hence not comparable to that of continuous or universal Hopfield networks [56, 57]. This capacity can be improved by implementing a fast and powerful memory writing operation that allows these models to store individual memories without overwriting existing ones. Models that incorporate memory writing also tend to facilitate the implementation of a *forget* operation that erases individual memories with little to no impact on overall model performance [58]. It is also possible to store memories in the latent variable  $\mathbf{x}_L$ , by learning a Gaussian mixture prior, whose centers correspond to each of the the individual memories [59]. This has also been implemented in the temporal domain, where the goal is to retrieve missing future frames of a video, given initial ones [55] (as a sort of priming stimulus).

### 3.1 Theoretical Results on PC

Here, we present theoretical results concerning the convergence properties of PC, as well as results that compare their learning capabilities against standard artificial neural networks trained with backprop. It is a common trend in the literature to compare the performance of biologically plausible algorithms to those of backprop, especially in supervised learning scenarios. Recent work has shown that PC can approximate the weight update of backprop, under specific conditions, on both MLPs (multilayer perceptrons) and within the more general framework of computational graphs [46, 60]. These conditions are restrictive in practice, as these results only hold if either the total prediction error on the network is infinitesimally small or the predictions are kept constant throughout the whole duration of the inference process, i.e.,  $\mathbf{u}_{i,t}^\ell = \mathbf{u}_{i,0}^\ell$  for every time step  $t$ . In practice, however, empirical studies have shown that for the approximation to hold, it suffices to have a small output error [60].

A similar line of work has also shown that simply adding a temporal scheduling to the updates of the weights and the neural activities leads to a weight update that is equivalent to that of backprop. This temporal scheduling, however, is only possible by adding an external control that triggers the updates at different time steps, hence reducing the biological plausibility of PC. Again, these results were first obtained in the setting of feedforward networks, and were later extended to the more general framework of computational graphs [61, 62]. Similar works have also investigated similarities between PC and other neuroscience-inspired algorithms, such as contrastive Hebbian learning [63], target propagation [64, 65, 66], and equilibrium propagation [15, 50].

**Robustness.** PC has been shown to perform better than standard models (such as backprop-trained deep neural networks) on problems that are faced by biological organisms, such as continual learning, online learning, and learning from a small amount of data [67, 68, 27]. This is due to the inference phase, which allows the error to be distributed

in the network in a way that avoids a phenomenon called *weight interference*, where the update rules of the single parameters do not consider the updates of the other parameters, leading to less stable training progress. Formally, PC networks trained for supervised learning naturally model *implicit* gradient descent [28], a more stable formulation that reduces numerical instability by using implicit gradients, instead of explicit ones. Specifically, a parameter update of implicit gradient descent is defined as follows:

$$\mathbf{W}_{t+1} = \mathbf{W}_t - \gamma \nabla \mathcal{L}(\mathbf{W}_{t+1}). \quad (8)$$

This formulation is called *implicit*, since  $\mathbf{W}_{t+1}$  appears on both sides of the equation, desirably reducing the sensitivity to the learning rate [69]. As a consequence, PC models tend to be more robust and better calibrated than standard ones, as has been shown in multiple classification tasks on both convolutional and graph networks [51, 70, 48].

### 3.2 Neural Generative Coding

Despite being developed to model information processing in different brain areas, the above formulation is still biologically implausible, the main implausibility being symmetric weight connections. In what follows, we survey a generalization of PC, to arbitrary wiring patterns, called neural generative coding (NGC). This variation has its roots grounded in cable theory [71, 72] and neuronal compartments [73]. As in PC, NGC instantiates a form of predict-then-correct learning and inference but crucially expands the iterative neural dynamics to incorporate other known neurobiological mechanisms, such as lateral competition, learned precision-weighting, and membrane potential leakage. Furthermore, NGC tackles the weight symmetry assumption inherent to standard PC by decoupling the forward generative pathway(s) (which are typically composed of matrices  $\mathbf{W}^\ell$ ) from the message passing feedback pathway(s) (which are composed of matrices  $\mathbf{E}^\ell$ ); this easily allows the introduction of skip connections in one or both pathways to create heterarchical structures [24]. Usefully, this means that NGC circuit models do not require that the feedback message passing connectivity structure mirror (in reverse) the same structure as the underlying generative model itself, offering a high degree of flexibility in designing the generative model and its requisite message passing pathways [24, 74, 75]. Furthermore, each error feedback matrix  $\mathbf{E}^\ell$  can be updated with local rules.

Compactly, given clamped sensory vectors, an NGC circuit undergoes a settling cycle where it processes input data signals over a stimulus window of  $T$  time steps. As in PC, each region of activity in an NGC circuit makes a local prediction of a nearby region (i.e., layer  $\ell + 1$  predicts  $\ell$  in a typical hierarchical structure) as follows:

$$\bar{\mathbf{x}}_t^\ell = g^\ell \left( \mathbf{W}^{\ell+1} \cdot \phi^{\ell+1}(\mathbf{x}_t^{\ell+1}) + \alpha_m \left( \sum_{k=2}^K \mathbf{M}^{\ell+k} \cdot \phi^{\ell+k}(\mathbf{x}_t^{\ell+k}) \right) \right) \quad (9)$$

$$\mathbf{e}_t^\ell = (\Sigma^\ell)^{-1} \cdot (\mathbf{x}_t^\ell - \bar{\mathbf{x}}_t^\ell), \quad (10)$$

where  $\mathbf{x}_t^0 = \mathbf{o}$  (the bottom layer is set to the observation) and  $g^\ell$  is a nonlinearity applied to a layer's predictive outputs.  $\mathbf{W}^\ell$  contains the generative synapses between layer  $\ell + 1$  and  $\ell$ ,  $\mathbf{M}^{\ell+k}$  houses skip generative synapses that connect layer  $\ell + k$  to  $\ell$ , and  $\Sigma^\ell$  is the cross-correlational matrix meant to modulate the error unit signals at each time step and is specifically constrained to ensure that its main diagonal is non-negative. The activities of the internal neurons themselves (i.e., all the neurons in between the clamped layers  $\ell = L \dots 0$ ) are updated according to the following equation (formulated for a single layer  $\ell$  in vector form):

$$\mathbf{x}_{t+\Delta t}^\ell = \mathbf{x}_t^\ell + \beta \left( -\gamma \mathbf{x}_t^\ell - \mathbf{e}_t^\ell + (\mathbf{E}^\ell \cdot \mathbf{e}_t^{\ell-1}) \odot f_D(\mathbf{x}_t^\ell) + \Phi(\mathbf{x}_t^\ell) \right) \text{ where } \ell > 0, \quad (11)$$

where  $\mathbf{E}^\ell$  is a matrix containing error feedback synapses that are meant to pass prediction errors from layer  $\ell - 1$  to  $\ell$ . Notice that while the above update is formulated as a single Euler integration step, one could employ other methods, e.g., the midpoint method, to calculate a new state update for time  $t + \Delta t$ .  $\beta$  is the neural state update coefficient (typically set according to  $\beta = \frac{\Delta t}{\tau}$ , where  $\tau$  is the state unit time constant, similar to a cellular membrane potential time constant, in the order of milliseconds), and  $f_D(\cdot)$  is a dampening function (which offers the update scaling benefits that  $\phi'(\cdot)$  provides in standard PC but without requiring differentiable activation functions).  $\Phi(\cdot)$  is a special lateral interaction function that can take many possible forms, ranging from a kurtotic distributional prior placed over the neural activities, as was classically done in [76, 20], or in the form of explicit lateral synapses [24], as presented below:

$$\Phi(\mathbf{x}_{i,t}^\ell) = - \left( \sum_{j \in J_\ell, j \neq i} \mathbf{V}_{i,j}^\ell \phi^\ell(\mathbf{x}_{j,t}^\ell) \right) + \mathbf{V}_{ii}^\ell \phi^\ell(\mathbf{x}_{i,t}^\ell), \quad (12)$$

where  $\mathbf{V}^\ell$  is a matrix containing the lateral cross-inhibitory and self-excitation synapses for layer/region  $\ell$ . Note that the state update equation (Equation 11) indicates that a vector of neural activity values changes, at each step within a settling cycle, according to (from left to right), a leak term/variable (the strength of which is controlled by  $\gamma$ ), a combined top-down and bottom-up pressure from mismatch signals in nearby neural regions/layers, and a lateral interaction term.

After processing the sensory input for  $T$  time steps (repeatedly applying Equation 11 for  $T$  times in a row), the synapses are then adjusted with a multi-factor Hebbian update:

$$\Delta \mathbf{W}^\ell = \mathbf{e}_t^\ell \cdot (\phi^{\ell+1}(\mathbf{x}_t^{\ell+1}))^T, \text{ and, } \Delta \mathbf{E}^\ell = \gamma_e (\phi^{\ell+1}(\mathbf{x}_t^{\ell+1} \cdot (\mathbf{e}_t^\ell)^T)), \quad (13)$$

where  $\gamma_e$  is a factor that controls the time-scale over which the error synapses are evolved ( $\gamma_e$  is typically less than one to ensure that the error feedback synapses change a bit more slowly than the generative synapses). Note that after the Hebbian updates prescribed by Equation 13 are applied to their corresponding weight matrices, either a form of synaptic scaling is applied or the synaptic matrices are instead normalized after an update [24] (much as was done in classical sparse coding), i.e.,  $\mathbf{W}^\ell \leftarrow \mathbf{W}^\ell / ||\mathbf{W}^\ell||_2$  and  $\mathbf{E}^\ell \leftarrow \mathbf{E}^\ell / ||\mathbf{E}^\ell||_2$ .

Another important functionality of an NGC circuit is the ability to project a vector through its underlying directed generative model ancestrally. In essence, this amounts to a feedforward pass, since no settling process is required. Formally, ancestrally projecting any vector  $\mathbf{x}_\epsilon$  through an NGC circuit is done as follows:

$$\mathbf{x}_t^\ell = \bar{\mathbf{x}}_t^\ell = g^\ell(\mathbf{W}^{\ell+1} \cdot \phi^{\ell+1}(\mathbf{x}_t^{\ell+1})), \forall \ell = (L-1), \dots, 0, \quad (14)$$

where  $\mathbf{z}_t^L = \mathbf{x}_\epsilon$  and  $\mathbf{x}_\epsilon$  is a sample from the NGC circuit's prior  $p(\mathbf{z}^L)$  or an explicit top-down vector that is clamped to layer  $L$ . Note that since the prior over a latent state  $p(\mathbf{z}^L)$  in an NGC circuit is unconstrained and multimodal, it is common to retro-fit a mixture model to samples of  $p(\mathbf{z}^L)$  in order to facilitate fast downstream ancestral sampling [24].

### 3.3 Biased Competition and Divisive Input Modulation (BC-DIM)

In the biased competition (BC) model of PC [77, 78], the neural dynamics generally involves a skip connection where a layer above the current one further mediates the state update:

$$\mathbf{x}_t^\ell = \mathbf{x}_t^\ell + \beta(\mathbf{W}^\ell)^T \cdot \mathbf{e}^{\ell-1} + \beta_m(\mathbf{V}^{\ell+1} \cdot \mathbf{x}^{\ell+1}) + \beta_a(\mathbf{A}^\ell \cdot \mathbf{x}^{\ell,A}) \quad (15)$$

$$\mathbf{e}_t^\ell = \mathbf{x}^\ell - (\mathbf{W}^{\ell+1} \cdot \mathbf{x}^{\ell+1}), \quad (16)$$

where we notice that, in this implementation, the error unit calculation remains the same as in standard PC and NGC. Note that  $\mathbf{A}^\ell$  is a third (optional) synaptic matrix introduced to map an external set of attentional feature values  $\mathbf{x}^{\ell,A}$  (for example, command control signals to induce an action-oriented behavior or labels to encourage the acquisition of discriminative latent activities). The coefficients  $\beta_m$  and  $\beta_a$  weigh the skip modulation and attentional feature pressures, respectively. Crucially, this model was later generalized/extended to incorporate an important neural mechanism known as divisive modulation (DIM) [79]:

$$\mathbf{e}_t^\ell = \mathbf{x}_t^\ell \oslash (\epsilon_1 + (\mathbf{W}^{\ell+1}) \cdot \mathbf{x}_t^{\ell+1}), \quad (17)$$

with the resulting neural dynamics becoming:

$$\mathbf{x}_t^\ell \leftarrow (\epsilon_2 + \mathbf{x}_t^\ell) \odot ((\mathbf{W}^\ell)^T \cdot \mathbf{e}^\ell) \quad (18)$$

$$\mathbf{x}_t^\ell \leftarrow \mathbf{x}_t^\ell \odot (1 + \beta((\mathbf{V}^{\ell+1}) \cdot \mathbf{x}^{\ell+1} + (\mathbf{A}^\ell) \cdot \mathbf{x}^{\ell,A})), \quad (19)$$

where we have (for consistency with the other PC frameworks) flipped the use of the transpose over the generative synaptic matrix  $\mathbf{W}^\ell$ , compared to the model's original presentation in [79]. Furthermore, in BC-DIM circuits,

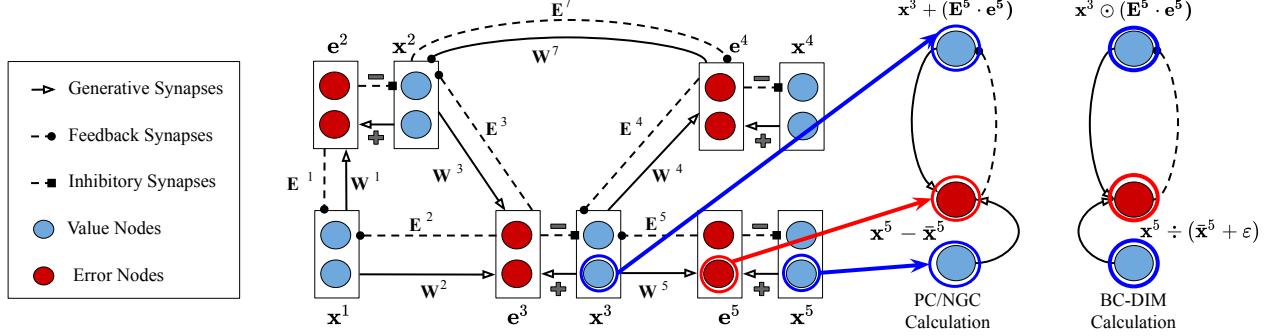


Figure 5: On the left is an arbitrary neural circuit (non-linearities are omitted for simplicity) that could be constructed under one of the three PC frameworks surveyed. Rao & Ballard PC (PC) only employs generative synapses  $\mathbf{W}^\ell$ , while NGC further employs separate feedback synapses (which may or may not correspond symmetrically to the generative pathway). Note that NGC/BC-DIM notably often employ skip connections ( $\mathbf{W}^7$ ). Finally, the right (which zooms in to a single value-error-value node triplet sub-circuit) depicts core differences in internal operations employed by PC/NGC and BC-DIM: PC/NGC computes error nodes via subtraction and updates value nodes using addition, while BC-DIM computes error nodes via division and updates value nodes using multiplication.

$\mathbf{V}^\ell = (n(\mathbf{W}^\ell))^\top$  is the transpose of the normalized forward synaptic matrix  $\mathbf{W}^\ell$ , while  $\epsilon_1$  and  $\epsilon_2$  are small coefficients used to prevent division or multiplication by zero (to ensure numerical stability).

While the formulation of biased competitive PC utilizes synaptic update rules similar to PC/NGC, the divisive modulative form requires rules that respect the new types of error units being used. Specifically, the synaptic update to the neural model above would be:

$$\Delta \mathbf{W}^\ell = \mathbf{W}^\ell \odot (\beta(\mathbf{z}^\ell \cdot ((\mathbf{e}^{\ell-1})^\top - 1))) \quad (20)$$

where we have further factorized the rule in [80] to make it compatible with the formulation of the standard PC synaptic update. The full computational instantiation of PC that leverages the above synaptic update as well as the error unit computation and state activity dynamics in Equations (17)–(19) is called the biased competition divisive input modulation (BC-DIM) form of PC.

In addition to enforcing the bio-physical constraint that both synaptic values and neural activities are strictly positive (by design), BC-DIM rests on several useful theoretical properties given its roots in one form of non-negative matrix factorization [81]. Specifically, the error units of BC-DIM computationally entail a minimization of the Kullback-Leibler (KL) divergence between sensory input targets and local model reconstructions. In addition, we can interpret one layer of BC-DIM probabilistically: we equate the prior ( $p(H)$ ) with its hidden state activity (any neuron in  $\mathbf{x}_t^\ell$ ), evidence ( $p(D)$ ) with the input activity ( $\mathbf{x}_t^{\ell-1}$ ), the posterior ( $p(H|D)$ ) with a single synapse inside of  $\mathbf{W}^\ell$ , and the likelihood ( $p(D|H)$ ) with a corresponding feedback synapses (or a single synaptic value inside  $(\mathbf{W}^\ell)^\top$ ). This means that the relationship between input activity (in layer  $\ell - 1$ ) and the steady-state hidden node activity (in layer  $\ell$ ) is consistent with Bayes' theorem [80]. Furthermore, the competition implicit in BC-DIM's neural activities could be viewed as performing a form of “explaining away” [82]: a node winning the competition within a layer could be viewed as the selection of a hypothesis that can explain the input, while suppressing (or reducing the support for) alternative hypotheses.

## 4 Predictive Coding in Machine Learning

So far, we have considered the reasons why PC might play a key role in machine intelligence. In this section, we discuss previous efforts that speak to empirical successes in this direction. Specifically, we review lines of work that have tackled different tasks in machine learning. Some of this work uses algorithms that differ in detail from the formalism of Section 3, but still conform to the definition of PC, in spirit.

**Supervised Learning.** The first application of PC to supervised learning involved training a small PC network to perform image classification on the MNIST dataset, achieving test and train errors comparable to those of an MLP of

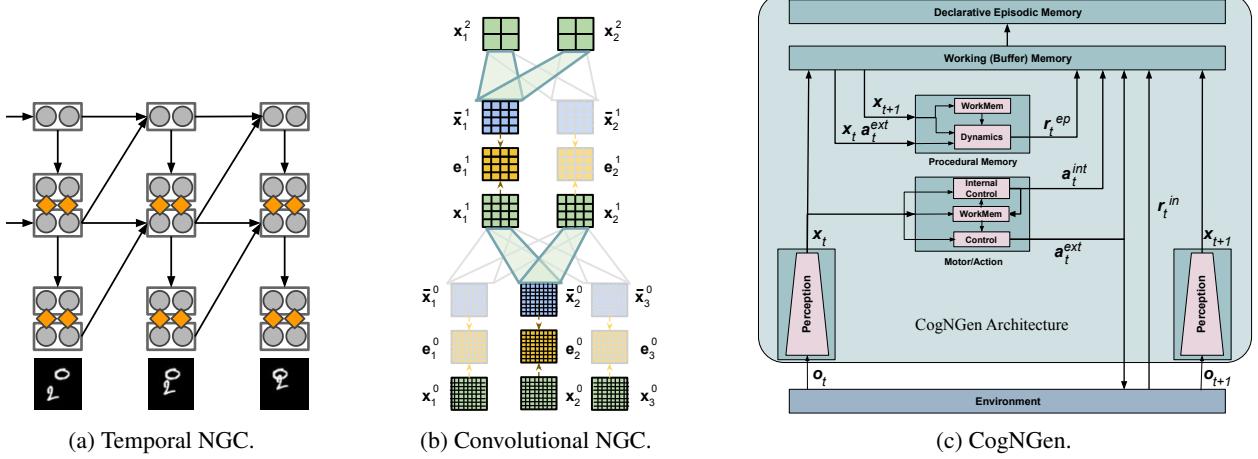


Figure 6: Various systems based on NGC-based PC: (a) a temporal NGC model (orange diamonds depict error nodes, grey circles depict state nodes, while arrows represent synaptic projections) for processing temporally-varying sequences of data patterns, e.g., frames from the moving MNIST dataset, (b) a convolutional NGC model (figure adapted from [75]; green grid blocks represent state feature maps, blue grid blocks represent prediction maps, yellow-orange grid blocks represent error maps, and blue parallelograms depict deconvolutional pathways) for extracting distributed representations of natural images, and (c) the CogNGen architecture (figure adapted from [86]), a modular cognitive control system that implements several core elements of the Common Model of Cognition [87] with PC and vector-symbolic memory ( $r$  depicts a reward, while  $a$  depicts an action vector).

the same complexity (depth and width) [46]. Since then, similar results have been achieved on convolutional networks trained on datasets of *RGB* images, such as CIFAR10 and SVHN [48]. In this work, the authors showed that updating the weight parameters alongside the neural activities (i.e., running Equations 5 and 6 in parallel), instead of waiting for the inference phase to converge, improves test accuracies as well as ensures a better convergence. These results also extend to structured datasets and graph neural networks, where PC is again able to match the performance of backprop on different benchmarks, with the advantage of learning models that are better calibrated and more robust to adversarial examples [51].

**Natural Language Processing.** Gaussian assumptions (that underwrite PC) can be limiting in scenarios where we need to model different distributions, such as categorical distributions or mixture models. One such scenario is found in transformer models [83]: the attention mechanism encodes a categorical distribution, computed via the softmax activation. To this end, it is possible to generalize the definition of the energy of a specific layer, originally defined as the squared distance between the predictions  $\mathbf{u}^\ell$  and the activities  $\mathbf{x}^\ell$ , to the KL divergence between two probability distributions, with prediction and activities serving as sufficient statistics. In detail, the PC model now has the following variational free energy:

$$\mathcal{E}_t = \sum_{\ell=0}^L \mathcal{E}_t^\ell \quad \text{where} \quad \mathcal{E}_t^\ell = D_{KL}[\mathcal{X}^\ell(\mathbf{u}_t^\ell) || \mathcal{X}^\ell(\mathbf{x}_t)], \quad (21)$$

where  $\mathcal{X}^\ell(x)$  is a probability distribution defined for every layer with sufficient statistics  $x$ . If every distribution is a Gaussian, this is equivalent to the energy defined in Equation 4. This generalization allows predictive-coding-based transformers to perform almost as well as standard transformers with the same model complexity [84]. In computational neuroscience, the use of hybrid generative models (with discrete and continuous state spaces) is fairly established: see, e.g., [85] for a first principles account of the requisite variational message passing, which can be regarded as a generalisation of PC within the setting of well-defined hierarchical generative models with mixed discrete and continuous states.

**Computer Vision.** When processing images, PC has shown promise, particularly, when generalizations that utilize convolutional operators are considered [88, 89]. Notably, BC-DIM has been shown to work well at extracting higher-level features from natural images and patches when the PC scheme employs convolution instead of matrix multiplications [90]. Other promising variants of PC have tackled certain sub-problems in vision, including object recognition and discrimination (using over-complete sparse representations) [91, 92].

With respect to NGC, early work relied on simplifying assumptions, particularly that images were grey-scale (or simply single-channel) and exhibited relatively low scene complexity, e.g., no backgrounds and objects were easily identifiable. Note that NGC/PC circuits can be learned with patches instead, where a natural image is deconstructed into a  $P \times P$  pixel grids; this allows the predictive synapses to acquire low-level patterns (such as strokes or edges for handwritten digits). Nevertheless, NGC has been generalized to natural images by directly integrating deconvolution/convolution [75], the standard operations used to build convolutional/deconvolutional neural networks, in a framework known as convolutional neural generative coding (Conv-NGC). In Conv-NGC, forward and feedback synapses are implemented to manipulate feature maps, or small clusters of neurons, which are coupled to equally shaped clusters of error units that compute the relevant mismatch signals needed to conduct iterative inference. Surprisingly, Conv-NGC models were shown to learn feature representations that implicitly embodied an image pyramid [93].

**Temporal Data.** PC has enjoyed some success in the much more difficult realm of temporal sequence modeling. Notably, [94, 89, 95, 96] developed a hierarchical neural generative modeling framework based on PC that focused on processing natural video data, where top-down information (inferred latent causal factors) was used to modulate the activities of lower-layers, aiming to extract locally invariant representations. Preceding this development was PC formulated as a Kalman filter [97, 98], which was demonstrated to work well on small sequential snippets of natural images, and deep hierarchies of local recurrent networks [99, 100] shown to work on a small symbol chunking task.

One of the earliest and first formulations of NGC was with respect to time-varying data, i.e., sequences made up of words/sub-words in a sentence or frames of a video [101]. This type of neural system was called the temporal neural coding network (TNCN) and was originally designed to operate as a top-down recurrent generative model and then later generalized to function as a hybrid recurrent and auto-regressive system [68], i.e., the parallel temporal neural coding network (P-TNCN). TNCN and P-TNCN were both shown to process pattern sequences without unfolding (over time), a core requirement for properly training deep recurrent networks (via backprop through time); thus making it local in space as well as time. Notably, both models (on different video simulations/benchmarks) were shown to generalize to unseen/out-of-distribution pattern sequences, exhibiting zero-shot capability, specifically with respect to video data, e.g., TNCN was shown to adapt to bouncing ball videos of different object quantities, while P-TNCN was shown to be capable of synthesizing frames of bouncing digits or characters of different quantities and qualities (without altering synaptic weights on the new samples). More recently, a formulation of PC, called dynamic PC [102], was developed by combining modeling tools from deep learning (i.e., using backprop-based neural circuitry such as hyper-networks) as well as mixture models. This dynamic PC system was demonstrated to acquire useful bio-physically plausible receptive fields in the context of small controlled sequential visual perception problems and tasks.

It is interesting to note that machine learning implementations of PC have been slow to deal with temporal data. This is surprising because PC can be viewed as an extended Kalman filter that should, in principle, handle temporal data in an efficient and Bayes optimal fashion. The generalization of PC as a Bayesian filter that encompasses learning leads to generalized filtering, in which model parameters can be treated as slowly varying latent variables or states. There are many instances of this form of PC; see [103] for a consistent variational treatment. One reason that machine learning may have yet to fully leverage PC in this context is its focus on classification problems that preclude dynamics. To deploy PC for time series assimilation and learning, it is necessary to move from static generative models to state-space models that have explicit dynamics, of the sort touched upon by [102] and implicit in recurrent neural networks.

**Continual Learning.** Another promising aspect of P-TNCNs described above was its ability/potential to conduct continual sequential learning, where [68] demonstrated that its generative ability on previously seen sequence modeling tasks did not degrade/deteriorate nearly as much as in recurrent networks (such as those based on gated recurrent units and long short-term memory cells). This meant that P-TNCNs exhibited some robustness to the catastrophic forgetting that appeared in recurrent networks when learning sequences of different types of patterns. This included recurrent networks trained with backprop but also with online forward mode training schemes that had access to full Jacobians, such as real-time recurrent learning (RTRL) and its noisy first-order approximation unbiased online recurrent learning. Additional effort [67] explored strengthening NGC’s memory retention ability by examining the challenging problem of online cumulative learning, where datasets (or tasks) were presented to the system in the form of a stream and with no indication of when the task was switched (creating a non-stationary, task boundary free variant of the lifelong machine learning problem setup). Surprisingly, the NGC-based model, without access to any task boundaries in [67] (namely, the sequential neural coding network (S-NCN)) was shown to outperform or be competitive with a wide swath of backprop-based approaches that relied on memory-buffers (replay), regularization, and/or auxiliary generative modeling in order to preserve prior knowledge. Stronger performance was seen when another neural circuit drove the S-NCN’s lateral recurrent synapses based on competitive learning (emulating the information routing behavior of the basal ganglia). This simple task mediating circuit was later improved in follow-up effort [104]). Another later effort developed a stochastic implementation of PC with readable/writable memory (BayesPCN) [58] that was shown to be robust to sample-level forgetting.

Research Domain	Tasks	References
Discriminative Learning	Categorization, Graph-based classification	[46, 48, 51]
Natural Language Processing	Language modeling, Masked language modeling	[68, 84, 121]
Computer Vision	Unsupervised reconstruction, Object classification, Feature extraction	[99, 20, 88, 89, 90, 91, 92, 75]
Temporal Modeling	Video sequence modeling, Sequence-based classification	[97, 98, 94, 89, 95] [96, 101, 68, 102]
Lifelong Learning	Continual classification, Continual sequence modeling	[67, 68, 104, 58]
Cognitive Control / Robotics	Reinforcement learning, Robotic control, maze navigation	[115, 110, 111, 112, 118, 87] [116, 86, 113, 117, 120]

Table 1: Overview of PC utilized and developed for machine learning, grouped by application/topic area. For a comprehensive study of the state of the art results in computer vision, we refer to [122].

**Active Inference and Robotics.** In computational neuroscience, early formulations of active inference were based on equipping PC with reflexes in order to simulate a variety of behaviors; ranging from handwriting and its observation [105], through oculomotor control [106, 107] to communication [108, 109]. This application of PC rests on the simple observation that perception and action are in the service of minimizing variational free energy, and action can be cast as minimizing (proprioceptive) prediction errors by changing (sensory) data. Machine learning implementations of PC are now starting to move beyond classification and generative modeling of static images to address dynamic control and reinforcement learning [110, 111, 112]. Active NGC (ANGC) [112] and active PC (ActPC) [113] formulate active inference in terms of predictive processing, much in contrast to machine learning implementations with deep neural networks trained via backprop. ANGC focused on a simple modular agent design, implementing a policy circuit and a generative transition dynamics that learned from sparse reward feedback by using the transition dynamics to produce a dynamically normalized epistemic signal that promoted intelligent exploration. ActPC builds on ANGC by implementing a policy circuit, an actor circuit, a generative transition dynamics circuit, and a prior preference circuit, further exploring how the temporal processing ability of each NGC component could be improved by integrating a simple form of working memory into the neural dynamics. ActPC and ANGC have been empirically shown to work well on standard reinforcement learning control problems and, more importantly, in the context of (simulated) robotic control [113], of which results for general PC also exist [114, 115, 116].

Parallel (independently developed) and homonym frameworks include active PC (APC) [117] and active PC networks (APCNs) [118], developed to learn part-whole hierarchies from natural images (tackling the difficult part-whole and reference frames learning problems), resulting in an interesting model of active, internally directed perception, i.e, the neural circuitry actively samples the natural image space to extract information for crafting internal representations. Notably, the more general APC model of [117] further offered a potential means of tackling the integrated state-action hierarchy learning problem, conducting a form of hierarchical reinforcement learning. The APC model was applied to a multi-room grid-world and was shown to work well. However, APC/APCNs utilize backprop in portions of their underlying architectures, having to train/adapt locally deep MLPs and recurrent networks (and deep hyper-networks) in order to obtain a desirable performance. ActPC, in contrast, rigidly commits to the principle of locality in terms of both inference and learning.

Beyond control agent design, a cognitive architecture known as the COGnitive Neural GENerative system (CogNGen) [87, 86], built on the ideas inherent to ActPC, has been proposed for tackling reinforcement learning problems. CogNGen instantiates elements of the Common Model of Cognition [119] and combines NGC with hyperdimensional / vector-symbolic models of human memory, implementing a module for the motor cortex, procedural memory, working memory neural buffers, and episodic declarative memory. CogNGen has been shown to perform well on maze-like exploration tasks [86, 120], including those that require maintaining memory within and across episodes.

## 5 Plausibility of Predictive Coding in Neuroscience

A common question in machine learning is: at what point can a particular algorithm be considered to be biologically plausible? This arises from the fact that no computer simulation can fully replicate the intricate workings of the brain in every respect, and, hence, there will invariably be certain nuances that render the simulation to be implausible in some way. Furthermore, different research agendas consider different properties for differentiating biologically plausible and non-plausible models. In this section, we discuss the key properties of PC that satisfy this distinction and which do not.

**Predictive Coding at Scale.** Broadly speaking, it can be said that PC already occurs at the level of individual brains. This notion is related to the Bayesian brain hypothesis [123, 124, 125, 126, 127, 128], a theory which states that our brain encodes a generative model of the world and perception is nothing more than a form of hypothesis testing [129, 130, 131, 132]. The inversion of this generative model conforms to the free energy principle, which can be read as the brain trying to minimise prediction errors, or variational free energy, given observations of the sensed world [38]. But how does this concept scale when we consider smaller “*things*”? Do individual brain regions perform PC on their own, and do the individual neurons also act so as to maximize the evidence of their own internal model of neighboring neurons [133]? Answering the above questions could serve as an inspiration to design neural systems and architectures that delegate error corrections across scale. In what follows, we will discuss the biological plausibility of PC at the neuronal level. However, we remark that developing a theory as well as empirical computational models of different scales of PC would prove invaluable.

**Error Neurons.** Our understanding of how PC might be implemented at the neuronal level has certainly changed over the last decade. The initial assumption was that the brain would encode two families of neurons/structures: one in charge of propagating predictions and one in charge of propagating errors [20, 46]. As of today, we have no definitive empirical evidence of the existence of single error neurons, though there is ample evidence for laminar-specific segregation of neuronal populations that may communicate predictions and errors, respectively [134, 135]. In addition, one could read the activity of midbrain dopamine neurons as reporting a certain kind of prediction error [136, 137]. Recent work has shown that error signals could potentially be computed by the local voltage dynamics in the dendrites [138, 139, 140]. For a more detailed description in the context of a possible biological neural implementation, see [141, 140]. Although existing technologies make it difficult to empirically demonstrate PC at the level of a single neuron, we have stronger evidence of PC at the level of neural populations, or brain regions [142]. PC can account for multiple brain phenomena, such as end-stopping and extra-classical receptive fields effects in V1 [20], bistable perception [143], illusory motion [144], repetition-suppression [145], and attentional modulation of cortical processing [146, 147]. It has also been shown that, when listening to speech, the human brain stores acquired information in a hierarchical fashion, where frontoparietal cortices predict the activities of higher level representations [148].

**Precision Engineering.** Another challenge in the implementation of PC is the management and updating of precision weighting. Typically, the covariance matrix  $\Sigma^\ell$  or its inverse, the precision matrix  $(\Sigma^\ell)^{-1}$ , must be adjusted or computed using matrix inversion [97, 24, 55]. However, implementations of PC in computational neuroscience have solved this problem using standard solutions from precision or covariance component analysis in a biologically plausible way: see [37] (Equation 57) and [149, 47] for details. This is an important aspect of PC, because precision weighting is thought to implement attention in a neuroscience setting. There is a substantial literature on PC in this setting that might usefully inform machine learning implementations [146, 150, 151, 147, 152, 153].

**Synaptic Constraints.** In standard PC networks, synaptic values, which are crucial for neural computation, are generally not subject to strict limitations after an update. This can cause the values to become highly positive or negative, which makes the model less stable overall. This is tackled in NGC, which introduces a constraint to ensure that the Euclidean norm of any row or column in the synaptic matrix does not exceed one, aiding in stability, a practice rooted in early classical sparse coding linear generative models [76]. Beyond this, there have been recent attempts to establish heuristic limits on the magnitude of synaptic values in order to thwart declines in classification performance [154]. A second implausibility of PC models is the frequent alterations in the signs of their synapses (or “sign-flipping”), that can go from negative to positive (and vice versa) during training, an aspect that is pivotal in emulating real cortical functionality. A potential solution to prevent sign-flipping would be to enforce non-negativity constraints on synaptic values and explicitly model groups of excitatory and inhibitory neurons, given that this configuration would apply the necessary positive and negative forces essential for PC inference and learning [155, 156, 157].

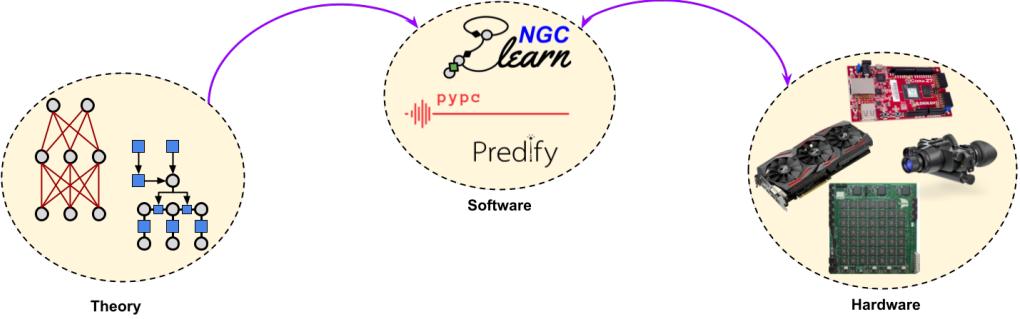


Figure 7: The theory-software-hardware cycle of predictive processing. In this setting, it is shown that theory and mathematical/computational development informs the structure and functionality of the required simulation software. The relationship between software and hardware has notably been depicted to be naturally bi-directional: software can inform the design of the hardware platform and vice-versa, i.e., co-design.

## 6 On Software Frameworks

Software plays a crucial role in engendering innovation, design, and development of models and algorithms for computational intelligence. In the realm of machine learning, software libraries provide the necessary back-end support and optimization needed for the GPU-driven, multi-CPU computation that powers the simulation of deep neural networks. Frameworks such as Theano [158], Caffe [159], Torch/PyTorch [160], and TensorFlow [161] have been among the key software platforms that have proven instrumental, both historically as well as for modern-day efforts in machine learning and neurobiological modeling. Furthermore, software libraries focused on particular subclasses of neural network and machine learning models facilitate reproducibility, an important element of scientific practice.

With respect to PC, software frameworks that facilitate research in PC are relatively sparse. Most research in PC design and development results in disjoint, scattered model and paper-specific code and scripts, often making it difficult to generalize those models and algorithms beyond the context in which they were developed. This prohibits the wider adoption of the principles that underlie PC and accompanying variational procedures; further preventing the education of future generations of researchers that could make important contributions to PC.

Nevertheless, there do exist several software libraries that could democratize PC research. Notably, *ngc-learn* [162], a general simulation and development library for computational neuroscience models, was one of the earliest historical libraries to support the construction of arbitrary PC models. Its theoretical grounding in neuronal cable theory and compartmental neurons allows computational modelers to prototype and simulate neural circuits, including those based on NGC and BC-DIM. To perform deep learning experiments, PCX [122] is a newer library built on top of Equinox, a deep learning framework in JAX, and hence allows an easy plug-and-play of deep learning models, trained using the neuronal updates of PC. Furthermore, the paper [122] accompanying the library also presents state-of-the-art results in the field for a large number of frameworks. Other examples of PC libraries include *pypc* [163], a library for the training of supervised and unsupervised hierarchical PC models, and *predify* [164], a PC-like software library that allows for the conversion of various deep learning architectures to systems that incorporate elements of PC, such as its top-down predictive circuitry. Newer PC-specialized libraries still emerge to this day, offering new elements of functionality such as specialized support for stochastic and Bayesian formulations of PC as in *pyhgf* [165]. Fig. 7 depicts the general PC, software, and hardware interaction cycle.

## 7 On Novel Hardware

Hardware limitations have historically played a pivotal role in shaping the direction of research by either enabling or hindering the practical implementation of theoretical ideas [166]. At present, graphics processing units (GPUs) and tensor processing units (TPUs) are predominantly used for training deep neural networks. However, emerging technologies such as memristors, spintronics, and optics have the potential to revolutionize the landscape [167, 168, 169]. Adapting algorithms to benefit from these new hardware technologies is crucial for advancing the field. PC is particularly well-suited for the development of algorithms for alternative hardware, as it is a simple energy based model that can be trained using equilibrium propagation, and bi-level optimization [15, 170]. It is also able to conduct iterative inference with layer-wise parallel computation, Hebbian synaptic adaptation, and optimisation resting on local (variational free) energy functions. These properties (in common with most neuro-mimetic schemes) could enable a parallelization of

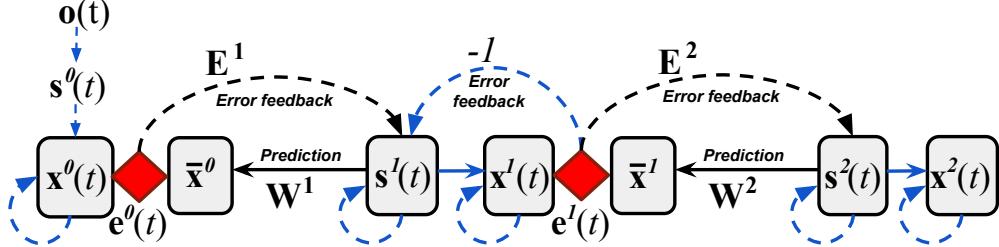


Figure 8: Spiking neural coding—a formulation of PC/NGC at the spike-train level, where  $s^\ell(t)$  represents an action potential (or spike) node, and  $x^\ell(t)$  is now treated as a trace meant to approximate a value node. Solid black arrows represent forward generative synapses, dashed black arrows represent error transmission synapses, and blue dashed arrows represent non-synaptic transformations (such as the recurrent electrical current and voltage calculations underlying a spike node  $s^\ell(t)$  or the trace/value node update underlying  $x^\ell(t)$ ). Note that  $\mathbf{o}(t)$ , which could be a static image or a video, is typically converted to a spike vector  $s^0(t)$  at time  $t$  (resulting in a sensory-level Poisson spike train).

its underlying operations, thus allowing for significant efficiency gains in training large-scale neural networks. The parallel nature of PC reduces communication and wait time, which are bottlenecks in the traditional backprop algorithm. Furthermore, the alignment of PC with neuromorphic hardware creates an opportunity for enabling energy-efficient learning methodologies [171]. A promising direction is that of using dynamical memristors, perfectly suitable for developing brain-inspired neuromorphic systems, which offer both high energy efficiency as well as high computing capacity [172].

**Biophysical Implementation.** Moving beyond conventional hardware, PC is poised to play a crucial role in “intelligence-in-a-dish” technology [173, 174, 175]. This involves adaptive neuromorphic computation through non-silicon bio-physical mediums. Due to the close association of PC with cortical computation and structure [176, 134, 177], it could be inherently compatible with organoid intelligence for performing fundamental calculations [178]. The early attempts to apply PC at the spike-communication level [179, 155] are particularly promising to mimic predictive processing in a dynamic context. Furthermore, PC is well-aligned with the constraints of biophysically oriented computations. Not only would these computational frameworks be natural first candidates for emulation in biophysical substrates, but their generalization ability might vastly improve given the natural evolution that the organoid structure lends itself. That is, the organoid’s “growth” and “decay” might offer a powerful means of facilitating model selection [180], improving the long-term generalization ability of a neural system. The road to robust synthetic general intelligence and neuromorphic cognition might lie in the intersection of neuroscientific (computational) models, such as PC, and the bio-engineering of neuronal micro-physiological systems.

## 7.1 Spiking Predictive Coding

A potential challenge for PC (and other neurobiological credit assignment processes in machine learning) is generalizing to spike-level temporal processing. Biological neurons communicate through discrete signals known as action potentials, creating spike trains that are sparse yet contain rich timing information [181]. These spike trains serve as the inspiration for spiking neural networks (SNNs), so-called third-generation neural networks, which encode information through the precise timing of spikes [182]. This sparse communication inherent to SNNs is one of their core strengths, allowing them to consume less energy through the use of high-information content spike trains, facilitating the construction of energy-efficient hardware to support their processing, i.e., neuromorphic hardware [183, 184, 185], where deep ANNs, on the other hand, require the use of energy-intensive, top-of-the-line graphics processing units (GPUs) for effective training. Unfortunately, with a few exceptions, most modern incarnations of PC fail to account for how learning and inference could occur under such a sparse, discrete communication scheme. This may reflect the fact that PC is, under the hood, a variational scheme that reproduces the idealized behavior of a sampling scheme (e.g., particle filtering) based on single particles or neurons: cf., [124]. That is, PC, by construction, describes ensemble or population dynamics, not the behavior of individual particles or neurons. For a comprehensive survey of spiking PC, we refer the reader to [186].

**The Spiking Neural Coding Framework.** The spiking neural coding framework is an attempt to formulate how PC could be implemented in spiking networks [187]. It builds on the premise that spike-based events can induce synaptic adjustments [155]. The framework employs an event-driven local adjustment rule that leverages variable traces for pre-synaptic and post-synaptic spikes. In SNNs, synaptic efficacies are updated using spike-timing-dependent plasticity (STDP) [188], where correlations in neural activities based on spike timing are used for synaptic modulation. Adapting

deep SNNs using STDP is challenging and often requires carefully hand-crafted layers. In contrast, spiking neural coding utilizes a more flexible approach, which involves synaptic conductance models, membrane potential models, spike emission functions, and trace mechanisms. Each layer in this framework attempts to estimate the trace activity of another layer, with the discrepancy being passed locally backward through iteratively evolved error feedback synapses (see Fig. 8). Importantly, spiking neural coding is adaptable to various spiking functions, from the leaky integrator to the Hodgkin-Huxley model [189]. Other implementations of spike-level PC have recently begun to emerge [190, 191, 140]. Notably, in contrast to the purely unsupervised nature of the original spiking neural coding framework, models such as [190] operate in a discriminative context. However, these newer models do not address the weight transport problem, because feedback synapses are shared with the forward/generative synapses.

## 8 Looking Forward: Important Directions for Predictive Coding Research

While it is often claimed that PC is the optimal inversion scheme for hierarchical Gaussian generative models, its performance can be quite below modern-day deep neural networks trained with backprop. The future of PC in machine intelligence strongly depends on our ability to address and fill this gap. Specifically, among the main directions for future work related to PC should be understanding the fundamental reasons behind this performance mismatch and using this acquired insight to develop and design novel PC schemas, mathematical frameworks, and computational models that work in large scale settings, where current deep learning models excel.

**Efficiency.** The first drawback of PC is its efficiency. This is a consequence of its underlying iterative inference process, which generally needs to be run until convergence. In practice, it is common to let a PC model run for a fixed number of iterations  $T$ , but this number must be large in order to reach high performance, and deeper networks require more iterations in order to perform well. To this end, it would be useful to derive different optimization techniques and methodologies that carry out the minimization of the variational free energy. Such techniques could come in the form of (faster) variations of the expectation-maximization (EM) algorithm (equivalent to gradient descent in the standard case). An example of such a scheme is the newly proposed *incremental* PC [48], based on incremental EM. The convergence of this method has also been proven using methods from dynamical systems, under the assumption of sufficiently small parameters [192]. Future work could investigate whether there are better alternatives or whether the optimal update rule can be learned with respect to specific tasks and datasets (drawing inspiration from the recent developments in deep meta-learning [193, 194, 195]). More advanced amortized inference algorithms and mechanisms might prove to be another critical ingredient for reducing the computational burden of the PC inference process itself, as, historically, the iterative inference of classical sparse coding linear generative models [76] was dramatically sped up when introducing a second recognition neural model [196]. It might be that the answer may lie in some variations of the EM algorithm that are lesser known to the machine learning community, such as *dynamical* expectation maximization (DEM) [197, 44, 44], or in alternative, more efficient implementations of precision-weighted prediction errors, as in [102]. Other possibilities may lie in methods based on different message passing frameworks, such as belief propagation and variational message passing over factor graphs.

**Optimization Tricks and Heuristics.** Future research will also need to focus on the study of optimization techniques that have proven useful and invaluable for variational inference, such as those that promote the inclusion of precision weighting parameters into the picture [198]. Despite interesting developments obtained over the last several years, and despite the fact that precisions are of primary importance in simulations used in the neurosciences, these techniques have only been tested in small and medium scale settings [199, 200, 201]. More generally, the field of deep learning has enjoyed immense benefits from simple optimization tricks developed throughout the last decade, such as dropout [202], batch normalization [203], adaptive learning rates such as Adam [204] and RMSprop [205], and the introduction of the ReLU activation [206] and its variants. Without these techniques, emerging from the joint effort of thousands of researchers, the training of extremely overparametrized neural models would not lead to the results that we observe today. Interestingly, backpropagation itself exhibited many flaws and limitations at the beginning that precluded it scaling to high-dimensional data spaces: in the late 90's, kernel learning methods were dominant and generally found to be more effective than artificial neural networks, which were generally disregarded due to the problem of vanishing gradients [207] as well as their strong requirement for heavy computational power. Most of these problems have now been addressed in over thirty years of research, again through a collective effort of thousands of people. Given the history of deep learning, one might ask: what are the dropout, batch norm, and Adam optimizer equivalents for PC? Addressing such a question would be of vital importance if the goal is to scale the applicability of PC, and will hopefully become a more prominent topic of interest of more research efforts going forward.

**Stochastic Generative Models and Sampling.** A different but important, direction, is that related to generative models. We have been discussing the importance of putting statistical models of joint distributions back into the

research agenda of generative AI; however, most of the research efforts that go beyond small-scale tasks focus on supervised learning [48, 84] (with small notable exceptions, such as the unsupervised neural circuit of [75]). To do so, we need to develop models that are capable of sampling data points from a well-computed posterior distribution, using simulation methods such those based on Langevin dynamics [208]. This would benefit different subfields of Bayesian inference, such as out-of-distribution (OOD) detection, uncertainty minimization, and data reconstruction. In fact, PC is particularly suitable to OOD detection, thanks to a measure of surprise that is always readily available to the model, that is, with respect to its variational free energy.

Another probabilistic generative modeling research direction for PC is to incorporate the uncertainty about model (i.e., synaptic) parameters into the variational bound on marginal likelihood. That is, one can equip synaptic parameters with probability distributions (as opposed to using point estimates). This move would take PC closer to its Bayesian roots: current machine learning implementations of PC do not treat the model parameters as random variables and can therefore be regarded as an expectation maximization (EM) procedure, where the M-step ignores uncertainty about the parameters [209]. The benefit of treating parameters as random variables is that one can evaluate the model evidence required for structure learning [210, 211, 212, 213], i.e., one could place prediction errors on the synaptic weights and evaluate the resulting variational free energy (or marginal likelihood) for structure learning or, in a biological setting, morphogenesis [214, 133]. This research direction takes PC into the world of generalized filtering and dynamic causal modeling, in which parameters can be regarded as latent states that change very slowly [103, 215]. In the case of dynamic causal modeling (i.e., the variational inversion of state-space models under Gaussian assumptions), structure learning can be rendered particularly efficient through particular instances of Bayesian model selection [216, 217, 218]; namely, Bayesian model reduction to remove or prune redundant parameters from a full or parent model [219]. Related generalizations of PC might also leverage advances in nonparametric Bayes to learn the structure of neuronal networks. Please see [217, 220, 221] for further details.

**Crafting Cognitive Control Systems.** PC brings with it the promise of learning a powerful generative process that is continuously and iteratively refined as more sensory samples are gathered over time. This has led some early work to consider such a process as the basis for world models that drive modular, brain-motivated cognitive models, capable of combining perception and action in the context of playing video games [91, 111] and robotic control tasks [114, 112, 113], as well as large-scale cognitive architectures [119, 86, 120]. This has important implications beyond machine learning, particularly for the domains of cognitive science and cognitive neuroscience where a key pathway is to craft computational theories of mind and to examine their fit to human subject data on controlled psychological tasks [222] as well as their ability to generalize to cognitive functionality. Hence, a promising future direction is to design modular, increasingly complex systems made up of PC circuitry, that rely on single fundamental PC circuits and low-level dynamics.

There are important lessons that come from crafting systems of PC circuitry that can inform the fundamentals of PC itself. For example, in the PC-centric cognitive architecture of [86], it was found that the synergy of PC with another important neural model, i.e., vector symbolic memory [223, 224, 225], facilitated effective complex auto-associative and hetero-associative memory operations that led to rapid convergence on complex maze navigation tasks and, furthermore, facilitated the design of a novel PC circuit that leveraged its neural dynamics to learn a policy for internally manipulating a flexible recurrent memory system [120].

Using PC as a fundamental neural building block for cognitive control systems is still in its earliest stages, and although more effort will be needed for it to become viable for building robust computational theories of mind, it presents a worthwhile long-term direction for crafting simulated natural intelligence. This promise is made even stronger when considering that deep backprop-based networks are beginning to find use in the field of cognitive science [226]. Making developments along this direction would also crucially benefit the research in active inference [227, 85, 19, 18], given that agent systems that engage in epistemic foraging often center around the use of dynamic generative models and can even be viewed as simple cognitive control models.

## 9 Conclusion and Outlook

Generative models will most likely play a large role in the future of artificial intelligence. Despite this, current research seems to mostly focus on a limited class of models, overlooking possible alternatives. On the one hand, this is justified by the exceptional results obtained by deep, backprop-trained artificial neural networks; on the other hand, more principled methods, whose formulations are grounded in statistics and information theory, may deserve attention. In this work, we have focused on inverting a specific class of continuous-state generative models, namely, predictive coding. More precisely, we have: (1) presented a review of predictive coding schemes in machine learning, highlighting previous art that has led us to the point that we are at today, (2) summarized important open questions in the field that need to be answered in order to unlock and utilize the full potential of predictive coding, and (3) identified possible

applications and future research directions. As of today, we are seeing some of the potential of PC, but we are still far away from large-scale applications that may call for a significant investment in PC research. Already in the past years, we have seen impressive growth in the field of predictive coding in machine learning: it was only in 2017 that Whittington and Bogacz demonstrated how to train a small predictive coding classifier on MNIST [46]. In addition, we have already seen how integrating a few ideas from predictive coding can lead to interesting and more powerful backprop-based deep models [228, 229, 49, 230, 231, 121].

One of the main goals of this survey is to encourage researchers to build on the results of decades of prior effort and focus on the challenges offered by predictive coding: no success story can come without an active community behind it, as evidenced by backpropagation-centric deep learning. We remark that a promising methodology is only as good as the efforts that are made to advance it, both empirically and theoretically. Community effort will be needed to advance predictive coding from both the software and the hardware standpoint; particularly, to develop computational schemes that exploit the advantages on offer, such as its parallelism and sparse, local, and potentially energy-efficient computations. Although research progress in predictive coding has been consistent over the past decades, we may be only starting to realize the benefits afforded to artificial intelligence by reverse engineering the cortex and other biological structures.

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## Appendices

Below, we provide comprehensive supplementary details that assist in understanding the essential aspects of the main survey. The structure of this appendix is designed as follows: First, a comprehensive table is provided that outlines and explicates the principal symbols and operations utilized in the core manuscript (Section 10). In Section 11, a robust analysis of the backpropagation of errors is conducted, in which we scrutinize its central issues and criticisms, the understanding of which motivates much of the research in neuro-mimetic computational intelligence. This research is not limited to predictive coding, but comprehends a large amount of message passing schemas and algorithms that different communities have developed and improved through the years. In Section 12, we discuss such biologically-inspired alternatives to backpropagation-centric credit assignment.

## 10 Table of Symbols and Operators

In Table 2, we provide a table that collects and briefly defines several acronyms/abbreviations, key symbols, and operators used throughout the survey.

Item	Explanation
Backprop	Backpropagation of errors
PC	Predictive coding
NGC	Neural generative coding
BC-DIM	Biased competition, divisive input modulation
TNCN	Temporal neural coding network
APC	Active predictive coding
ActPC	Active predictive coding (NGC, active inference generalization)
DPC	Dynamic predictive coding
SNN	Spiking neural network
STDP	spike-timing-dependent plasticity
.	Matrix/vector multiplication
$\odot$	Hadamard product (element-wise multiplication)
$\oslash$	Element-wise division
$\mathbf{z}_j$	$j$ th scalar of vector $\mathbf{z}$
$\ \mathbf{v}\ _2$	Euclidean norm of vector $\mathbf{v}$
$L$	Number of layers
$\mathbf{z}^\ell$	State representation at layer $\ell$
$\bar{\mathbf{z}}^{\ell-1}$	State prediction at layer $\ell$
$\mathbf{e}^\ell$	Error/mismatch signal at layer $\ell$
$\phi^\ell()$	Activation/transfer nonlinear activation applied to the state tensor
$g^\ell()$	Activation/transfer nonlinear activation applied to the state tensor prediction
$\leftarrow$	Variable override
$\beta$	Constant value, which controls the state correction rate
$\gamma$	Strength factor to control leak variable
$\top$	Transpose operation
$\lambda$	Modulation factor to control the evolution of the error filters
$p(\mathbf{o})$	Bayesian model evidence over observation $\mathbf{o}$
$q(\mathbf{x})$	Approximate posterior distribution on the latent space
$\mathbf{x}_{i,t}^\ell$	Value node of the $i$ -th neuron of the $\ell$ -th layer at time $t$ (adjustable/dynamic model parameter)
$\mathbf{u}_{i,t}^\ell$	Prediction signal
$\mathbf{E}^\ell$	Learnable matrix containing error feedback synapses
$\mathbf{W}^\ell$	Learnable matrix of generative forward synapses
$\mathcal{E}^\ell$	(Free) Energy functional
$\mathbf{M}_W$ and $\mathbf{M}_E$	Modulation matrices that enable a form of synaptic scaling
$\mathbf{V}^\ell$	Matrix containing the lateral cross-inhibitory and self-excitation synapses

Table 2: Key symbols, operators, abbreviations, and definitions.

## 11 On Backpropagation of Errors and Biophysical Credit Assignment

In this section, we provide relevant context with respect to backpropagation of errors (backprop), the workhorse algorithm for training deep neural networks today. First, we discuss the core criticisms/issues of this algorithm, which research on predictive coding (and other neuro-mimetic learning algorithms) attempts to address. Next, we provide a simple treatment of backprop from the perspective of this survey’s notation/symbols as review.

### 11.1 What is Wrong with Backprop? Criticisms and Limitations

The problem of *credit assignment* is vital in scenarios in which only incomplete performance evaluations are available. During learning, this problem reduces identifying which neuronal units have a larger influence on a specific objective function and modifying their relevant synapses to improve performance. From a purely error-driven algorithmic perspective on learning, credit assignment is performed by allocating error values to every neuron (based on this objective). The consequent update of the incoming synapses is performed to minimize this error. A similar behavior has been first theorized [20, 36, 42] and then observed in the brain [232, 233]. However, the way in which backprop specifically performs this allocation of error is considered implausible, i.e., this is not likely to happen in the brain. Historically, the first discussions about the implausibility of backprop date back to 1989, with Francis Crick’s work [234]. After more than three decades of progress in understanding biological neurons and synapses, the fact that backprop is implausible is even more obvious.

**Forward and Backward Signals.** The first, and historically major criticism [141], about the plausibility of backprop is given by the presence of a forward and a backward pass [13, 235], which propagates input information forward, and back-propagates information about gradients of an objective function (also sometimes called “teaching signals”). There are two reasons for the implausibility of this approach: first, biological neurons are not believed to have the storage capabilities needed to memorize the forward signals; second, the rule governing the synaptic updates is not local but depends on the minimization of a (global) loss function that depends on the value of neurons that can be many layers below in the hierarchy. This contrasts with plasticity rules and the belief that synaptic updates only rely on local information [23].

**Symmetric Synaptic Connections.** In backprop, presynaptic neurons receive error information from postsynaptic ones through the same synapses used to originally forward the input information; this has also been called the “weight transport problem” [236]. This operation is not feasibly possible in chemical synapses, where neurotransmitters and receptors force a one-directional flow of information. Hence, feedback loops in the brain are created by using two different synapses [237, 235, 101, 141, 14]. Note that even feedback loops are not guaranteed, as they may not be present at all [238].

**Arbitrary Topologies.** Models trained via backprop are not limited to a sequential structure: thanks to automatic differentiation, it is possible to perform multiple kinds of operations. Most used models are, in fact, composed of different kinds of layers, such as convolutional layers [11] or the (multi-head) attention operators that characterize transformers [83]. However, backprop is limited to training networks that take the form of directed acyclic graphs. If a cycle is present inside the neural structure of a network, an infinite loop that would make learning impossible is created during the first forward pass. To address this limitation, researchers have developed a time-dependent variation of backprop that stores vectors on neural activities over time [239], called backprop-through-time. However, this further increases the implausibility of this type of error-driven learning, as the neural activities that were earlier stored for error computations are now additionally stored over time [16]. This limits biological plausibility and prevents reproducing the message-passing structure that characterizes processing in brain, as the structure of biological networks is extremely complex, full of cycles, and heterarchically organized with small-world connections [26]. These topologies are likely highly optimized by evolution, where different topological attributes promote different types of communication mechanisms [240, 241, 242].

**Credit Assignment.** The models trained using backprop often struggle with issues with the commonly known issue of credit assignment [243], particularly leading to vanishing or exploding gradients [207], making the entire network unstable. The issues related to credit assignment over deep hierarchies of computational units become more problematic when training sequential neural networks through time, such as recurrent neural networks [244]. The problem of using a long chain of recursive operations (such as those that collectively characterize backprop) has been referred to as the “global feedback pathway problem” [101, 245] and have been argued to be a particularly important driving mechanism of error-driven learning that needs to be dispensed with if more parallel, local learning is desired.

**Sensitivity to Weight Initialization.** One key ingredient that guarantees convergence and generalization is based on the initial condition of the weights derived from some parametric space. However, the model trained using backprop is sensitive to initial conditions [246], thus hampering its overall performance. Despite recent advances in initialization approaches, this issue still exists. One of the widely popular initialization techniques in modern-day ML is based on Glorot initialization. However, recently, [247] and [248] showed that blindly adopting Glorot initialization leads to suboptimal performance.

**Dependence on Normalization.** The models trained using backprop are often heavily dependent on initialization strategies at the data level [249] and activation level [250, 203], the choice of which can help to ensure faster convergence and better generalization. However, these approaches introduce additional computational overhead and have several problems, such as: working with small batch sizes [250], only work operating across certain input patterns or particular activation functions, struggling when there are dependencies between samples in a mini-batch, not operating stably when the distribution during test-time inference is different or drifts away from the training distribution, and not working well when used in tandem with other normalization strategies or even simple noise injection schemes.

## 11.2 Credit Assignment by Backpropagating Error Derivatives

We next proceed to develop a basic formal understanding of the learning dynamics of the backprop algorithm.

**The Case of the Feedforward Network.** To illustrate the credit assignment process induced by backprop, we examine the case of a popularly-used ANN structure known as the feedforward network. A feedforward network, in essence, is a stack of nonlinear transformations, or  $\{f_\ell(\mathbf{z}^{\ell-1}; \theta_\ell)\}_{\ell=1}^L$ , applied to the input  $\mathbf{x}$ . If the ANN is specifically a multilayer perceptron (MLP), each transformation  $\mathbf{z}^\ell = f_\ell(\mathbf{z}^{\ell-1})$  will produce an output  $\mathbf{z}^\ell$  from the value  $\mathbf{z}^{\ell-1}$  of the previous layer using a synaptic weight matrix  $\theta_\ell = \{W^\ell\}$ .  $f_\ell$  is concretely decomposed into two operations (we omit biases for clarity):

$$\mathbf{z}^\ell = \phi^\ell(\mathbf{h}^\ell), \quad \mathbf{h}^\ell = \mathbf{W}^\ell \cdot \mathbf{z}^{\ell-1}, \quad (22)$$

where  $\phi^\ell$  is an activation function,  $\mathbf{z}^\ell \in \mathcal{R}^{J_\ell}$  is the post-activation of layer  $\ell$ , and  $\mathbf{h}^\ell \in \mathcal{R}^H$  is the pre-activation vector of layer  $\ell$ .<sup>2</sup> For convenience, we set  $\mathbf{z}_0 = \mathbf{o}$  (this layer is the input vector), and  $\mathbf{z}_L$  is the final output prediction made by the stacked model  $f_\Theta(\mathbf{o})$ . The goal of a backprop-centric credit assignment process used to train any such deep network will be to adjust  $\Theta$  to minimize an output loss/cost function (or a function that evaluates the quality of the performance/fitting ability of the overall network for a given task).

The output activation function (for layer  $L$ ) and the cost function of a feedforward network are generally chosen based on the task/problem at hand. For example, in the case of regression over continuous, unbounded values, an identity activation function could be used  $\mathbf{z}^L = \phi^L(\mathbf{h}^L) = \mathbf{h}^L$ , and the cost function set to be squared error, i.e.,  $\mathcal{L}(\mathbf{y}, \mathbf{z}^L) = \frac{1}{2} \sum_i (\mathbf{z}_i^L - \mathbf{y}_i)^2$ . For classification, the output activation function is typically set to be the softmax, i.e.,  $p(\mathbf{y}|\mathbf{z}^L) = \phi_L(\mathbf{z}^L) = \exp(\mathbf{z}^L) / (\sum_j \exp(\mathbf{z}_j^L))$ . Any element in the output vector (i.e.,  $\mathbf{y}_j \equiv \phi_L(\mathbf{v})_j = p(j|\mathbf{v})$ ) is the specific scalar probability for class  $j$ . In this case, the cost function typically chosen is the categorical negative log-likelihood, or  $\mathcal{L}(\mathbf{y}, \mathbf{z}^L) = - \sum_i (\mathbf{y} \odot \log p(\mathbf{y}|\mathbf{z}^L))_i$ .

To conduct credit assignment in a network such as the one characterized by Equation 22, we take gradients of  $\mathcal{L}(\mathbf{y}, \mathbf{z}^L)$  with respect to each underlying weight matrix, i.e., for each synaptic matrix our goal is to obtain another matrix  $\frac{\partial \mathcal{L}(\mathbf{y}, \mathbf{z}^L)}{\partial \mathbf{W}^\ell}$  that contains synaptic deltas or adjustments; this adjustment matrix can then be used in an optimization rule such as stochastic gradient descent/ascent. However, to obtain these necessary adjustment matrices, we must employ reverse-mode differentiation (or the computational implementation of the chain rule of calculus) starting from the global cost function and moving (recursively) backward through the operations defining the network<sup>3</sup>, i.e., a process also well-known as backprop. Formally, calculating the required delta matrices is done in the following way (where we

<sup>2</sup>Note that the terms “pre-activation” and “post-activation” are used a bit differently in the literature, particularly with respect to deep ANNs and neurobiologically-motivated models. In this survey, in the context of deep learning models, the terms are defined as we have done so here, whereas in the context of biological models, we use pre-activation to refer to an incoming layer of neural activities (i.e.,  $\mathbf{z}^{\ell-1}$ ) and post-activation to refer to an outgoing layer of activity values (i.e.,  $\mathbf{z}^\ell$ ).

<sup>3</sup>As noted before, working through this long chain of operations step by step, layer by layer, has been referred to as the moving back along a global feedback pathway [14, 245] and further represents a strong criticism of learning in modern-day ANNs, as there is no evidence that the neural circuits in the brain transmit backward error derivatives back along the same pathways that information was transmitted along. This crucially prohibits parallel computing across layers in the system.

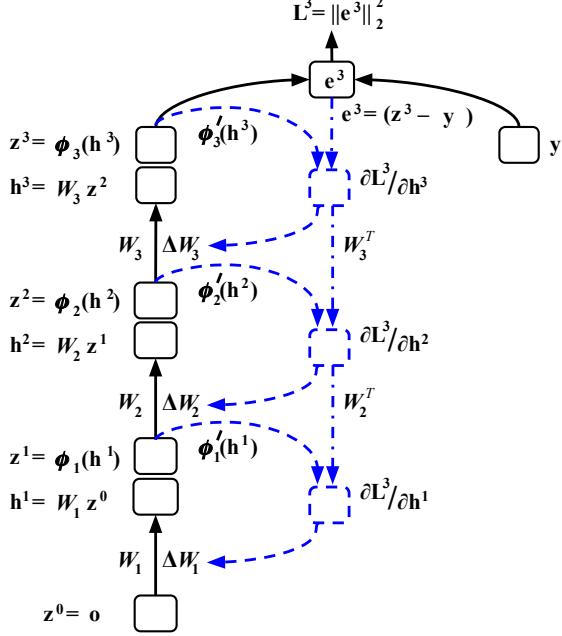


Figure 9: Illustration of back-propagation of errors (backprop) applied to a three-layer multi-layer perceptron, i.e.,  $L = 3$ , trained to minimize mean squared error. The blue lines indicate the reverse propagation calculation. For notational consistency,  $\mathbf{z}^0 = \mathbf{o}$  denotes the input datum. The blue dash-dotted lines mark the global feedback pathway that backprop depends upon to calculate the updates to synaptic parameters in the lower levels of the model.

show first how to compute the adjustment for the output matrix and then how to compute the neural system's internal intermediate synaptic parameter matrices):

$$\Delta \mathbf{W}^L \propto \frac{\partial \mathcal{L}(\mathbf{y}, \mathbf{z}^L)}{\partial \mathbf{W}^L} = \frac{\partial \mathcal{L}(\mathbf{y}, \mathbf{z}^L)}{\partial \mathbf{h}^L} \frac{\partial \mathbf{h}^L}{\partial \mathbf{W}^L} = \frac{\partial \mathcal{L}(\mathbf{y}, \mathbf{z}^L)}{\partial \mathbf{h}^L} \cdot (\mathbf{z}^{L-1})^\top \quad (23)$$

$$= \left( \frac{\partial \mathcal{L}(\mathbf{y}, \mathbf{z}^L)}{\partial \mathbf{z}^L} \frac{\partial \mathbf{z}^L}{\partial \mathbf{h}^L} \right) \cdot (\mathbf{z}^{L-1})^\top = (\mathbf{e}^L \odot \phi'(\mathbf{h}^L)) \cdot (\mathbf{z}^{L-1})^\top \quad (24)$$

$$\Delta \mathbf{W}^\ell \propto \frac{\partial \mathcal{L}(\mathbf{y}, \mathbf{z}^L)}{\partial \mathbf{W}^\ell} = \frac{\partial \mathcal{L}(\mathbf{y}, \mathbf{z}^L)}{\partial \mathbf{h}^\ell} \frac{\partial \mathbf{h}^\ell}{\partial \mathbf{W}^\ell} = \left( \frac{\partial \mathcal{L}}{\partial \mathbf{h}^\ell} \frac{\partial \mathbf{h}^\ell}{\partial \mathbf{z}^{L-1}} \frac{\partial \mathbf{z}^{L-1}}{\partial \mathbf{h}^{L-1}} \cdots \frac{\partial \mathbf{h}^{\ell+1}}{\partial \mathbf{z}^\ell} \frac{\partial \mathbf{z}^\ell}{\partial \mathbf{h}^\ell} \right) \frac{\partial \mathbf{h}^\ell}{\partial \mathbf{W}^\ell} \quad (25)$$

$$= \left( \left( (\mathbf{W}^\ell)^\top \cdot \frac{\partial \mathcal{L}}{\partial \mathbf{h}^{\ell+1}} \right) \odot \phi'(\mathbf{h}^\ell) \right) \cdot (\mathbf{z}^{\ell-1})^\top, \quad (26)$$

where  $\phi'(\mathbf{h}^\ell)$  is the first derivative of the activation function  $\phi^\ell()$  applied to pre-activation vector  $\mathbf{h}^\ell$ . Note that  $\mathbf{e}^L = \frac{\partial \mathcal{L}(\mathbf{y}, \mathbf{z}^L)}{\partial \mathbf{z}^L} \frac{\partial \mathbf{z}^L}{\partial \mathbf{h}^L}$ , which allows us to think of the first derivative of the global cost function with respect to the output units as a set of *error neurons* or error units (an idea that will be touched on frequently throughout the main survey). Note that, to speed up the simulation of the above synaptic adjustment equations, one could use more than one data point at a time for the calculations (also known as a mini-batch). That is, one could either use a single vector input  $\mathbf{o}$  to the equations above, i.e.,  $\mathbf{z}^0 = \mathbf{o}$  (online learning), or one could substitute  $\mathbf{o}$  with matrix  $\mathbf{o} \in \mathcal{R}^{J_0 \times B}$  where  $B > 1$  is the batch size (batch-based learning). Figure 9 illustrates the full process of a forward and backward pass in a two hidden-layer MLP.

Once the delta/adjustment matrices have been calculated via Equations 24 and 26, we may change the actual values of the MLP's synaptic values (or synaptic efficacies) in a subsequent step, such as through  $\mathbf{W}^\ell \leftarrow \mathbf{W}^\ell - \eta \Delta \mathbf{W}^\ell$  (stochastic gradient descent with step size  $\eta$ ) or through a more sophisticated procedure, such as Adam [204], RMSprop [205], or AdamW.

## 12 Neuro-Mimetic Credit Assignment: Alternatives to Backpropagation

Due to the aforementioned limitations (of backprop), the research community has focused on finding alternatives to backprop-centric optimization. These alternatives are mostly neuroscience-inspired and differ in the way that credit assignment is specifically conducted. In this section, we review the following influential frameworks: *target propagation* [64, 65, 245], *local representation alignment* [101, 245], *equilibrium propagation* [15], which builds on *contrastive Hebbian learning* [63], *feedback alignment* [237], and the recently proposed *forward-forward* algorithm [16].

**Target Propagation.** As the name suggests, the main peculiarity of this algorithm lies in the fact that it backpropagates targets as opposed to gradients. To this end, every level of the hierarchy can be seen as a shallow autoencoder, where every latent variable aims to generate itself via asymmetric forward and backward connections. Here, the target of the layer below acts as a latent representation. This mechanism allows it to have asymmetric weight connections and learn via local information only. This algorithm has been applied to sequential structures, such as natural language tasks [251, 252, 253]. In all cases, however, the performance is not comparable to backprop's. A theoretical study has shown that target propagation (TP) is related to Gaussian-Newton optimization and claimed this as the underlying reason for this mismatch [254]. This work also partially addresses this limitation by proposing an algorithm formulation that can be seen as a hybrid between gradient descent and Gauss-Newton optimization. This variation is, however, less biologically plausible and still not convincing in terms of performance. To this end, it has been shown that adding a prior distribution that makes TP learn a target similar to that of backprop restores bio-plausibility and largely improves performance [255]. This is thanks to the implementation of a loss function that pushes the Jacobian of the feedback operator towards the feedforward weights. Recent work has also investigated whether we actually need to learn the feedback weights and has shown that the algorithm could perform well even when these are kept fixed [256]. Thus targetprop can be considered as an approximation of predictive coding, where instead of local loss, targets are pushed. Thus, assuming the underlying function to be approximated is Lipschitz continuous, and the difference between forward and backward activity is less than some  $\epsilon$  (where  $\epsilon$  is some small value), the network can be shown to converge to an optimal point. In predictive coding, this is achieved by minimizing an energy function over an arbitrary number inference steps, which empirically reduces uncertainty and leads to a stable and robust performance.

**Local Representation Alignment.** This algorithm can be seen as a fast, noisy approximation of predictive coding [245], and advocates a form of indirectly coordinated learning by minimizing a pseudo-energy functional per neural activity layer [101, 245]. These approaches have been mainly tested on classification tasks focused on the domain of computer vision and have been shown to operate and generalize well on large-scale (image) benchmarks such as ImageNet [74]. As opposed to target propagation, local representation alignment (LRA) minimizes an approximate form of (variational) free energy; under some mild assumptions, it can also be shown that LRA approximates backprop [257] and, thus, by induction predictive coding.

**Contrastive Hebbian Learning and Equilibrium Propagation.** These algorithm are the ones that share the most similarities with PC, as they are utilized to learn an energy-based model that iteratively relaxes to a solution. In equilibrium propagation (EP), two different phases are required to perform credit assignment: a prediction phase, where energy is minimized in order to make a prediction based on some available information, and a learning phase, where the neurons in charge of making the prediction are slowly nudged towards a supervised signal. At the end of both phases, a synaptic weight update is performed. Notably, EP builds on the classical dual-phase adjustment process of the framework of contrastive Hebbian learning, which is one of the earlier biologically-plausible algorithms used to adapt parameters of Hopfield networks [63] and later extended to those with latent variables, i.e., Boltzmann machines [258], and Helmholtz and neural heat exchange machines [259, 259, 260]. While this model has been shown to approximate backprop and recurrent backprop [261], the original formulation fails to scale up to complex tasks. To this end, different variations of this framework have been developed that improve efficiency and performance in specific tasks [262, 263, 264]. It has also been shown that defining the energy function on the complex plane allows one to avoid nudging, making the algorithm more robust [265]. A recent review of methods similar to EP has developed the theory of this class of algorithm in terms of bilevel optimization problems [170]. In a few prior efforts, this algorithm has been further implemented on neuromorphic chips [266, 171, 267].

**Feedback Alignment and Sign Symmetry.** The original goal of this particular line of work was to show that learning was possible without the need to use symmetric backward connections (hence, resolving the weight transport problem mentioned earlier). In the first work that introduced feedback alignment, the authors showed that, by having fixed backward connections, the forward connections tended to align with them when possible [237]. This result was then used and extended to develop new training algorithms where learning is performed by simply propagating error information to single layers via random matrices [268]. This is interesting, as feedback alignment allows to perform machine learning tasks via forward passes only, a fundamental property for implementations on photonic chips

[269, 270]. Direct feedback alignment (DFA) has also been shown to scale to large-scale datasets and tasks [271, 272]. An important extension/generalization of feedback alignment is known as sign symmetry, where the feedback weights (used to generate the teaching signals) share only the sign but not the magnitude of the feedforward weights [273]. Sign symmetry-based approaches lack theoretical justification given that they do not accurately propagate either the magnitude or the sign of the error gradient. Nevertheless, their performance is empirically only slightly worse than backprop, even when using tensor connections such as those that define convolution neural networks [274].

**Forward-Forward Learning.** The newest addition to the realm of biologically-plausible algorithms in machine learning is the forward-forward algorithm, proposed by Geoffrey Hinton [16]. It has a layer-wise loss function similar to algorithms such as PC and EP but differs in that it uses auto-generated adversarial examples. Its goal is to minimize the “goodness” of the objectives for adversarial data, and maximize it for samples taken from a provided dataset. Recent work has also proposed the predictive forward-forward (PFF) algorithm, integrating learnable lateral inhibitory and self-excitation synapses and merging the forward-only adaptation process with predictive coding to perform generative/reconstruction tasks [275]. Notably, PFF and FF have been generalized to work in training spiking neural networks through a bio-physically plausible credit assignment process known as contrastive-signal-dependent plasticity [157]. Another similar approach that shares similarity with FF and PFF is the signalProp algorithm family [276]; however, signalProp requires that the hidden representations of the label(s) and image(s) remain separate and distinct. Another algorithm, which shares similarity with FF, is called "Present the Error to Perturb the Input To modulate the Activity learning rule (PEPITA)" [277], which is local in space but not local in time and relies on weight-mirroring in order to obtain a stable performance.