A biologically plausible neural network for multi-channel Canonical Correlation Analysis

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Abstract

Cortical pyramidal neurons receive inputs from multiple distinct neural populations and integrate these inputs in separate dendritic compartments. We explore the possibility that cortical microcircuits implement Canonical Correlation Analysis (CCA), an unsupervised learning method that projects the inputs onto a common subspace so as to maximize the correlations between the projections. To this end, we seek a multi-channel CCA algorithm that can be implemented in a biologically plausible neural network. For biological plausibility, we require that the network operates in the online setting and its synaptic update rules are local. Starting from a novel CCA objective function, we derive an online optimization algorithm whose optimization steps can be implemented in a single-layer neural network with multi-compartmental neurons and local non-Hebbian learning rules. We also derive an extension of our online CCA algorithm with adaptive output rank and output whitening. Interestingly, the extension maps onto a neural network whose neural architecture and synaptic updates resemble neural circuitry and synaptic plasticity observed experimentally in cortical pyramidal neurons.

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1 Introduction

One approach to understanding brain function is to identify mathematical algorithms implemented by neuronal circuits. Here, we apply this approach to the simplified cortical microcircuit composed of pyramidal neurons and inhibitory interneurons. The pyramidal neurons are multi-compartmental: they separately integrate inputs to apical and basal dendritic (somatic) compartments [47, 28] and signal coincidence of the two inputs by firing action potentials [29, 28]. In addition, synaptic plasticity in cortical pyramidal neurons is non-Hebbian in that it depends on correlations between inputs to the two compartments [8, 9, 32].

We explore the possibility that these circuits implement an algorithm for Canonical Correlation Analysis (CCA), a statistical method for analyzing a dataset with two views. Essentially, CCA finds projections of the views onto a common subspace such that the projections are maximally correlated. Since its introduction by Hotelling [24], CCA has found widespread use in applications, including time series analysis [1], regression [25], clustering [13], and word embedding [16]. Furthermore, CCA has a useful probabilistic interpretation [4], and is closely related to mutual information [10] and influential information theoretic methods [6, 5, 14].

To serve as a viable model of a neural circuit, the CCA algorithm must map onto a neural network consistent with basic biological facts. For our purposes, we say that a network is “biologically plausible” if it satisfies the following two minimal requirements: (i) the network operates in the online setting, i.e., upon receiving an input, it computes the corresponding output without relying on the storage of any significant fraction of the full dataset, and (ii) the learning rules are local in the sense that each synaptic update depends only on the variables that are available as biophysical quantities represented in the pre- or post-synaptic neurons.

There are a number of neural network implementations of CCA [27, 41, 20, 50]; however, most of these networks use non-local learning rules and are therefore not biologically plausible. One exception is the work by Pehlevan et al. [40]. They propose a biologically plausible implementation of single-channel CCA in a pyramidal neuron with multiple dendritic compartments, which allow the neuron to simultaneously represent multiple variables. Starting from an objective for single-channel CCA, they derive an online optimization algorithm that models both the neural activities and synaptic updates. However, the natural generalization of their objective to multi-channel CCA leads to an online algorithm with non-local learning rules. To address this, they resort to deflation, which requires the circuit to sequentially find projections of the two views. While this resolution yields a multi-channel network with local learning rules, it is not truly online because the projections must be learned sequentially.

In this work, we derive an online multi-channel CCA algorithm (Algorithm 2), which can be implemented in a single-layer biologically plausible network with multi-compartmental neurons and local non-Hebbian synaptic updates, Figure 1. In the
Figure 1: Single-layer network architecture with $k$ multi-compartmental neurons for outputting the sum of the canonical subspace projections (CCSPs) $z = (z_1, \ldots, z_k)$. Here $a = W_x x$ and $b = W_y y$ are projections of the views $x = (x_1, \ldots, x_m)$ and $y = (y_1, \ldots, y_n)$ onto a common $k$-dimensional subspace. The output, $z = M^{-1}(a + b)$, is the sum of the CCSPs and is computed using recurrent lateral connections. The components of $a$, $b$ and $z$ are represented in separate compartments of the neurons. Filled circles denote non-Hebbian synapses and empty circles denote anti-Hebbian synapses. Importantly, each synaptic update depends only on variables represented locally.

process, we also derive a novel offline CCA algorithm (Algorithm 1). Our approach is inspired by recent works which use similarity matching objectives to derive algorithms for single-view tasks that have biologically plausible implementations in single-layer networks [37]. Starting from a novel similarity matching objective for CCA, we derive an optimization algorithm whose optimization steps naturally correspond to neural activities and synaptic updates.

While our neural network implementation of CCA captures salient features of cortical microcircuits — the network consists of multi-compartmental neurons with non-Hebbian synaptic updates — the network includes direct lateral connections between the principal neurons (see Figure 1), which is in contrast to cortical microcircuits where lateral influence between cortical pyramidal neurons is often indirect.
and mediated by interneurons. With this in mind, we derive an extension of our online CCA algorithm (Algorithm 3), which adaptively chooses the rank of the output based on the level of correlation captured, and also whitens the output. The extension naturally maps onto a neural network with multi-compartmental principal neurons and without direct lateral connections between the principal neurons (see Figure 3 of Section 6). Interestingly, both the neural architecture and local, non-Hebbian plasticity resemble neural circuitry and synaptic plasticity in cortical microcircuits.

There are a number of existing consequential models of cortical microcircuits with multi-compartmental neurons and non-Hebbian plasticity [26, 48, 21, 44, 22, 43, 35]. These models provide mechanistic descriptions of the neural dynamics and synaptic plasticity and account for many experimental observations, including the nonlinearity of neural outputs and the layered organization of the cortex. While our neural network model is single-layered and linear, it is derived from a principled CCA objective function, which has several advantages. First, since biological neural networks evolved to adaptively perform behaviorally relevant computations, it is natural to view them as optimizing a relevant objective. Second, our approach clarifies which features of the network (e.g., multi-compartmental neurons and non-Hebbian synaptic updates) are central to computing correlations. Finally, since the optimization algorithm is derived from a CCA objective that can be solved offline, the neural activities and synaptic weights can be analytically predicted for any input without resorting to numerical simulation. In this way, our neural network model is interpretable and analytically tractable, and provides a useful contrast to nonlinear, layered neural network models.

**Organization:** The remainder of this work is organized as follows. We state the CCA problem in Section 2. In Section 3, we introduce our novel objective for the CCA problem, and in Section 4, we derive offline and online CCA algorithms. In Section 5, we derive an extension of our CCA algorithm, and in Section 6, we map the extension onto a simplified cortical microcircuit. We provide results of numerical simulations in Section 7.

**Notation:** For positive integers $p, q$, let $\mathbb{R}^p$ denote $p$-dimensional Euclidean space, and let $\mathbb{R}^{p \times q}$ denote the set of $p \times q$ real-valued matrices equipped with the Frobenius norm $\| \cdot \|_F$. We use boldface lower-case letters (e.g., $\mathbf{v}$) to denote vectors and boldface upper-case letters (e.g., $\mathbf{M}$) to denote matrices. We let $O(p)$ denote the set of $p \times p$ orthogonal matrices and $\mathcal{S}_+^p$ denote the set of $p \times p$ positive definite matrices. We let $\mathbf{I}_p$ denote the $p \times p$ identity matrix.
2 Canonical correlation analysis

Given $T$ pairs of centered input data samples $(x_1, y_1), \ldots, (x_T, y_T) \in \mathbb{R}^m \times \mathbb{R}^n$ and $k \leq \min(m, n)$, the CCA problem is to find $k$-dimensional linear projections of the views $x_1, \ldots, x_T$ and $y_1, \ldots, y_T$ that are maximally correlated. To be precise, consider the CCA objective

$$\arg \max_{V_x \in \mathbb{R}^{m \times k}, V_y \in \mathbb{R}^{n \times k}} \text{Tr} \left( V_x^\top C_{xy} V_y \right)$$

subject to the whitening constraint

$$V_x^\top C_{xx} V_x + V_y^\top C_{yy} V_y = I_k,$$

where we have defined the sample covariance matrices

$$C_{xx} := \frac{1}{T} \sum_{t=1}^{T} x_t x_t^\top, \quad C_{xy} := \frac{1}{T} \sum_{t=1}^{T} x_t y_t^\top, \quad C_{yy} := \frac{1}{T} \sum_{t=1}^{T} y_t y_t^\top.$$

In addition, we let $C_{yx} := C_{xy}^\top$.

To compute the solution of the CCA objective (1)–(2), define the $m \times n$ correlation matrix

$$R_{xy} := C_{xx}^{-1/2} C_{xy} C_{yy}^{-1/2},$$

and set $R_{yx} := R_{xy}^\top$. Let $\rho_1 \geq \cdots \geq \rho_{\min(m,n)}$ denote the singular values, and let $U_x \in O(m)$ and $U_y \in O(n)$ denote the matrices whose column vectors are respectively the left- and right-singular vectors of the correlation matrix. The $i^{th}$ singular value $\rho_i$ is referred to as the $i^{th}$ canonical correlation, and the $i^{th}$ column vectors of $C_{xx}^{-1/2} U_x$ and $C_{yy}^{-1/2} U_y$ are jointly referred to as the $i^{th}$ pair of canonical correlation basis vectors, for $i = 1, \ldots, \min(m, n)$. The maximal value of the trace in Equation (1) is the normalized sum of canonical correlations $(\rho_1 + \cdots + \rho_k)/2$. For simplicity, we assume $\rho_k > \rho_{k+1}$ so the subspace spanned by the first $k$ canonical correlation basis vectors is unique. In this case, every solution of the CCA objective (1)–(2), which we denote by $(\bar{V}_x, \bar{V}_y)$, is of the form

$$\bar{V}_x = C_{xx}^{-1/2} U_x^{(k)} Q, \quad \bar{V}_y = C_{yy}^{-1/2} U_y^{(k)} Q,$$

where $U_x^{(k)}$ (resp. $U_y^{(k)}$) is the $m \times k$ (resp. $n \times k$) matrix whose $i^{th}$ column vector is equal to the $i^{th}$ column vector of $U_x$ (resp. $U_y$) for $i = 1, \ldots, k$, and $Q \in O(k)$ is any orthogonal matrix. Since the column vectors of any solution $(\bar{V}_x, \bar{V}_y)$ span the same subspaces as the first $k$ pairs of canonical correlation basis vectors, we refer

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1This constraint differs slightly from the usual CCA whitening constraint $V_x^\top C_{xx} V_x = V_y^\top C_{yy} V_y = I_k$; however, the constraints are equivalent up to a scaling factor of 2.
to the column vectors of $\overrightarrow{V}_x$ and $\overrightarrow{V}_y$ as basis vectors. We refer to the $k$-dimensional projections $\overrightarrow{V}_x^\top x_t$ and $\overrightarrow{V}_y^\top y_t$ as canonical correlation subspace projections (CCSPs).

Whereas many existing CCA networks output both CCSPs [27, 41, 20, 50], we choose to output the following sum of the CCSPs:

$$z_t := \overrightarrow{V}_x^\top x_t + \overrightarrow{V}_y^\top y_t. \quad (5)$$

Biologically, this choice is motivated by the fact that the output of a neuron at any time step is a scalar which combines information from both views. Conceptually, the choice is motivated by a probabilistic interpretation of CCA in which the sum of the CCSPs is useful for estimating the state of a relevant latent variable, see Figure 2.

Figure 2: Graphical model for CCA. Here, $s$ is a latent $k$-dimensional mean-zero Gaussian random vector with identity covariance matrix, and the conditional distribution of the observed random vector $x$ (resp. $y$) given $s$ is Gaussian. Bach and Jordan [4] showed that the posterior expectation of the latent vector $s$ given the observation $(x,y)$ is a linear transformation of the sum of the $k$-dimensional CCSPs $z$, i.e., $E[s|(x,y)] = Lz$ for some $k \times k$ matrix $L$. To see this, set $M_1 = M_2 = P_d^{1/2}R$ in the paragraph following [4, Theorem 2].

The focus of this work is to derive a single-layer biologically plausible network whose input at each time $t$ is the pair $(x_t, y_t)$ and the output is the sum of the CCSPs $z_t$. The components of the two input vectors $x_t$ and $y_t$ are represented by the activity of upstream neurons belonging to two different populations. The components of the output vector $z_t$ are represented by the activity of the principal neurons in our network, see Figure 1.

While CCA is typically viewed as an unsupervised learning method, it can also be interpreted as a special case of the supervised learning method Reduced-Rank Regression, in which case $x_t$ is the feature vector and $y_t$ is the label (see, e.g., page 38 of [49]). With this supervised learning view of CCA, the natural output of a CCA network is the CCSP of $x_t$. In separate work [19], we derive a network for the general Reduced-Rank Regression problem, which includes CCA as a special case, for outputting the projection of the feature vector $x_t$. 

7
3 A similarity matching objective

To derive a network that computes the sums of CCSPs for arbitrary input datasets, we adopt a normative approach in which we identify an appropriate cost function whose optimization leads to an online algorithm that can be implemented by a network with local learning rules. Here, we take advantage of the previously developed similarity matching approach, which leads to biologically plausible neural networks for multi-channel PCA and related objectives [37], by rewriting the CCA objective in the PCA form. To this end, we proceed in two steps, which are summarized here and detailed below. First, we recall that the sums of CCSPs $z_1, \ldots, z_T$ are equal to the principal subspace projections of the data $\xi_1, \ldots, \xi_T$, where $\xi_t$ is the following $d$-dimensional vector of concatenated whitened inputs (recall $d := m + n$):

$$\xi_t := \begin{bmatrix} C^{-1/2}_{xx} x_t \\ C^{-1/2}_{yy} y_t \end{bmatrix}. \quad (6)$$

Second, we formulate a similarity matching objective for the sums of CCSPs.

Sums of CCSPs as principal subspace projections.

We begin by writing a generalized eigenproblem formulation of the CCA objective (1)–(2):

$$\arg \max_{V_x \in \mathbb{R}^{m \times k}, V_y \in \mathbb{R}^{n \times k}} \text{Tr} \left[ V_x^\top \begin{bmatrix} C_{xx} & C_{xy} \\ C_{yx} & C_{yy} \end{bmatrix} \begin{bmatrix} V_x \\ V_y \end{bmatrix} \right], \quad (7)$$

subject to the whitening constraint

$$\begin{bmatrix} V_x^\top \\ V_y^\top \end{bmatrix} \begin{bmatrix} C_{xx} & C_{xy} \\ C_{yx} & C_{yy} \end{bmatrix} \begin{bmatrix} V_x \\ V_y \end{bmatrix} = I_k. \quad (8)$$

The equivalence can be readily verified by expanding the matrix products in Equations (7)–(8). Next, we transform this generalized eigenproblem formulation (7)–(8) into a standard eigenproblem formulation. Since the trace of the left hand side of Equation (8) is constrained to equal $k$, we can add it to the trace in Equation (7), without affecting the output of the argmax, to arrive at the CCA objective:

$$\arg \max_{V_x \in \mathbb{R}^{m \times k}, V_y \in \mathbb{R}^{n \times k}} \text{Tr} \left[ V_x^\top \begin{bmatrix} C_{xx} & C_{xy} \\ C_{yx} & C_{yy} \end{bmatrix} \begin{bmatrix} V_x \\ V_y \end{bmatrix} \right], \quad (9)$$

subject to the whitening constraint in Equation (8). Our final step is a substitution of variables. To this end, we define the $d \times k$ matrix

$$V_\xi := \begin{bmatrix} C^{-1/2}_{xx} V_x \\ C^{-1/2}_{yy} V_y \end{bmatrix}, \quad (10)$$
and the $d \times d$ matrix covariance matrix of the concatenated whitened inputs $\xi_1, \ldots, \xi_T$

\[
C_{\xi\xi} := \frac{1}{T} \sum_{t=1}^{T} \xi_t \xi_t^\top = \begin{bmatrix} I_m & R_{xy} \\ R_{yx} & I_n \end{bmatrix}.
\]  

(11)

After substituting these variables into Equations (9) and (8), we see that $(V_x, V_y)$ is a solution of the CCA objective (1)–(2) if and only if $V_{\xi}$, defined via Equation (10), is solution of:

\[
\arg \max_{V_{\xi} \in \mathbb{R}^{d \times k}} \text{Tr} V_{\xi}^\top C_{\xi\xi} V_{\xi} \quad \text{subject to} \quad V_{\xi}^\top V_{\xi} = I_k.
\]

(12)

Importantly, Equation (12) is the variance maximization objective for the standard PCA eigenproblem, which is optimized when the column vectors of $V_{\xi}$ form an orthonormal basis spanning the $k$-dimensional principal subspace of the data $\xi_1, \ldots, \xi_T$. Therefore, by Equations (5), (6) and (10), the projection of the vector $\xi_t$ onto its principal subspace is precisely the desired sum of CCSPs: $z_t = \nabla_x x_t + \nabla_y y_t = \nabla_{\xi t}$.

**A similarity matching objective for sums of CCSPs.**

We now take advantage of the fact that the principal subspace projections can be expressed in terms of solutions of similarity matching objectives. To this end, we define the matrices $\Xi := [\xi_1, \ldots, \xi_T] \in \mathbb{R}^{d \times T}$ and $Z := [z_1, \ldots, z_T] \in \mathbb{R}^{k \times T}$, so that $Z$ is a linear projection of $\Xi$ onto its $k$-dimensional principal subspace. As shown in [15, 51], the principal subspace projection $Z$ is a solution of following similarity matching objective:

\[
\arg \min_{Z \in \mathbb{R}^{k \times T}} \frac{1}{2T^2} \| Z^\top Z - \Xi^\top \Xi \|^2_{F}.
\]

(13)

The objective, which comes from classical multidimensional scaling [15], minimizes the difference between the similarity of output pairs, $z_i^\top z_{i'}$, and the similarity of input pairs, $\xi_i^\top \xi_{i'}$, where similarity is measured in terms of inner products. The fact that the objective is minimized when $Z$ is the projection of $\Xi$ onto its principal subspace can be seen by noting that the objective is minimized when the $k$ non-zero singular values (and corresponding right-singular vectors) of $Z$ match the top $k$ singular values (and corresponding right-singular vectors) of $\Xi$. Finally, we note that, by Equation (6), the Gram matrix $\Xi^\top \Xi$ is equal to $X^\top C_{xx}^{-1} X + Y^\top C_{yy}^{-1} Y$, where we have defined the data matrices $X := [x_1, \ldots, x_T] \in \mathbb{R}^{m \times T}$ and $Y := [y_1, \ldots, y_T] \in \mathbb{R}^{n \times T}$. Substituting this relation into Equation (13), we can express our similarity matching objective directly in terms of the data matrices $X$ and $Y$:

\[
\arg \min_{Z \in \mathbb{R}^{k \times T}} \frac{1}{2T^2} \| Z^\top Z - X^\top C_{xx}^{-1} X - Y^\top C_{yy}^{-1} Y \|^2_{F}.
\]

(14)
The similarity matching objective (14) is the starting point for our derivation of offline and online CCA algorithms in the next section.

4 A biologically plausible CCA algorithm

With our similarity matching objective function in hand, we now derive offline and online CCA algorithms. While the objective (14) can be minimized by taking gradient descent steps with respect to $Z$, this would not lead to an online algorithm because such computation requires combining data from different time steps. Rather, we introduce auxiliary matrix variables, which store sufficient statistics allowing for the CCA computation using solely contemporary inputs and will correspond to synaptic weights in the network implementation, and rewrite the minimization problem (14) as a min-max problem. By taking stochastic gradient descent-ascent steps, we obtain our online CCA algorithm.

4.1 A min-max objective

Expanding the square in Equation (14) and dropping terms that do not depend on $Z$ yields the minimization problem

$$
\min_{Z \in \mathbb{R}^{k \times T}} - \frac{1}{T^2} \operatorname{Tr} \left( Z^\top ZX^\top C_{xx}^{-1}X \right) - \frac{1}{T^2} \operatorname{Tr} \left( Z^\top ZY^\top C_{yy}^{-1}Y \right) + \frac{1}{2T^2} \operatorname{Tr} \left( Z^\top ZZ^\top Z \right).
$$

Next, we introduce dynamic matrix variables $W_x, W_y$ and $M$ in place of the matrices $\frac{1}{T}ZX^\top C_{xx}^{-1}, \frac{1}{T}ZY^\top C_{yy}^{-1}$ and $\frac{1}{T}ZZ^\top$, respectively, and rewrite the minimization problem as a min-max problem:

$$
\min_{Z \in \mathbb{R}^{k \times T}} \min_{W_x \in \mathbb{R}^{k \times m}} \min_{W_y \in \mathbb{R}^{k \times n}} \max_{M \in \mathcal{S}_+^k} L(W_x, W_y, M, Z)
$$

where

$$
L(W_x, W_y, M, Z) := \frac{1}{T} \operatorname{Tr} \left( -2Z^\top W_x X - 2Z^\top W_y Y + Z^\top MZ \right)
$$

$$
+ \operatorname{Tr} \left( W_x C_{xx} W_x^\top + W_y C_{yy} W_y^\top - \frac{1}{2}M^2 \right) . \quad (15)
$$

To verify the above substitutions are valid, it suffices to optimize over the matrices $W_x, W_y$ and $M$; e.g., by differentiating $L(W_x, W_y, M, Z)$ with respect to $W_x, W_y$ or $M$, setting the derivative equal to zero, and solving for $W_x, W_y$, or $M$. Finally, we interchange the order of minimization with respect to $Z$ and $(W_x, W_y)$, as well
as the order of minimization with respect to $Z$ and maximization with respect to $M$:

$$
\min_{W_x \in \mathbb{R}^{k \times m}} \min_{W_y \in \mathbb{R}^{k \times n}} \max_{M \in S_{++}^k} \min_{Z \in \mathbb{R}^{k \times T}} L(W_x, W_y, M, Z). \tag{16}
$$

The second interchange is justified by the fact that $L(W_x, W_y, M, Z)$ satisfies the saddle point property with respect to $Z$ and $M$, which follows from its strict convexity in $Z$ (since $M$ is positive definite) and strict concavity in $M$.

Given an optimal quadruple of the min-max problem (16), we can compute the basis vectors, as follows. First, minimizing the objective $L(W_x, W_y, M, Z)$ over $Z$ yields the relation

$$
Z := \arg \min_{Z \in \mathbb{R}^{k \times T}} L(W_x, W_y, M, Z) = M^{-1}W_xX + M^{-1}W_yY. \tag{17}
$$

Therefore, if $(W_x, W_y, M, Z)$ is an optimal quadruple of the min-max problem (16), it follows from Equation (5) that the corresponding basis vectors satisfy

$$
\tilde{V}_x^\top = \tilde{M}^{-1}W_x \quad \text{and} \quad \tilde{V}_y^\top = \tilde{M}^{-1}W_y. \tag{18}
$$

### 4.2 An offline CCA algorithm

Before deriving our online CCA algorithm, we first demonstrate how the objective (16) can be optimized in the offline setting, where one has access to the data matrices $X$ and $Y$ in their entirety. In this case, the algorithm solves the min-max problem (16) by alternating minimization and maximization steps. First, for fixed $W_x$, $W_y$ and $M$, we minimize the objective function $L(W_x, W_y, M, Z)$ over $Z$ to obtain the minimum $\tilde{Z}$ defined in Equation (17). Then, with $\tilde{Z}$ fixed, we perform a gradient descent-ascent step with respect to $(W_x, W_y)$ and $M$:

$$
W_x \leftarrow W_x - \eta \frac{\partial L(W_x, W_y, M, \tilde{Z})}{\partial W_x}
$$

$$
W_y \leftarrow W_y - \eta \frac{\partial L(W_x, W_y, M, \tilde{Z})}{\partial W_y}
$$

$$
M \leftarrow M + \frac{\eta}{\tau} \frac{\partial L(W_x, W_y, M, \tilde{Z})}{\partial M}.
$$

Here $\eta$ is the learning rate for $W_x$ and $W_y$, which may depend on the iteration, and $\tau > 0$ is the ratio of the learning rates of $W_x$ (or $W_y$) and $M$. To ensure that $M$ remains positive definite given a positive definite initialization, we assume that $\eta \in (0, \tau)$. Substituting in the explicit expressions for the partial derivatives of $L(W_x, W_y, M, \tilde{Z})$ yields our offline CCA algorithm (Algorithm 1), which we refer to as Offline-CCA.
Algorithm 1: Offline-CCA

\begin{algorithm}
\begin{align*}
\text{input:} & \quad \text{data matrices } X, Y; \text{ dimension } k \\
\text{initialize:} & \quad \text{matrices } W_x, W_y \text{ and positive definite matrix } M \\
C_{xx} & \leftarrow \frac{1}{T} XX^\top; \quad C_{yy} & \leftarrow \frac{1}{T} YY^\top \quad \triangleright \text{covariance matrices} \\
\text{repeat} & \\
Z & \leftarrow M^{-1}W_x X + M^{-1}W_x Y \quad \triangleright \text{optimize over output} \\
W_x & \leftarrow W_x + 2\eta \left( \frac{1}{T} ZX^\top - W_x C_{xx} \right) \quad \triangleright \text{gradient descent-ascent steps} \\
W_y & \leftarrow W_y + 2\eta \left( \frac{1}{T} ZY^\top - W_y C_{yy} \right) \\
M & \leftarrow M + \frac{\eta}{T} (ZZ^\top - M) \\
\text{until convergence}
\end{align*}
\end{algorithm}

4.3 An online CCA algorithm

In the online setting, the input data \((x_t, y_t)\) are streamed one at a time and the algorithm must compute its output \(z_t\) without accessing any significant fraction of \(X\) and \(Y\). To derive an online algorithm, it is useful to write the cost function as an average over time-separable terms:

\[ L(W_x, W_y, M, Z) = \frac{1}{T} \sum_{t=1}^{T} l_t(W_x, W_y, M, z_t), \]

where

\[ l_t(W_x, W_y, M, z_t) := -2z_t^\top W_x x_t - 2z_t^\top W_y y_t + z_t^\top M z_t \]

\[ + \text{Tr} \left( W_x x_t x_t^\top W_x^\top + W_y y_t y_t^\top W_y^\top - \frac{1}{2} M^2 \right). \quad (19) \]

At iteration \(t\), to compute the output \(z_t\), we minimize the cost function \(l_t(W_x, W_y, M, z_t)\) with respect to \(z_t\) by running the following gradient descent dynamics to equilibrium:

\[ \frac{dz_t(\gamma)}{d\gamma} = a_t + b_t - M z_t(\gamma), \quad (20) \]

where we have defined the following \(k\)-dimensional projections of the inputs: \(a_t := W_x x_t\) and \(b_t := W_y y_t\). These dynamics, which will correspond to recurrent neural dynamics in our network implementation, are assumed to occur on a fast timescale, allowing \(z_t(\gamma)\) to equilibrate at \(Z_t := M^{-1}(a_t + b_t)\) before the algorithm outputs its value. After \(z_t(\gamma)\) equilibrates, we update the matrices \((W_x, W_y, M)\) by taking a stochastic gradient descent-ascent step of the cost function \(l_t(W_x, W_y, M, z_t)\) with
respect to \((W_x, W_y)\) and \(M\):

\[
W_x \leftarrow W_x - \eta \frac{\partial l_t(W_x, W_y, M, z_t)}{\partial W_x} \\
W_y \leftarrow W_y - \eta \frac{\partial l_t(W_x, W_y, M, z_t)}{\partial W_y} \\
M \leftarrow M + \frac{\eta}{\tau} \frac{\partial l_t(W_x, W_y, M, z_t)}{\partial M}.
\]

Substituting in the explicit expressions for the partial derivatives of \(l_t(W_x, W_y, M, z_t)\) yields our online CCA algorithm (Algorithm 2), which we refer to as Bio-CCA.

**Algorithm 2: Bio-CCA**

- **input** data \(\{(x_1, y_1), \ldots, (x_T, y_T)\}\); dimension \(k\)
- **initialize** matrices \(W_x, W_y\), and positive definite matrix \(M\).
- for \(t = 1, 2, \ldots, T\) do
  - \(a_t \leftarrow W_x x_t\); \(b_t \leftarrow W_y y_t\) \(\triangleright\) projection of inputs
  - run \(\frac{da_t(\gamma)}{d\gamma} = a_t + b_t - Mz_t(\gamma)\) \(\triangleright\) neural dynamics
  - until convergence
  - \(W_x \leftarrow W_x + 2\eta(z_t - a_t)x_t^T\) \(\triangleright\) synaptic updates
  - \(W_y \leftarrow W_y + 2\eta(z_t - b_t)y_t^T\)
  - \(M \leftarrow M + \frac{\eta}{\tau}(z_t z_t^T - M)\)
- end for

Algorithm 2 can be implemented in a biologically plausible single-layer network with \(k\) neurons that each consist of three separate compartments, Figure 1. At each time step, the inputs \(x_t\) and \(y_t\) are multiplied by the respective feedforward synapses \(W_x\) and \(W_y\) to yield the \(k\)-dimensional vectors \(a_t\) and \(b_t\), which are represented in the first two compartments of the \(k\) neurons. Lateral synapses, \(-M\), connect the \(k\) neurons. The vector of neuronal outputs, \(z_t\), equals the normalized sum of the CCSPs, and is computed locally using recurrent dynamics in Equation (20). The synaptic updates can be written elementwise, as follows:

\[
W_{x,ij} \leftarrow W_{x,ij} + \eta(z_{t,i} - a_{t,i})x_{t,j}, \quad 1 \leq i \leq k, 1 \leq j \leq m, \\
W_{y,ij} \leftarrow W_{y,ij} + \eta(z_{t,i} - b_{t,i})y_{t,j}, \quad 1 \leq i \leq k, 1 \leq j \leq n, \\
M_{ij} \leftarrow M_{ij} + \frac{\eta}{\tau}(z_{t,i}z_{t,j} - M_{ij}), \quad 1 \leq i, j \leq k.
\]

As shown above, the update to synapse \(W_{x,ij}\) (resp. \(W_{y,ij}\)), which connects the \(j^{th}\) input \(x_{t,j}\) (resp. \(y_{t,j}\)) to the \(i^{th}\) output neuron, depends only on the quantities \(z_{t,i}\), \(a_{t,i}\) (resp. \(b_{t,i}\)), and \(x_{t,j}\) (resp. \(y_{t,j}\)), which are represented in the pre- and post-synaptic
neurons, so the updates are local, but non-Hebbian due to the contribution from the \(a_{t,i}\) (resp. \(b_{t,i}\)) term. Similarly, the update to synapse \(M_{ij}\), which connects the \(j^{th}\) output neuron to the \(i^{th}\) output neuron, depends only the quantities \(z_{t,i}\) and \(z_{t,j}\), which are the outputs of the pre- and post-synaptic neurons, so the updates are local and anti-Hebbian.

5 Online adaptive CCA with output whitening

We now introduce an extension of Bio-CCA which addresses two biologically relevant issues. First, Bio-CCA a priori sets the output rank at \(k\); however, it may be advantageous for a neural circuit to instead adaptively set the output rank depending on the level of correlation captured. In particular, this can be achieved by projecting each view onto the subspace spanned by the canonical correlation basis vectors which correspond to canonical correlations that exceed a threshold. Second, it is useful from an information theoretic perspective for neural circuits to whiten their outputs [42], i.e., by enforcing that the non-zero singular values of the output are all equal to one. Both adaptive output rank and output whitening modifications were implemented for a PCA network by Pehlevan and Chklovskii [36], and can be adapted to the CCA setting. Here we present the modifications without providing detailed proofs, which can be found in the supplement of [36].

In order to implement these extensions, we need to appropriately modify the similarity matching objective function (14). First, to adaptively choose the output rank, we add a quadratic penalty \(\text{Tr}(Z^\top Z)\) to the objective function (14):

\[
\arg \min_{Z \in \mathbb{R}^{k \times T}} \frac{1}{2T^2} \|Z^\top Z - X^\top C_{xx}^{-1} X - Y^\top C_{yy}^{-1} Y\|_F^2 + \frac{\alpha}{T} \text{Tr}(Z^\top Z).
\]  
(21)

The effect of the quadratic penalty is to rank constrain the output, with \(\alpha \geq 0\) acting as a threshold parameter on the eigenvalues values of the output covariance.

Next, to whiten the output, we expand the square in Equation (21) and replace the quartic term \(\text{Tr}(Z^\top Z Z^\top Z)\) by a Langrange constraint enforcing \(Z^\top Z \preceq TI_T\) (i.e., \(TI_T - Z^\top Z\) is positive semi-definite):

\[
\arg \min_{Z \in \mathbb{R}^{k \times T}} \max_{N \in \mathbb{R}^{k \times T}} \frac{1}{T^2} \text{Tr}(Z^\top Z X^\top C_{xx}^{-1} X - Z^\top Z Y^\top C_{yy}^{-1} Y + \alpha T Z^\top Z) \\
+ \frac{1}{T^2} \text{Tr}[N^\top (Z^\top Z - TI_T)].
\]  
(22)

The effect of the Lagrange constraint in Equation (22) is to enforce that all non-zero eigenvalues of the output covariance are set to one.

Solutions of the objective (22) can be expressed in terms of the eigendecomposition of the Gram matrix \(\Sigma^\top \Sigma = T U_{\xi} \Lambda_{\xi} U_{\xi}^\top\), where \(U_{\xi} \in O(T)\) is a matrix of eigenvectors and \(\Lambda_{\xi} = \text{diag}(\lambda_1, \ldots, \lambda_d, 0, \ldots, 0)\) is the \(T \times T\) diagonal matrix whose
non-zero entries \( \lambda_1 \geq \cdots \geq \lambda_d > 0 \) are the eigenvalues of the covariance matrix \( C_{\xi \xi} \) defined in Equation (11). Assume, for technical purposes, that \( \alpha \not\in \{ \lambda_1, \ldots, \lambda_d \} \).

Then, as shown in [38, Theorem 3], every solution \( \hat{Z} \) of objective (22) is of the form

\[
\hat{Z} = Q \sqrt{T \hat{\Lambda}_{\xi}^{(k)} U_{\xi}^{(k)^\top}}, \quad \hat{\Lambda}_{\xi}^{(k)} = \text{diag}(H(\lambda_1 - \alpha), \ldots, H(\lambda_k - \alpha)),
\]

where \( Q \in O(k) \) is any orthogonal matrix, \( U_{\xi}^{(k)} \in \mathbb{R}^{T \times k} \) is the \( T \times k \) matrix whose \( i \)th column vector is equal to the \( i \)th column vector of \( U_{\xi} \), for \( i = 1, \ldots, k \), and \( H \) is the heaviside step function defined by \( H(r) = 1 \) if \( r > 0 \) and \( H(r) = 0 \) otherwise. Finally, we note that, in view of Equation (11) and the singular value decomposition of \( R_{xy} \), the top \( \min(m,n) \) eigenvalues of \( C_{\xi \xi} \) satisfy

\[
\lambda_i = 1 + \rho_i, \quad i = 1, \ldots, \min(m,n),
\]

where we recall that \( \rho_1, \ldots, \rho_{\min(m,n)} \) are the canonical correlations. Thus, \( H(\lambda_i - \alpha) = H(\rho_i - (\alpha - 1)) \), for \( i = 1, \ldots, k \). In other words, the objective (22) outputs the sum of the projections of the inputs \( x_t \) and \( y_t \) onto the canonical correlation subspace spanned by the (at most \( k \)) pairs of canonical correlation basis vectors associated with canonical correlations exceeding the threshold \( \max(\alpha - 1, 0) \), and sets the non-zero output covariance eigenvalues to one, thus implementing both the adaptive output rank and output whitening modifications.

With the modified objective (22) in hand, the next step is to derive an online algorithm. To derive the network, we rewrite the objective by introducing auxiliary matrix variables, which we solve by taking gradient steps. Since the general outline is similar to the approach taken in Section 4 to derive Bio-CCA, we defer the details to Appendix A and simply state the online algorithm (Algorithm 3), which we refer to as Adaptive Bio-CCA with output whitening.

6 Relation to cortical microcircuits

We now show that Adaptive Bio-CCA with output whitening (Algorithm 3) naturally maps onto a network with local, non-Hebbian synaptic update rules that emulate synaptic plasticity found experimentally in cortical microcircuits (both in the neocortex and the hippocampus). Cortical microcircuits contain two classes of neurons: excitatory pyramidal neurons and inhibitory interneurons. Pyramidal neurons receive excitatory synaptic inputs from two distinct sources via their apical and basal dendrites. The apical dendrites are all oriented in a single direction and the basal dendrites branch from the cell body in the opposite direction [47, 28], Figure 3. The excitatory synaptic currents in the apical and basal dendrites are first integrated separately in their respective compartments [47, 28]. If the integrated excitatory current in either compartment exceeds the corresponding inhibitory input
Algorithm 3: Adaptive Bio-CCA with output whitening

**input** data \( \{(x_1, y_1), \ldots, (x_T, y_T)\} \); max output-dimension \( k \); threshold \( \alpha \)

**initialize** weight matrices \( W_x, W_y, \) and \( P \).

**for** \( t = 1, 2, \ldots, T \) **do**

\[ a_t \leftarrow W_x x_t \; ; \; b_t \leftarrow W_y y_t \] **▷** projection of inputs

\[ \frac{d\gamma}{dz_t(\gamma)} = b_t - a_t - P \gamma(\gamma) - a_t z_t(\gamma) \] **▷** neural dynamics

\[ \frac{dn_t(\gamma)}{dz_t(\gamma)} = P^T z_t(\gamma) - n_t(\gamma) \]

**until** convergence

\[ W_x \leftarrow W_x + \eta (z_t - a_t) x_t^T \] **▷** synaptic updates

\[ W_y \leftarrow W_y + \eta (z_t - b_t) y_t^T \]

\[ P \leftarrow P + \frac{\eta}{\tau} (z_t n_t^T - P) \]

**end for**

(the source of which is explained below) it produces a calcium plateau potential that propagates through the rest of the neuron [47, 28, 8]. Pyramidal neurons combine the apical and basal dendrite contributions to produce spikes (or sodium action potentials). Inhibitory interneurons integrate pyramidal outputs and reciprocally inhibit the apical dendrites of pyramidal neurons, thus closing the loop.

We propose that a network of \( k \) pyramidal neurons implements CCA on the inputs received by apical and basal dendrites and outputs the whitened sum of CCSPs (Algorithm 3). The two datasets \( X \) and \( Y \) are represented as activity vectors \( x_t \) and \( y_t \) streamed onto the apical and basal dendrites respectively, Figure 3. At each time step the activity vectors are multiplied by the corresponding synaptic weights to yield localized apical and basal dendritic currents, \( a_t = W_x x_t \) and \( b_t = W_y y_t \), thus implementing projection onto the common subspace. This is followed by linear recurrent neural dynamics (30)–(31), where the components of \( z_t \) are represented by the spiking activity of pyramidal neurons, the components of \( n_t \) are represented by the activity of inhibitory interneurons, and \( \alpha \) is the threshold parameter of the adaptive algorithm. These dynamics equilibrate at \( n_t = P^T z_t \) and

\[ z_t = (P P^T + \alpha I_k)^{-1} (a_t + b_t). \] (23)

Rearranging Equation (23) and substituting into the synaptic update rules in Algorithm 3 yields

\[ W_x \leftarrow W_x + \eta (c_t^b + (1 - \alpha) z_t) x_t^T \]

\[ W_y \leftarrow W_y + \eta (c_t^a + (1 - \alpha) z_t) y_t^T \]

\[ P \leftarrow P + \frac{\eta}{\tau} (z_t n_t^T - P) , \]

where \( c_t^a := a_t - P n_t \) and \( c_t^b := b_t - P n_t \). The components of \( c_t^a \) (resp. \( c_t^b \)) are
Figure 3: Cortical microcircuit implementation of Adaptive Bio-CCA with output whitening (Algorithm 3). The black cell bodies denote pyramidal neurons, with the apical tufts pointing upwards. The red and blue lines arrows denote the axons respectively transmitting the apical input $x$ and basal input $y$. The black lines originating from the base of the pyramidal neurons are their axons, which transmit their output $z$. The green cell bodies denote the interneurons and the green lines are their axons, which transmit their output $n$. Filled circles denote non-Hebbian synapses whose updates are proportional to the input (i.e., $x$ or $y$) and the weighted sum of the calcium plateau potential plus backpropogating somatic output [i.e., $c^b + (1 - \alpha)z$ or $c^a + (1 - \alpha)z$]. The directions of travel of these weighted sums are depicted using dashed lines with arrows. Empty circles denote (anti-)Hebbian synapses whose updates are (inversely) proportional to the pre- and post-synaptic activities.
represented by the apical (resp. basal) calcium plateau potentials within each pyramidal neuron. The learning signal for the basal (resp. apical) synaptic updates of this circuit is the correlation between the apical (resp. basal) calcium plateau potentials plus the scaled spiking activity of the pyramidal neurons, and the synaptic inputs to the basal (resp. apical) dendrites, $x_t$ (resp. $y_t$). If $\alpha = 1$ then the spiking (action potentials) of the post-synaptic neuron is not required for synaptic plasticity matching closely the experimental observations in the hippocampus [18, 9, 32]. If $\alpha \neq 1$ then the spiking of the post-synaptic neuron may affect synaptic plasticity along with the calcium plateau as observed in the neocortex [45]. Unlike Hebbian learning rules which depend only on the correlation of the spiking output of the post-synaptic neuron with the pre-synaptic spiking, the mechanisms involving the calcium plateau potential represented internally in a neuron are called non-Hebbian. Because synapses have access to both the corresponding presynaptic activity and to the calcium plateau potential, the learning rule remains local. Furthermore, provided $\alpha > 0$, we can rearrange Equation (23) to write the output as

$$z_t = \alpha^{-1}(b_t + c_t^a).$$

In other words, the output is proportional to the sum of the basal dendritic current and the apical calcium plateau potential, which is consistent with experimental evidence showing that the output depends on both the basal inputs and apical calcium plateau potential [8, 9, 32].

Multi-compartmental models of pyramidal neurons have been invoked previously in the context of biological implementation of the backpropagation algorithm [26, 48, 21, 22, 44, 43]. In this context, the apical compartment represents the target output, the basal compartment represents the algorithm prediction and calcium plateau potentials communicate the error from the apical to the basal compartment which is used for synaptic weight updates. The difference between these models and ours is that we use a normative approach to derive not only the learning rules but also the neural dynamics of the CCA algorithm ensuring that the output of the network is known for any input. On the other hand, the linearity of neural dynamics in our network means that stacking our networks will not lead to any nontrivial results expected of a deep learning architecture. We leave introducing nonlinearities into neural dynamics and stacking our network to future work.

7 Numerical experiments

We now evaluate the performance of the online algorithms, Bio-CCA and Adaptive Bio-CCA with output whitening. In each plot, the lines and shaded regions respectively denote the means and 90% confidence intervals over 10 runs. Detailed descriptions of the implementations are given in Appendix B. All experiments were
performed in Python on an iMac Pro equipped with a 3.2 GHz 8-Core Intel Xeon W CPU.

7.1 Datasets

We first describe the two evaluation datasets.

**Synthetic.** We generated a synthetic dataset with $T = 100,000$ samples according to the graphical model described in Figure 2. In particular, let $s_1, \ldots, s_T$ be i.i.d. 8-dimensional latent mean-zero Gaussian vectors with identity covariance. Let $T_x \in \mathbb{R}^{50 \times 8}$, $T_y \in \mathbb{R}^{30 \times 8}$, $\Psi_x \in \mathbb{S}^{50}_{++}$ and $\Psi_y \in \mathbb{S}^{30}_{++}$ be randomly generated matrices and define the 50-dimensional observations $x_1, \ldots, x_T$ and 30-dimensional observations $y_1, \ldots, y_T$ by

$$x_t := T_x s_t + \phi_t, \quad y_t := T_y s_t + \psi_t, \quad t = 1, \ldots, T,$$

where $\phi_1, \ldots, \phi_T$ are i.i.d. 50-dimensional mean-zero Gaussian vectors with covariance $\Psi_x$ and $\psi_1, \ldots, \psi_T$ are i.i.d. 30-dimensional mean-zero Gaussian vectors with covariance $\Psi_y$. Thus, conditioned on the latent random variable $s$, the observation $x$ (resp. $y$) has a Gaussian distribution with mean $T_x s$ (resp. $T_y s$) with covariance $\Psi_x$ (resp. $\Psi_y$), i.e.,

$$x|s \sim N(T_x s, \Psi_x), \quad y|s \sim N(T_y s, \Psi_y),$$

which matches the graphical model in Figure 2. The first 10 canonical correlations are plotted in Figure 4 (left).

**Mediamill.** The dataset Mediamill [46] consists of $T = 43,907$ samples (including training and testing sets) of video data and text annotations, and has been previously used to evaluate CCA algorithms [2, 40]. The first view consists of 120-dimensional visual features extracted from representative video frames. The second view consists of 101-dimensional vectors whose components correspond to manually labeled semantic concepts associated with the video frames (e.g., “basketball” or “tree”). To ensure that the problem is well-conditioned, we add Gaussian noise with covariance matrix $\varepsilon I_m$ (resp. $\varepsilon I_n$), for $\varepsilon = 0.1$, to the first (resp. second) view to generate the data matrix $X$ (resp. $Y$). The first 10 canonical correlations are plotted in Figure 4 (right).

7.2 Bio-CCA

We now evaluate the performance of Algorithm 2 on the two datasets. We compare the performance with the top online machine learning algorithms Gen-Oja [7], which
Figure 4: Top 10 canonical correlations $\rho_1, \ldots, \rho_{10}$ of the synthetic dataset (left) and dataset Mediamill (right).

implements single-channel CCA (i.e., $k = 1$), and MSG-CCA [2], which implements multi-channel CCA (i.e., $k \geq 1$).

To evaluate the performance of the algorithms, we use the following $[0, 2]$-valued relative error function:

$$\text{Error}(t) := \frac{\rho_{\text{max}} - \text{Tr}(V_x^\top C_{xy} V_y)}{\rho_{\text{max}}}. \quad (24)$$

Here $\rho_{\text{max}} := (\rho_1 + \cdots + \rho_k)/2$ is the optimal value of the CCA objective (1)–(2), and $(V_x, V_y)$ are the basis vectors reported by the respective algorithm after iteration $t$, normalized to ensure they satisfy the orthonormality constraint (2). In Figure 5 we plot the performance of our Bio-CCA algorithm against competing online algorithms for target dimensions $k = 1, 2, 4, 8$ on the synthetic dataset (presented once in a randomly permuted order) and the dataset Mediamill (presented 3 times with a randomly permuted order in each presentation). When tested on the synthetic dataset, the sample efficiency of Bio-CCA initially lags behind the competing algorithms, but outperforms them when given sufficiently many samples. When tested on the dataset Mediamill, the sample efficiency of Bio-CCA is comparable to the best performing competing algorithm.

To verify that the Bio-CCA basis vectors asymptotically satisfy the orthonormality constraint (2), we use the following orthonormality error function:

$$\text{Orthonormality Error}(t) := \frac{\|M^{-1}(W_x C_{xx} W_x^\top + W_y C_{yy} W_y^\top)M^{-1} - I_k\|_F^2}{k}. \quad (25)$$
Figure 5: Comparisons of Bio-CCA with Gen-Oja (for $k = 1$) and MSG-CCA on the synthetic dataset (top) and the dataset Mediamill (bottom), in terms of the error defined in Equation (24).

Figure 6: The deviation of the Bio-CCA solution from the CCA orthonormality constraint, in terms of the orthonormality error defined in Equation (25), on the synthetic dataset (top) and dataset Mediamill (bottom).
In Figure 6 we demonstrate that Bio-CCA asymptotically satisfies the CCA orthonormality constraints (2) on both the synthetic dataset and the dataset Mediamill.

### 7.3 Adaptive Bio-CCA with output whitening

Next, we evaluate the performance of Algorithm 3 on the two datasets. To evaluate the performance of the algorithm, we use the subspace alignment error. In particular, for $k \geq 1$ and $\alpha \geq 0$, let $r$ denote the number of canonical correlations $\rho_1, \ldots, \rho_k$ greater than $\max(\alpha - 1, 0)$, i.e., $r := \max\{1 \leq i \leq k : \rho_i > \max(\alpha - 1, 0)\}$. The subspace error function is defined, for $\zeta \in \{x, y\}$, by

$$\text{Subspace Error}(t) := \|\tilde{U}_\zeta \tilde{U}_\zeta^T - \nabla_\zeta (\nabla_\zeta^T \nabla_\zeta)^{-1} \nabla_\zeta^T \|_F^2, \quad (26)$$

where $\tilde{U}_x$ (resp. $\tilde{U}_y$) is the $m \times r$ (resp. $n \times r$) matrix whose column vectors are the top $r$ right-singular vectors of $W_x$ (resp. $W_y$), and $\nabla_x$ and $\nabla_y$ are defined as in Equation (4), but with $k$ replaced by $r$. To verify that the top $r$ eigenvalues of the output covariance are asymptotically approach 1, we let $\lambda_1(t) \geq \cdots \geq \lambda_k(t)$ denote the ordered eigenvalues of the covariance matrix $C_{zz}(t) := \frac{1}{t} \sum_{s=1}^{t} z_s z_s^T$, and define the whitening error by

$$\text{Whitening Error}(t) := \frac{\sum_{i=1}^{r} |\lambda_i(t) - 1|^2 + \sum_{i=r+1}^{k} |\lambda_i(t)|^2}{k}. \quad (27)$$

**Synthetic.** From Figure 4 (left) we see that the first 8 canonical correlations are close to one and the remaining canonical correlations are approximately zero. Therefore, for $k \geq 8$ and $\alpha \in (1.1, 1.9)$, Algorithm 3 should project the inputs $x_t$ and $y_t$ onto the 8-dimensional subspace spanned by the top 8 pairs of canonical correlation basis vectors, and set the non-zero output covariance eigenvalues to one. In Figure 7 we plot the performance of Algorithm 3 with $k = 10$ for $\alpha = 1.2, 1.4, 1.6, 1.8$ on the synthetic dataset (presented once times with a randomly permuted order).

**Mediamill.** From Figure 4 (right) we see that the canonical correlations of the dataset Mediamill exhibit a more gradual decay than the canonical correlations of the synthetic dataset. As we increase the threshold $\alpha$ in the interval (1.1, 1.4), the rank of the output of Algorithm 3 decreases. In Figure 8 we plot the performance of Algorithm 3 with $k = 5$ for $\alpha = 1.15, 1.2, 1.25, 1.3$ on the dataset Mediamill (presented three times with a randomly permuted order in each presentation).
Figure 7: Performance of Adaptive Bio-CCA with output whitening on the synthetic dataset in terms of the subspace error (top) defined in Equation (26) and the whitening error (bottom) defined in Equation (27).

Figure 8: Performance of Adaptive Bio-CCA with output whitening on the dataset Mediamill in terms of the subspace error (top) defined in Equation (26) and the whitening error (bottom) defined in Equation (27).
8 Discussion

In this work, we derived an online algorithm for CCA that can be implemented in a neural network with multi-compartmental neurons and local, non-Hebbian learning rules. We also derived an extension that adaptively chooses the output rank and whitens the output. Remarkably, the neural architecture and non-Hebbian learning rules of our extension resembled neural circuitry and non-Hebbian plasticity in cortical pyramidal neurons. Thus, our neural network model may be useful for understanding the computational role of multi-compartmental neurons with non-Hebbian plasticity.

While our neural network model captures salient features of cortical microcircuits, there are important biophysical properties that are not explained by our model. First, our model uses linear neurons to solve the linear CCA problem, which substantially limits its computational capabilities and is a major simplification of cortical pyramidal neurons which can perform nonlinear operations [17]. However, studying the analytically tractable and interpretable linear neural network model is useful for understanding more complex nonlinear models. Such an approach has proven successful for studying deep networks in the machine learning literature [3]. In future work we plan to incorporate nonlinear neurons in our model.

Second, the output of our neural network is the equally weighted sum of the basal and apical projections. However, experimental evidence suggests that the pyramidal neurons integrate their apical and basal inputs asymmetrically [30, 28, 33]. In addition, in our model, the apical learning rule is non-Hebbian and depends on a calcium plateau potential that travels from the basal dendrites to the apical tuft. Experimental evidence for calcium plateau potential dependent plasticity is focused on the basal dendrites, with inconclusive evidence on the plasticity rules for the apical dendrites [18, 45].

To provide an alternative explanation of cortical computation, in a separate work [19], we derive an online algorithm for the general supervised learning method Reduced-Rank Regression, which includes CCA as a special case. The algorithm also maps onto a neural network with multi-compartmental neurons and non-Hebbian plasticity in the basal dendrites. Both models adopt a normative approach in which the algorithms are derived from principled objective functions. This approach is highly instructive as the differences between the models highlight which features of the network that are central to implementing an unsupervised learning method versus a supervised learning method.

There are two main differences between the models. First, the output of the network in [19] is the projection of the basal inputs, with no apical contribution. Second, the network in [19] allows for a range of apical synaptic update rules, including Hebbian updates. These differences can be compared to experimental outcomes to provide evidence that cortical microcircuits implement unsupervised algorithms, supervised algorithms, or mixtures of both. Thus, we find it informative to put
forth and contrast the two models.

Finally, we did not prove theoretical guarantees that our algorithms converge. As we show in Appendix C, Offline-CCA and Bio-CCA can be viewed as gradient descent-ascent and stochastic gradient descent-ascent algorithms for solving a nonconvex-concave min-max problem. While gradient descent-ascent algorithms are natural methods for solving such min-max problems, they are not always guaranteed to converge to a desired solution. In fact, when the gradient descent step size not sufficiently small relative to the gradient ascent step size (i.e., when $\tau$ is not sufficiently small), gradient descent-ascent algorithms for solving nonconvex-concave min-max problems can converge to limit cycles [23, 34]. Establishing local or global convergence, and convergence rate guarantees for general gradient descent-ascent algorithms is active area of research, and even recent advances [31] impose assumptions that are not satisfied in our setting. In Appendix C, we discuss these challenges and place our algorithms within the broader context of gradient descent-ascent algorithms for solving nonconvex-concave min-max problems.

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A Derivation of Algorithm 3

Recall the objective for adaptive CCA with output whitening given in Equation (22):

$$\min_{Z \in \mathbb{R}^{k \times T}} \max_{N \in \mathbb{R}^{k \times T}} \frac{1}{T^2} \mathrm{Tr}(-Z^T ZX^T C_{xx}^{-1} X - Z^T ZY^T C_{yy}^{-1} Y + \alpha T Z^T Z)$$

$$+ \frac{1}{T^2} \mathrm{Tr}[N^T N(Z^T Z - TI_T)].$$

Similar to Section 4.1, we introduce dynamic matrix variables $W_x$, $W_y$ and $P$ in place of $\frac{1}{T} ZX^T C_{xx}^{-1}$, $\frac{1}{T} ZY^T C_{yy}^{-1}$ and $\frac{1}{T} ZN^T$ to rewrite the objective (22) as follows:

$$\min_{Z \in \mathbb{R}^{k \times T}} \max_{N \in \mathbb{R}^{k \times T}} \min_{W_x \in \mathbb{R}^{k \times m}} \min_{W_y \in \mathbb{R}^{k \times n}} \max_{P \in \mathbb{R}^{k \times k}} \tilde{L}(W_x, W_y, P, Z, N),$$

(28)

where

$$\tilde{L}(W_x, W_y, P, Z, N) := \frac{1}{T} \mathrm{Tr}(-2Z^T W_x X - 2Z^T W_y Y + \alpha Z^T Z)$$

$$+ \frac{1}{T} \mathrm{Tr}(2N^T P^T Z - N^T N)$$

$$+ \mathrm{Tr}(W_x C_{xx} W_x^T + W_y C_{yy} W_y^T - PP^T).$$
Since $\tilde{L}(W_x, W_y, P, Z, N)$ is strictly convex in $W_x$, $W_y$ and $Z$, and strictly concave in $P$ and $N$, we can interchanged the order of optimization to obtain:

$$\min_{w_x \in \mathbb{R}^{k \times m}} \min_{w_y \in \mathbb{R}^{k \times n}} \max_{p \in \mathbb{R}^{k \times k}} \max_{z \in \mathbb{R}^{k \times k}} \max_{n \in \mathbb{R}^{k \times T}} \tilde{L}(W_x, W_y, P, Z, N). \quad (29)$$

The interchange of the maximization with respect to $N$ and the minimization with respect to $W_x$ and $W_y$ is justified by the fact that, for fixed $Z$ and $P$, $\tilde{L}(W_x, W_y, P, Z, N)$ is strictly convex in $(W_x, W_y)$ and strictly concave in $N$. Similarly, the interchange of the minimization with respect to $Z$ and the maximization with respect to $P$ is justified by the fact that, for fixed $N, W_x$ and $W_y$, $\tilde{L}(W_x, W_y, P, Z, N)$ is convex in $Z$ and strictly concave in $P$. In order to derive an online algorithm, we write the objective in terms of time-separable terms:

$$\tilde{L}(W_x, W_y, P, Z, N) = \frac{1}{T} \sum_{t=1}^{T} \tilde{l}_t(W_x, W_y, P, z_t, n_t),$$

where

$$\tilde{l}_t(W_x, W_y, P, z_t, n_t) := -2z_t^T W_x x_t - 2z_t^T W_y y_t + \alpha z_t^T z_t + 2n_t^T P^T z_t - n_t^T n_t$$

$$+ Tr \left( W_x x_t x_t^T W_x^T + W_y y_t y_t^T W_y^T - PP^T \right).$$

At each time step $t$, for fixed $W_x, W_y$ and $M$, we first simultaneously maximize the objective function $\tilde{l}_t(W_x, W_y, P, z_t, n_t)$ over $n_t$ and minimize over $z_t$ by running the following fast gradient descent-ascent dynamics to equilibrium:

$$\frac{dz_t(\gamma)}{d\gamma} = a_t + b_t - P n_t(\gamma) - \alpha z_t(\gamma) \quad (30)$$

$$\frac{dn_t(\gamma)}{d\gamma} = P^T z_t(\gamma) - n_t(\gamma), \quad (31)$$

where we recall that $a_t = W_x x_t$ and $b_t = W_y y_t$. Since $\tilde{l}_t(W_x, W_y, P, z_t, n_t)$ is convex in $z_t$ and concave in $n_t$, these fast dynamics equilibriate at the saddle point where $z_t = (PP^T + \alpha I_k)^{-1}(a_t + b_t)$ and $n_t = P^T z_t$. Then, with $(n_t, z_t)$ fixed, we perform a gradient descent-ascent step of the objective function with respect to $(W_x, W_y)$ and $P$:

$$W_x \leftarrow W_x - \frac{\eta}{2} \frac{\partial \tilde{l}_t(W_x, W_y, P, z_t, n_t)}{\partial W_x}$$

$$W_y \leftarrow W_y - \frac{\eta}{2} \frac{\partial \tilde{l}_t(W_x, W_y, P, z_t, n_t)}{\partial W_y}$$

$$P \leftarrow P + \frac{\eta}{2 \tau} \frac{\partial \tilde{l}_t(W_x, W_y, P, z_t, n_t)}{\partial P}.$$

Substituting in with the partial derivatives yields Algorithm 3.
B Experimental details

Bio-CCA: We implemented Algorithm 2. We initialized $\mathbf{W}$ to be a random matrix with i.i.d. standard normal entries and $\mathbf{M} = \mathbf{I}_k$. We used the time-dependent learning rate of the form $\eta_t = \eta_0/(1 + \gamma t)$. To find the optimal hyperparameters, we performed a grid search over $\eta_0 \in \{10^{-2}, 10^{-3}, 10^{-4}\}$, $\gamma \in \{10^{-3}, 10^{-4}, 10^{-5}\}$ and $\tau \in \{10, 1, 0.1\}$. The best performing parameters are reported in Table 1. Finally, to ensure the reported basis vectors satisfy the orthonormality constraints (2), we report the following normalized basis vectors:

$$V_x^\top := \left\{ \mathbf{M}^{-1}(\mathbf{W}_x \mathbf{C}_{xx}^\top \mathbf{W}_x + \mathbf{W}_y \mathbf{C}_{yy} \mathbf{W}_y^\top) \mathbf{M}^{-1} \right\}^{-1/2} \mathbf{M}^{-1} \mathbf{W}_x, \quad (32)$$

$$V_y^\top := \left\{ \mathbf{M}^{-1}(\mathbf{W}_x \mathbf{C}_{xx}^\top \mathbf{W}_x + \mathbf{W}_y \mathbf{C}_{yy} \mathbf{W}_y^\top) \mathbf{M}^{-1} \right\}^{-1/2} \mathbf{M}^{-1} \mathbf{W}_y. \quad (33)$$

|                       | Bio-CCA ($\eta_0, \gamma, \tau$) | Gen-Oja ($\beta_0, \gamma$) |
|-----------------------|-----------------------------------|------------------------------|
| synthetic ($k = 1$)   | $(10^{-3}, 10^{-4}, 0.1)$         | $(10^{-2})$                  |
| synthetic ($k = 2$)   | $(10^{-3}, 10^{-4}, 0.1)$         | N/A                          |
| synthetic ($k = 4$)   | $(10^{-3}, 10^{-4}, 0.1)$         | N/A                          |
| synthetic ($k = 8$)   | $(10^{-3}, 10^{-4}, 0.1)$         | N/A                          |
| Mediamill ($k = 1$)   | $(10^{-2}, 10^{-4}, 0.1)$         | $(10^{-2}, 10^{-3})$         |
| Mediamill ($k = 2$)   | $(10^{-2}, 10^{-4}, 0.1)$         | N/A                          |
| Mediamill ($k = 4$)   | $(10^{-2}, 10^{-4}, 0.1)$         | N/A                          |
| Mediamill ($k = 8$)   | $(10^{-2}, 10^{-4}, 0.1)$         | N/A                          |

Table 1: Optimal learning rates for Bio-CCA and Gen-Oja.

MSG-CCA: We implemented the online algorithm stated in [2]. Following [2], we use the learning rate $\eta_t = 0.1/\sqrt{t}$. MSG-CCA requires a training set to estimate the covariance matrices $\mathbf{C}_{xx}$ and $\mathbf{C}_{yy}$. We provided the algorithm with 1000 samples to initially estimate the covariance matrix.

Gen-Oja: We implemented the online algorithm stated in [7]. The algorithm includes 2 learning rates: $\alpha_t$ and $\beta_t$. As stated in [7], the Gen-Oja’s performance is robust to changes in the learning parameter $\alpha_t$, but sensitive to changes in the learning rate $\beta_t$. Following [7], we set $\alpha_t$ to be constant and equal to $1/R^2$ where $R^2 := \text{Tr}(\mathbf{C}_{xx}) + \text{Tr}(\mathbf{C}_{yy})$. To optimize over $\beta_t$, we used a time-dependent learning rate of the form $\beta_t = \beta_0/(1 + \gamma t)$ and performed a grid search over $\beta_0 \in \{1, 10^{-1}, 10^{-2}\}$ and $\gamma \in \{10^{-1}, 10^{-2}, 10^{-3}\}$. The best performing parameters are reported in Table 1.
Adaptive Bio-CCA with output whitening: We implemented Algorithm 2. We initialized $W_x$, $W_y$ and $P$ to be random matrices with i.i.d. standard normal entries. For the synthetic dataset, we used the time-dependent learning rate $\eta_t = 10^{-3}/(1 + 10^{-4}t)$ and set $\tau = 0.03$. For the dataset Mediamill, we used the time-dependent learning rate $\eta_t = 0.1/(1 + 10^{-3}t)$ and set $\tau = 0.5$.

C Convergence of CCA algorithms

To better interpret our offline and online CCA algorithms (Algorithms 1 & 2), we first make the following observation. Both algorithms optimize the min-max objective (16), which includes optimization over the neural outputs $Z$. In this way, the neural activities can be viewed as optimization steps, which is useful for a biological interpretation of the algorithms. However, since we assume a separation of time-scales in which the neural outputs equilibriate at their optimal values before the synaptic weight matrices are updated, the neural dynamics are superfluous when analyzing the algorithms from a mathematical perspective. Therefore, we set $Z$ equal to its equilibrium value $\bar{Z} = M^{-1}(W_xX + W_yY)$ in the cost function $L(W_x, W_y, M, Z)$ to obtain a min-max problem in terms of the synaptic weights:

$$
\min_{W \in \mathbb{R}^{k \times d}} \max_{M \in S_{++}^k} F(W, M),
$$

where $W := [W_x \ W_y]$ is the matrix of concatenated weights and $F(W, M) := L(W_x, W_y, M, \bar{Z})$. After substitution, we see that $F : \mathbb{R}^{k \times d} \times S_{++}^k \to \mathbb{R}$ is the nonconvex-concave function

$$
F(W, M) = \text{Tr} \left( -M^{-1}WAW^\top + WBW^\top - \frac{1}{2}M^2 \right),
$$

with partial derivatives

$$
-\frac{\partial F(W, M)}{\partial W} = 2M^{-1}WA - 2WB
$$

$$
\frac{\partial F(W, M)}{\partial M} = M^{-1}WAW^\top M^{-1} - M.
$$

where we have defined

$$
A := \begin{bmatrix} C_{xx} & C_{xy} \\ C_{yx} & C_{yy} \end{bmatrix}, \quad B := \begin{bmatrix} C_{xx} \\ C_{yy} \end{bmatrix}.
$$

The synaptic updates in both our offline and online algorithms can be viewed as (stochastic) gradient descent-ascent algorithms for solving the nonconvex-concave min-max problem (34). To make the comparison with our offline algorithm, we
substitute the optimal value $\bar{Z}$ into the synaptic weight updates in Algorithm 1 to obtain:

$$W \leftarrow W + 2\eta(M^{-1}WA - WB) \quad (36)$$

$$M \leftarrow M + \frac{\eta}{\tau}(M^{-1}WAW^TM^{-1} - M) \quad (37)$$

Comparing these updates to the partial derivatives of $F$, we see that Offline-CCA is naturally interpreted as a gradient descent-ascent algorithm for solving the min-max problem (34), with descent step size $\eta$ and ascent step size $\frac{\eta}{\tau}$. Similarly, to make the comparison with our online algorithm, we substitute the explicit expression for the equilibrium value $z_t = M^{-1}(a_t + b_t)$, where $a_t = W_x x_t$ and $b_t = W_y y_t$, into the synaptic weight updates in Algorithm 2 to rewrite the updates:

$$W \leftarrow W + 2\eta(M^{-1}WA_t - WB_t)$$

$$M \leftarrow M + \frac{\eta}{\tau}(M^{-1}WA_tW^TM^{-1} - M),$$

where

$$A_t := \begin{bmatrix} x_t x_t^T & x_t y_t^T \\ y_t x_t^T & y_t y_t^T \end{bmatrix}, \quad B_t := \begin{bmatrix} x_t x_t^T \\ y_t x_t^T \end{bmatrix}.$$ 

Comparing these updates to the partial derivatives of $F$, we see that our online algorithm is naturally interpreted as a stochastic gradient descent-ascent algorithm for solving the min-max problem (34), using the time $t$ rank-1 approximations $A_t$ and $B_t$ in place of $A$ and $B$, respectively.

There have been relatively few works establishing theoretical guarantees for solving nonconvex-concave min-max problems of the form (34) via stochastic gradient descent-ascent. Borkar [11, 12] proved asymptotic convergence to the solution of the min-max problem for a two time-scale stochastic gradient descent-ascent algorithm, where the ratio between the learning rates for the minimization step and the maximization step, $\tau$, depends on the iteration and converges to zero in the limit as the iteration number approaches infinity. Lin et al. [31] established convergence rate guarantees for a two time-scale stochastic mini-batch gradient descent-ascent algorithm to an equilibrium point (not necessarily a solution of the min-max problem). Both these results, however, impose assumptions that do not hold in our setting: the partial derivatives of $F$ are Lipschitz continuous and $M$ is restricted to a bounded convex set. Therefore, establishing global stability with convergence rate guarantees for our offline and online CCA algorithms requires new mathematical techniques that are beyond the scope of this work.

Even proving local convergence properties is non-trivial. In the special case that $B = I_d$, Pehlevan et al. [39] carefully analyzed the continuous dynamical system obtained by formally taking the step size $\eta$ to zero in Equations (36)–(37). They
computed an explicit value $\tau_0 \geq 1/2$, in terms the eigenvalues of $A$ such that if $\tau \leq \tau_0$, then solutions of the min-max problem (34) are linearly stable fixed points of the continuous dynamics. The case that $B \neq I_d$ is more complicated, and the approach in [39] is not readily extended. In a separate work, we take a step towards understanding the asymptotics of our algorithms by analyzing local stability properties for a general class of gradient descent-ascent algorithms, which includes Offline-CCA and Bio-CCA as special cases.

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