General analytical solution to Linsker’s application of Hebbian rules in neural networks

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\section*{Abstract}

Previous work by Linsker revealed how simple cells can emerge in the absence of structured environmental input, via a self-organisation learning process. He empirically showed the development of spatial-opponent cells driven only by input noise, emerging as a result of structure in the initial synaptic connectivity distribution. To date, a complete set of radial eigenfunctions have not been provided for this multi-layer network. In this paper, the complete set of eigenfunctions and eigenvalues for a three-layered network is for the first time analytically derived. Initially a simplified learning equation is considered for which the homeostatic parameters are set to zero. To extend the eigenfunction analysis to the full learning equation, including non-zero homeostatic parameters, a perturbation analysis is used.

\section{Introduction}

Synaptic plasticity underpins learning as the mechanism describing how synaptic weights change in response to environmental inputs. Plasticity has traditionally been modelled as rate-based, in which synapse weights change in response to short-time averaged pre- and post-synaptic neuron spiking rates. Over the past two decades the importance of pre- and post-synaptic neuron spike timing has been recognized, particularly for contexts in which high resolution temporal information is required such as microsecond resolution (Kempter et al., 1999; Gerstner et al., 1996), prompting the emergence of spike timing dependent plasticity (STDP) (Gerstner et al., 1996; Markram et al., 1997). Spike-based plasticity updates synaptic strength in response to the relative timing of pre- and post-synaptic spikes, amplifying synaptic strength if the presynaptic neuron contributes to the postsynaptic neuron’s action potential, and depressing a synapse if the presynaptic neuron fires after the postsynaptic neuron and thus did not contribute to its action potential.

Plasticity mechanisms have played a fundamental role in explaining the emergence of simple cells in the early layers of cortical processing, such as the primary visual cortex (V1). Plasticity has successfully explained the emergence of simple cells such as orientation selective cells (Bienenstock et al., 1982; Wimbauer et al., 1998; Yamakazi, 2002), direction selective cells (Wimbauer et al., 1997a,b; Senn and Buchs, 2003), ocular dominance (Miller, 1990), and feature maps in which sensitivity to a particular feature changes as the lamina is traversed (Goodhill, 2007).

Much of the research on learning in a cortical networks has been empirical and computational because of the analytical complexity of learning in response to number of layers, connectivity structure, and neuron type. A notable exception is the analysis of the network proposed by Linsker (1986b), in which he showed the emergence of a spatial opponent cell in the third layer of a three-layered network of Poisson neurons with Gaussian connectivity kernels. Learning in this network is a linear
function of correlation in presynaptic neural activity, with two learning constants that control the homeostatic equilibrium. The linearity of the learning system enables an eigenfunction analysis to be used to identify the independent contributors to a postsynaptic neuron’s synaptic weight structure. Eigenvalues provide a means to distinguish the eigenfunction that is the most significant contributor and hence determines the receptive field of the postsynaptic neuron. Although [Linsker (1986b)] focused on empirical results, there has been significant work aimed at extending the analytical framework for the network he proposed. [MacKay and Miller (1990)] proposed the first three radial eigenfunctions based on the work by [Tang (1990)], but without providing a derivation. The proposed eigenfunctions were for a simplified learning system in which homeostatic constants were assumed zero, so that all plasticity was driven by correlation between pre-synaptic inputs, and there was no non-competitive plasticity. They provided an empirical examination of the impact of non-zero homeostatic constants, showing that the eigenfunction of the leading eigenvalue can change in response to a change in the homeostatic equilibrium.

Miller (1990) employed Linsker’s (1986b) network in a model of learning in the primary visual cortex, with overlapping left and right eye inputs processed by the lateral geniculate nucleus (LGN). The network structure prompted correlation and anti-correlation in two afferents originating from either the same eye or the opposite eye, leading to the emergence of an ocular dominance feature map. Miller (1990) provided a description of an analytical derivation for the eigenfunctions of ocular dominance feature maps across the cortex.

Wimbauer et al. (1998) extended Linsker’s (1986b) network by incorporating lateral inhibitory connections in the third layer, showing the emergence of orientation selective cells in the third layer. They provided a derivation of Cartesian eigenfunctions for learning with homeostatic constants set to zero, and empirically extended the solution to the general learning equation with non-zero homeostatic constants. They simulated the development of an orientation selective feature map distributed across the primary visual cortex, using a model slightly more complex than for which they derived the eigenfunctions.

Analytical solutions to Linsker’s (1986b) learning system have played a central role in explaining the emergence of spatial opponent and orientation selective cells in the network. However, thus far no general analytical solution has been provided, with analytical results to date being for the simplified system with homeostatic constants set to zero. We provide here a solution for the eigenfunctions of Linsker’s (1986b) network in polar coordinates. As the system is radially symmetric, polar coordinates provide a natural coordinate system that enables an easy extension of polar eigenfunctions to the general learning system with non-zero homeostatic constants. One of the benefits of a full analytical solution for the network is insight into why the receptive field changes in response to changes in the homeostatic equilibrium, and the framework to determine exactly when this change occurs.

This paper is organised as follows. Section 2 introduces the network and neuron models used, based on Linsker’s (1986b) network. Radial eigenfunctions and eigenvalues are analytically derived for the simplified learning equation, for which the homeostatic parameters are set to zero, and then extended via perturbation analysis to the full system in Section 3. Finally, eigenfunctions and eigenvalues are found in Cartesian coordinates in Section 4 and compared to the radial eigenfunctions.

2 Network specification

We find the both the radial and Cartesian eigenfunctions of the three-layered, feed-forward, topographic network proposed by Linsker (1986b). The network is driven by spontaneous neural activity in the first layer, layer A, which inputs to layer B, which in turn inputs to layer C. Layers are comprised of populations of homogeneous neurons equispaced in a square grid across the lamina. The distance between the parallel layers is assumed to dominate sufficiently such that propagation delay experienced by action potentials from the presynaptic layer can be assumed approximately equal. A schematic diagram of the network is shown in Fig 1. Neurons $m$ and $n$ of layer A have synaptic inputs to neurons $i$ and $j$ of layer B, respectively, which both input to neuron $p$ of layer C.

Each postsynaptic neuron has a Gaussian synaptic connection distribution, centred on its two-dimensional position in the lamina, that ensures that radially proximate neurons are more likely to connect to it than a neuron more distal in the presynaptic lamina. The connectivity distributions are parameterised by a distance-dependent standard deviation, or radius, that is homogeneous across a layer, denoted $\sigma^{AB}$ and $\sigma^{BC}$, for synaptic connections between layers A and B and layers B and C, respectively. Consequently, the probability of neuron $m$ in layer A connecting to neuron $i$ in layer B is given by

$$p_{ni}(x_{mi}, y_{mi}) = \frac{1}{\sqrt{\pi} \sigma^{AB} \sigma^{BC}} \exp\left(-\frac{x_{mi}^2 + y_{mi}^2}{\sigma^{AB} \sigma^{BC}}\right),$$

(1)
where \((x_{mi}, y_{mi})\) is the two-dimensional radial distance between \(m\) and \(i\). Note that this definition differs from the standard definition by a factor of \(\sqrt{2}\) in accordance with the definition used by Linsker (1986b), and is specifically chosen for later convenience.

For postsynaptic neurons in layer \(C\), it is useful to write the connection probability in polar coordinates by assuming, without loss of generality, that the postsynaptic neuron is at position \((0, 0)\); the probability of presynaptic neuron \(j\) in layer \(B\) connecting to postsynaptic neuron \(p\) in layer \(C\) in polar coordinates is

\[
p_{NP} \left( r_{jp}, \theta_{jp} \right) = \frac{1}{\sigma_{BC}^2} \exp \left( -\frac{r_{jp}^2}{\sigma_{BC}^2} \right),
\]

where \(r_{jp}\) is the radial distance from the centre of the laminar to neuron \(i\) in layer \(C\), and \(\theta_{jp}\) is the angle to \(i\) within the two-dimensional laminar.

Linsker (1986b) showed that despite spontaneous neural activity in layer \(A\) being uncorrelated, the Gaussian connectivity distributions introduce spatial correlations in the inputs to layer \(B\) neurons. Layer \(B\) neurons that are spatially more proximate will have a greater number of shared connections, and therefore more correlated input, when compared to layer \(B\) neurons that are positioned further apart in the lamina. The expected number of shared presynaptic inputs between two postsynaptic neurons in layer \(B\) can easily be shown to be (see Appendix A for full derivation)

\[
E \left[ N_{BB} (d) \right] = \frac{(N_{AB})^2}{2\pi(\sigma_{AB})^2} \exp \left( -\frac{(d_{ij})^2}{2(\sigma_{AB})^2} \right),
\]

where \(N_{AB}\) denotes the expected number of synaptic connections from layer \(A\) to each neuron in layer \(B\), and \(d_{ij}\) represents the distance between neurons \(i\) and \(j\) such that \(d_{ij} = \sqrt{x_{mi}^2 + y_{mi}^2}\).

### 2.1 Neuron model

The network is driven by spontaneous Poisson activity of the layer \(A\) cells. This implies that there are no spike-based temporal correlations between input and output neurons other than what is captured in the rate-based signals and that the rates change slowly when compared to the period they are averaged over (Kempter et al., 1999). Activity of a layer \(A\) neuron is modelled as \(f_m^A (t) \sim \text{Poisson} (\lambda^A)\), where \(f_m^A (t)\) is the spiking rate of layer \(A\) neuron \(m\) at time \(t\).

As in Linsker (1986b) we use a Poisson neuron model so that the network is linear when operating within the weight bounds, discussed below. The update equations for neural activity in layers \(B\) and \(C\) is

\[
f_i^B (t) = R_a^B + R_b^B \sum_m w_{mi}^A (t) f_m^A (t),
\]

\[
f_i^C (t) = R_a^C + R_b^C \sum_i w_{ip}^B (t) f_p^B (t),
\]

where \(R_a^B, R_a^C\) denote spontaneous firing rates, while \(R_b^A, R_b^B\) represent scaling constants, and \(w_{mi}^A (t), w_{ip}^B (t)\) depict synaptic strengths between neurons \(m\) and \(i\) in layers \(A\) and \(B\), respectively, and neurons \(i\) and \(p\) in layers \(B\) and \(C\), respectively. Note that an implicit assumption in this Poisson model of neural activity is that propagation delay is negligible or, equivalently, is dominated by inter-layer distances between neurons and can therefore be considered approximately equal for all inputs to a postsynaptic neuron.

### 2.2 Learning dynamics

The adiabatic assumption is that incremental weight changes occur slowly with respect to neural dynamics, which occur on a millisecond timescale. Furthermore, neurons within the same population are assumed to have the same statistical properties of neural activity and synaptic connectivity. Consequently, the system is ergodic and the spike rate can be determined from the ensemble average, or from a temporal mean over the timescale of learning. Under these assumptions, the learning equation...
Figure 1: Schematic diagram showing the three layered feed-forward network, where layer A neurons, m (grey) and n (grey), feed into layer B neurons, i (red) and j (blue), respectively, which in turn are input to a layer C neuron, p (green). Synaptic connections between neurons are shown by solid, coloured lines connecting from a presynaptic neuron, to a postsynaptic neuron of the same colour. Synaptic strength, for example between neurons m and i, is denoted \( w_{mi}^{AB} \). Synaptic connection distributions are homogeneous within a layer, and modelled as being Gaussian, parameterised by distance-dependent standard deviation, or radius, denoted \( \sigma_{AB} \) and \( \sigma_{BC} \), between layers A and B, and layers B and C, respectively. The radial distance between two neurons within a lamina, for example between neuron m from layer A and i from layer B, is denoted \( d_{mi} \).

A

B

C

can be expressed as a differential equation (Linsker, 1986b). The general learning equations for synaptic weights between neurons in layers A and B, and synapses connecting layers B and C, network is given by (Linsker, 1986b)

\[
\eta w_{mi}^{AB} = k_1^{AB} + \frac{1}{N^{AB}} \sum_n w_{ni}^{AB} Q_{mn}^{AB} + k_2^{AB} , \quad w_{min} \leq w_{mi}^{AB} \leq w_{max} , \tag{5a}
\]

\[
\eta w_{ij}^{BC} = k_1^{BC} + \frac{1}{N^{BC}} \sum_j w_{ji}^{BC} Q_{ij}^{BC} + k_2^{BC} , \quad w_{min} \leq w_{ij}^{BC} \leq w_{max} , \tag{5b}
\]

where \( \eta \ll 1 \) is the learning rate that ensures that learning is slow on a millisecond timescale, \( w_{min} \) and \( w_{max} \) are the lower and upper bounds on the weights, respectively, and the parameters \( k_1^{AB}, k_2^{AB}, k_1^{BC}, k_2^{BC} \) are layer specific constants controlling homeostasis (i.e. independent of the correlation structure of the inputs). The definition for normalised covariance has the same structure for each layer; for example the normalised covariance between layer A neurons m and n is defined by \( Q_{mn}^{A} = f_0^{-2} \left\langle \frac{f_m^A - \bar{f}^A}{\max} \right\rangle \left\langle \frac{f_n^A - \bar{f}^A}{\max} \right\rangle \), where \( \langle \rangle \) depicts an ensemble average, \( \bar{f}^A \) denotes the temporal average of layer A neural activity, and \( f_0^2 \) is a scaling factor to normalise the covariance matrix Q.

For a Gaussian synaptic density distribution, the covariance between layer B neurons is a function of the radial distance separating the neurons,

\[
\text{cov} \left( f_m^B, f_n^B \right) = \left( \frac{\rho_{BC}^{2} N^{BC} \sigma_{AB}^2}{2\pi (\sigma_{AB}^2)} \right)^2 \exp \left( -\frac{d_{mn}^2}{2 (\sigma_{AB}^2)} \right) , \tag{6}
\]

Note that vector distances are given with respect to the layer C cell, so we define the two dimensional radial distance of presynaptic neuron, m, from postsynaptic neuron, i, by vector, \( \mathbf{x}_{mi} = [x_{mi}, y_{mi}] \text{T} \), and \( d_{ij} = \| \mathbf{x}_{mi} - \mathbf{x}_{nj} \| \). Only radial distances are considered, so that distances between layers are assumed to have negligible impact on learning dynamics, since the inter-layer transmission delay is uniform.
Normalising this result, and incorporating into the learning equation in Eq. (5), gives
\[ \eta w_{mi} = k_1 + \frac{1}{N} \sum_n w_{ni} \left( \exp \left( -\frac{|x_{mi} - x_{ni}|^2}{2(\sigma^2)^2} \right) + k_2 \right), \]  
where it is assumed that the covariance is normalised, and we have removed the layer superscripts for readability.

It is assumed that a deeper layer cannot be learned until its presynaptic layer has converged to a stable weight structure, and hence layers are learned sequentially. This accords with the approach employed by [Linsker, 1986b], and does not impact the final weight structure across the network. Consequently, synapses connecting layers A and B evolve to a stable structure before learning begins for synapses connecting layers B and C.

[Linsker, 1986b] demonstrated that individual synapses are unstable and, for excitatory synapses, all or all-but-one necessarily reach the upper bound, \( w_{\text{max}} \). However, under an assumption of weak covariance of the inputs [MacKay and Miller, 1990] the mean weight of synapses input to a postsynaptic neuron is not necessarily unstable, but rather controlled by the homeostatic constants. For excitatory connections the mean weight of a postsynaptic neuron’s synapses will converge to
\[ w = -\frac{k_1}{k_2}, \quad \text{if} \quad k_2 < 0, \quad \text{and} \quad 0 < \frac{k_1}{k_2} < 1, \]  
where the conditions on \( k_1 \) and \( k_2 \) are required to ensure that the mean synaptic weight does not diverge to the bounds. For all synapses to grow until they reach the upper bound requires that \( k_1 + k_2 > 0 \). In this case the system is unstable so that the mean synaptic weight grows until all individual synapses, or all-but-one, have reached the upper bound [Linsker, 1986b].

[Linsker, 1986b] selected homeostatic constants for synapses connecting layers A and B such that the mean weight was unstable and, consequently, all synapses diverged to the upper bound. For connections between layers B and C the homeostatic constants are chosen such that the mean weight is stable, requiring some individual synapses to diverge to the lower bound, and others to the upper bound.

With synaptic connections between layers A and B assumed to all reach the upper bound, the focus is on determining the learned synaptic structure for postsynaptic neurons in layer C. Given that the learning equation in Eq. (5b) is linear within the weight bounds the system lends itself to an eigenfunction analysis. That is, we wish to identify the independent eigenfunctions that contribute to the evolution of synaptic weights. Given that the system is driven by unstructured noise, it will self-organise such that the eigenfunction with the leading eigenvalue will ultimately dominate the synaptic weight structure.

In order to conduct an eigenfunction analysis we approximate the discrete grid of neurons by its continuous limit. The probability of a synaptic connection existing between neuron \( m \) at position \( (x_{mi}, y_{mi}) \) in the presynaptic layer, and postsynaptic neuron \( i \), detailed in Eq. (1), becomes a synaptic density describing the expected proportion of the total number of presynaptic inputs originating from \( (x_{mi}, y_{mi}) \). The synaptic strength is then considered the average weight of synapses at this location. In the continuous limit the learning equation in Eq. (7) becomes
\[ \eta w(x) = k_1 + \int_{-\infty}^{\infty} A \exp \left( -\frac{|x - x'|^2}{2(\sigma^2)^2} \right) \exp \left( -\frac{|x|^2 + |x'|^2}{(\sigma^2)^2} \right) w(x') d^2x', \]  
where neuron \( i \) in layer B is denoted by its continuous position vector \( x = (x_ip, y_ip) \), and neuron \( j \) in layer B is represented by its continuous vector, \( x' = (x_{jp}, y_{jp}) \), and subscripts have been omitted for readability. The Cartesian coordinates have been centred on the layer C neuron. Note that \( A \) contains coefficients to normalise covariance and connection probabilities, such that \( A = \pi(\sigma^2)^2 \). To characterise the system in terms of its eigenfunctions, we need to solve the eigenvalue problem for the following system,
\[ \lambda \eta w(x) = \int_{-\infty}^{\infty} A \exp \left( -\frac{|x - x'|^2}{2(\sigma^2)^2} \right) \exp \left( -\frac{|x|^2 + |x'|^2}{(\sigma^2)^2} \right) w(x') d^2x', \]  

5
3 Radial eigenfunctions of the learning equation

3.1 Radial eigenfunctions of the simplified learning equation

To proceed we initially set $k_2$ to zero, and later consider the more general case in which $k_2$ is non-zero. Converting to polar coordinates such that $r$ and $\theta$ give the magnitude and phase of $x$, and transforming $r$ to be unitless by scaling it by $\frac{1}{\sigma \sigma}$, the eigenvalue problem in Eq. (10) becomes:

$$\lambda \eta w (r, \theta) = A (\sigma^{AB})^2 \exp \left( -\frac{r^2}{2} \left( \frac{2(\sigma^{AB})^2 + (\sigma^{BC})^2}{(\sigma^{BC})^2} \right) \right) \int_0^{2\pi} d\tilde{\theta} \exp \left( -\frac{r^2}{2} \left( \frac{2(\sigma^{AB})^2 + (\sigma^{BC})^2}{(\sigma^{BC})^2} \right) \right) \int_0^{2\pi} d\tilde{\theta} \exp \left( -\frac{r^2}{2} \left( \frac{2(\sigma^{AB})^2 + (\sigma^{BC})^2}{(\sigma^{BC})^2} \right) \right) w (\tilde{r}, \tilde{\theta}).$$

(11)

The weight functions can be decomposed into a sum of independent components that are dense in the space using a Fourier series. Therefore, expressing the exponential in its infinite series form, we get

$$\eta \sum_{l=0}^{\infty} \lambda_l \left( g_l (r) \cos (l \theta) + \tilde{g}_l (r) \sin (l \theta) \right) = A (\sigma^{AB})^2 \exp \left( -\frac{r^2}{2} \left( \frac{2(\sigma^{AB})^2 + (\sigma^{BC})^2}{(\sigma^{BC})^2} \right) \right) \int_0^{2\pi} d\tilde{\theta} \exp \left( -\frac{r^2}{2} \left( \frac{2(\sigma^{AB})^2 + (\sigma^{BC})^2}{(\sigma^{BC})^2} \right) \right) \int_0^{2\pi} d\tilde{\theta} \exp \left( -\frac{r^2}{2} \left( \frac{2(\sigma^{AB})^2 + (\sigma^{BC})^2}{(\sigma^{BC})^2} \right) \right) \sum_{n=0}^{\infty} \frac{1}{n!} \sum_{l'=0}^{\infty} (\tilde{g}_{l'} (\tilde{r}) \cos (l' \tilde{\theta}) + \tilde{g}_{l'} (\tilde{r}) \sin (l' \tilde{\theta})).$$

(12)

Rearrange the sum and integral terms to give

$$\eta \sum_{l=0}^{\infty} \lambda_l \left( g_l (r) \cos (l \theta) + \tilde{g}_l (r) \sin (l \theta) \right) = A (\sigma^{AB})^2 \exp \left( -\frac{r^2}{2} \left( \frac{2(\sigma^{AB})^2 + (\sigma^{BC})^2}{(\sigma^{BC})^2} \right) \right) \int_0^{2\pi} d\tilde{\theta} \exp \left( -\frac{r^2}{2} \left( \frac{2(\sigma^{AB})^2 + (\sigma^{BC})^2}{(\sigma^{BC})^2} \right) \right) \sum_{l=0}^{\infty} \sum_{n=0}^{\infty} \frac{1}{n!} (\tilde{r})^n \int_0^{2\pi} d\tilde{\theta} \cos^n (\tilde{\theta}) \left( \tilde{g}_{l'} (\tilde{r}) \cos (l' \tilde{\theta}) + \tilde{g}_{l'} (\tilde{r}) \sin (l' \tilde{\theta}) \right).$$

(13)

Now we consider just the inner integral over $\tilde{\theta}$,

$$\int_0^{2\pi} d\tilde{\theta} \cos^n (\tilde{\theta}) \left( \tilde{g}_{l'} (\tilde{r}) \cos (l' \tilde{\theta}) + \tilde{g}_{l'} (\tilde{r}) \sin (l' \tilde{\theta}) \right).$$

(14)

A general expression for $\cos^n (\phi)$ can be found by writing it as

$$\cos^n (\phi) = \frac{1}{2^n} \left( e^{-i\phi} + e^{i\phi} \right)^n$$

$$= \frac{1}{2^n} \sum_{k=0}^{n} \binom{n}{k} \left( e^{-i\phi} \right)^k \left( e^{i\phi} \right)^{n-k}$$

$$= \frac{1}{2^n} \sum_{k=0}^{n} \binom{n}{k} \left( e^{-i\phi(n-2k)} \right)$$

$$= \frac{1}{2^n} \sum_{k=0}^{n} \binom{n}{k} \left( e^{-i\phi(n-2k)} + e^{i\phi(n-2k)} \right)$$

$$= \frac{1}{2^n} \sum_{k=0}^{n} \binom{n}{k} \cos (\phi (n-2k))$$

$$= \left\{ \begin{array}{ll} \frac{1}{2} \binom{n}{2} + \frac{1}{2^n} \sum_{k=0}^{n-1} \binom{n}{k} \cos (\phi (n-2k)), & \text{for } n \text{ odd} \\
\frac{1}{2} \binom{n}{2} & \text{for } n \text{ even} \end{array} \right.$$
Application of this result to Eq. \([14]\) gives

\[
\begin{align*}
\int_0^{2\pi} d\tilde{\theta} \cos^n (\theta - \tilde{\theta}) \left( g_{\ell'} (\tilde{r}) \cos (\ell' \tilde{\theta}) + \tilde{g}_{\ell'} (\tilde{r}) \sin (\ell' \tilde{\theta}) \right) \\
= \frac{1}{2^n} \int_0^{2\pi} d\tilde{\theta} \sum_{k=0}^{n} \left( \begin{array}{c} n \\ k \end{array} \right) \cos ((\theta - \tilde{\theta})(n-2k)) \left( g_{\ell'} (\tilde{r}) \cos (\ell' \tilde{\theta}) + \tilde{g}_{\ell'} (\tilde{r}) \sin (\ell' \tilde{\theta}) \right) \\
= \frac{1}{2^n} \sum_{k=0}^{n} \left( \begin{array}{c} n \\ k \end{array} \right) \int_0^{2\pi} d\tilde{\theta} \cos ((\theta - \tilde{\theta})(n-2k)) g_{\ell'} (\tilde{r}) \cos (\ell' \tilde{\theta}) \\
+ \frac{1}{2^n} \sum_{k=0}^{n} \left( \begin{array}{c} n \\ k \end{array} \right) \int_0^{2\pi} d\tilde{\theta} \cos ((\theta - \tilde{\theta})(n-2k)) \tilde{g}_{\ell'} (\tilde{r}) \sin (\ell' \tilde{\theta}) \\
= \frac{1}{2^{n+1}} \sum_{k=0}^{n} \left( \begin{array}{c} n \\ k \end{array} \right) \int_0^{2\pi} d\tilde{\theta} g_{\ell'} (\tilde{r}) \left( \cos ((\theta - \tilde{\theta})(n-2k)+\ell' \tilde{\theta}) + \cos (-(\theta - \tilde{\theta})(n-2k)+\ell' \tilde{\theta}) \right) \\
+ \frac{1}{2^{n+1}} \sum_{k=0}^{n} \left( \begin{array}{c} n \\ k \end{array} \right) \int_0^{2\pi} d\tilde{\theta} \tilde{g}_{\ell'} (\tilde{r}) \left( \sin ((\theta - \tilde{\theta})(n-2k)+\ell' \tilde{\theta}) - \sin (-(\theta - \tilde{\theta})(n-2k)+\ell' \tilde{\theta}) \right) \\
= \frac{1}{2^n} \sum_{k=0}^{n} \left( \begin{array}{c} n \\ k \end{array} \right) \int_0^{2\pi} d\tilde{\theta} g_{\ell'} (\tilde{r}) \cos \left( \theta(n-2k)+\tilde{\theta}(l'-(n-2k)) \right) + \cos \left( \theta(n-2k)+\tilde{\theta}(l'+(n-2k)) \right) \\
+ \frac{1}{2^n} \sum_{k=0}^{n} \left( \begin{array}{c} n \\ k \end{array} \right) \int_0^{2\pi} d\tilde{\theta} \tilde{g}_{\ell'} (\tilde{r}) \sin \left( \theta(n-2k)+\tilde{\theta}(l'-(n-2k)) \right) - \sin \left( \theta(n-2k)+\tilde{\theta}(l'+(n-2k)) \right) , \\
= \left\{ \begin{array}{ll}
\frac{1}{2^n} \sum_{k=0}^{n} \left( \begin{array}{c} n \\ k \end{array} \right) \int_0^{2\pi} d\tilde{\theta} \left( g_{\ell'} (\tilde{r}) \cos (\theta(n-2k)+\tilde{\theta}(l'-(n-2k))) + \cos (\theta(n-2k)+\tilde{\theta}(l'+(n-2k))) \right) \\
+ \frac{1}{2^n} \sum_{k=0}^{n} \left( \begin{array}{c} n \\ k \end{array} \right) \int_0^{2\pi} d\tilde{\theta} \left( \tilde{g}_{\ell'} (\tilde{r}) \sin (\theta(n-2k)+\tilde{\theta}(l'-(n-2k))) + \sin (\theta(n-2k)-\tilde{\theta}(l'-(n-2k))) \right) , \\
\text{for } n \text{ odd}
\end{array} \right.
\end{align*}
\]

(16)

All of the integrals within the binomial sum term will evaluate to zero since the functions are periodic in \(2\pi\) and centred around a mean of zero, except those for which \(l' = n - 2k\), because in these cases the \(\tilde{\theta}\) terms cancel, and therefore the integration is over a constant. For odd \(l'\), this can only happen for odd \(n\), and for even \(l'\), this can only happen for even \(n\), when \(k = \frac{n-l}{2}\) such that \(0 \leq k \leq \frac{n-1}{2}\). Consequently, the sinusoidal term for which the \(\tilde{\theta}\) coefficient is \(l' + n - 2k\) will always integrate to 0, since \(l' + 2k - n \geq 0\) for all \(k\). The additional term for even \(n\) will only be non-zero when \(l' = 0\). Thus equation Eq. \([16]\) evaluates to

\[
\begin{align*}
\int_0^{2\pi} d\tilde{\theta} \cos^n (\theta - \tilde{\theta}) \left( g_{\ell'} (\tilde{r}) \cos (\ell' \tilde{\theta}) + \tilde{g}_{\ell'} (\tilde{r}) \sin (\ell' \tilde{\theta}) \right) \\
= \left\{ \begin{array}{ll}
\frac{2\pi}{2^n} \left( \begin{array}{c} n \\ 2 \end{array} \right) g_{\ell'} (\tilde{r}), \\
\text{for } l' = 0 \text{ and } n \text{ even}
\end{array} \right.
\end{align*}
\]

(17)

otherwise.

Note that for \(n - l' \geq 0\) we require \(n \geq l'\), and thus the infinite sum over \(l'\) in Eq. \([13]\) can be truncated.

Incorporating this result into the infinite sums from Eq. \([13]\), separating the odd and even terms for \(n\) and \(l'\), and focussing only on the cosine components for the interim, gives,
\[
\sum_{\ell=0}^{\infty} \sum_{n=0}^{\infty} \int_{0}^{2\pi} d\tilde{\theta} \cos^n (\theta - \tilde{\theta}) A(\tilde{\rho}) \cos (\ell' \tilde{\theta}) \\
= \sum_{n=0}^{\infty} \sum_{\ell=0}^{n} \left[ \frac{2\pi}{2\ell} \left( \frac{2n}{n-\ell} \right) g_{2\ell}(\tilde{\rho}) \cos (2\ell' \theta) + \frac{2\pi}{2n+1} \left( \frac{2n+1}{n-\ell} \right) g_{2\ell+1}(\tilde{\rho}) \cos ((2\ell' + 1) \theta) \right] \\
= \sum_{\ell'=0}^{\infty} \sum_{n'=0}^{\infty} \left[ \frac{2\pi}{2\ell' + 1} \left( \frac{2n'}{n'-\ell'} \right) g_{2\ell'}(\tilde{\rho}) \cos (2\ell' \theta) + \frac{2\pi}{2n'+1} \left( \frac{2n'+1}{n'-\ell'} \right) g_{2\ell'+1}(\tilde{\rho}) \cos ((2\ell' + 1) \theta) \right]. \quad (18)
\]

Let \( n' = n - \ell' \), so that
\[
\sum_{\ell'=0}^{\infty} \sum_{n'=0}^{\infty} \int_{0}^{2\pi} d\tilde{\theta} \cos^n (\theta - \tilde{\theta}) g_{\ell'}(\tilde{\rho}) \cos (\ell' \tilde{\theta}) \\
= \sum_{\ell'=0}^{\infty} \sum_{n'=0}^{\infty} \left[ \frac{2\pi}{2(n'+\ell')} \left( \frac{2(n'+\ell')}{n'+\ell'} \right) g_{2\ell'}(\tilde{\rho}) \cos (2\ell' \theta) + \frac{2\pi}{2n'+1} \left( \frac{2(n'+\ell') + 1}{n'+\ell'} \right) g_{2\ell'+1}(\tilde{\rho}) \cos ((2\ell' + 1) \theta) \right]. \quad (19)
\]

Note that \( n' \) and \( \ell' \) can now be set independently so that the odd and even terms for \( \ell' \) can now be recombined.
\[
\sum_{\ell'=0}^{\infty} \sum_{n'=0}^{\infty} \int_{0}^{2\pi} d\tilde{\theta} \cos^n (\theta - \tilde{\theta}) g_{\ell'}(\tilde{\rho}) \cos (\ell' \tilde{\theta}) = \sum_{\ell'=0}^{\infty} \sum_{n'=0}^{\infty} \frac{2\pi}{2\ell'+1} \left( \frac{2n'+\ell'}{n'+\ell'} \right) g_{\ell'}(\tilde{\rho}) \cos (\ell' \tilde{\theta}). \quad (20)
\]

Incorporating this sum into the full equation for Eq. (13), gives,
\[
\eta \sum_{l=0}^{\infty} \lambda_l (g_l (r) \cos (l \theta) + \tilde{g}_l (r) \sin (l \theta)) \\
= A(\sigma_{AB})^2 \exp \left( -\frac{r^2}{2} \left( \frac{2(\sigma_{AB})^2 + (\sigma_{BC})^2}{(\sigma_{BC})^2} \right) \right) \int_{0}^{\infty} d\tilde{\rho} \exp \left( -\frac{r^2}{2} \left( \frac{2(\sigma_{AB})^2 + (\sigma_{BC})^2}{(\sigma_{BC})^2} \right) \right) \\
\sum_{l'=0}^{\infty} \sum_{n'=0}^{\infty} \left( \frac{2n'+\ell'}{2n'+1} \right) g_{\ell'}(\tilde{\rho}) \cos (\ell' \tilde{\theta}) + \tilde{g}_{\ell'}(\tilde{\rho}) \sin (\ell' \tilde{\theta}) \\
= A(\sigma_{AB})^2 \exp \left( -\frac{r^2}{2} \left( \frac{2(\sigma_{AB})^2 + (\sigma_{BC})^2}{(\sigma_{BC})^2} \right) \right) \int_{0}^{\infty} d\tilde{\rho} \exp \left( -\frac{r^2}{2} \left( \frac{2(\sigma_{AB})^2 + (\sigma_{BC})^2}{(\sigma_{BC})^2} \right) \right) \\
\sum_{l'=0}^{\infty} \sum_{n'=0}^{\infty} \left( \frac{2n'+\ell'}{2n'+1} \right) g_{\ell'}(\tilde{\rho}) \cos (\ell' \tilde{\theta}) + \tilde{g}_{\ell'}(\tilde{\rho}) \sin (\ell' \tilde{\theta}) \\
= 2\pi A(\sigma_{AB})^2 \exp \left( -\frac{r^2}{2} \left( \frac{2(\sigma_{AB})^2 + (\sigma_{BC})^2}{(\sigma_{BC})^2} \right) \right) \int_{0}^{\infty} d\tilde{\rho} \exp \left( -\frac{r^2}{2} \left( \frac{2(\sigma_{AB})^2 + (\sigma_{BC})^2}{(\sigma_{BC})^2} \right) \right) \\
\sum_{l'=0}^{\infty} \sum_{n'=0}^{\infty} \left( \frac{2n'+\ell'}{2n'+1} \right) g_{\ell'}(\tilde{\rho}) \cos (\ell' \tilde{\theta}) + \tilde{g}_{\ell'}(\tilde{\rho}) \sin (\ell' \tilde{\theta}) \\
= 2\pi A(\sigma_{AB})^2 \exp \left( -\frac{r^2}{2} \left( \frac{2(\sigma_{AB})^2 + (\sigma_{BC})^2}{(\sigma_{BC})^2} \right) \right) \int_{0}^{\infty} d\tilde{\rho} \exp \left( -\frac{r^2}{2} \left( \frac{2(\sigma_{AB})^2 + (\sigma_{BC})^2}{(\sigma_{BC})^2} \right) \right) I_{\ell'}(\tilde{\rho}) (g_{\ell'}(\tilde{\rho}) \cos (\ell' \tilde{\theta}) + \tilde{g}_{\ell'}(\tilde{\rho}) \sin (\ell' \tilde{\theta})), \quad (21)
\]

where \( I_{\alpha}(x) \) is a modified Bessel function of the first kind, of order \( \alpha \), such that
\[
I_{\alpha}(x) = \sum_{m=0}^{\infty} \frac{1}{m! \Gamma(m + \alpha + 1)} \left( \frac{x}{2} \right)^{2m + \alpha}. \quad (22)
\]

We can consider each component in the sum separately, such that
\[
\eta \lambda_l (g_l (r) \cos (l \theta) + \tilde{g}_l (r) \sin (l \theta)) \\
= 2\pi A(\sigma_{AB})^2 \exp \left( -\frac{r^2}{2} \left( \frac{2(\sigma_{AB})^2 + (\sigma_{BC})^2}{(\sigma_{BC})^2} \right) \right) \int_{0}^{\infty} d\tilde{\rho} \exp \left( -\frac{r^2}{2} \left( \frac{2(\sigma_{AB})^2 + (\sigma_{BC})^2}{(\sigma_{BC})^2} \right) \right) I_{\ell'}(\tilde{\rho}) (g_{\ell'}(\tilde{\rho}) \cos (\ell' \tilde{\theta}) + \tilde{g}_{\ell'}(\tilde{\rho}) \sin (\ell' \tilde{\theta})). \quad (23)
\]
To derive the eigenfunctions that satisfy Eq. (23), we require weight functions with an exponential of the same form, and polynomials in \( r \) that will be of the same order after evaluating the integral. Furthermore, it is well known that Laguerre polynomials are orthogonal over the interval \([0, \infty)\), with respect to the weight function \( x^n e^{-x} \). Consequently, we propose eigenfunctions of the form

\[
\psi^l_n(r) = N_l n^l \exp \left( -\frac{r^2}{2C} \right) L_n^{l-n} \left( \frac{r^2}{C} \right) \cos ((l-n)\theta),
\]

where the additional index, \( n \), denotes the index into eigenvalues of the same order, \( l \), since the solutions are degenerate, and \( N_l n \) is a normalisation factor. \( L_n^{l-n} () \) is an associated Laguerre polynomial. Since \( \int_0^\infty x^n e^{-x} L_n^p(x)^2 \, dx = (p + q)!/q! \), the normalisation factor can be derived as,

\[
N_l n = \begin{cases} \frac{2^{l-n} \pi^{\frac{l-n}{2}}}{\sqrt{\Gamma(l-n+1)\sigma^{l+n+1}}} & l = n \\ \frac{n^l \pi^{\frac{l-n}{2}}}{\sqrt{\Gamma(l-n+1)\sigma^{l+n+1}}} & \text{otherwise,} \end{cases}
\]

where the factor of 2 difference occurs for the case \( l = n \), because the integral for the angular component is over \( \cos (0\theta) \), a constant.

Separating the \( \cos \) and \( \sin \) terms in Eq. (23) since they are independent components, and letting

\[
\alpha = \frac{(\sigma BC)^2}{2(\sigma AB)^2 + (\sigma BC)^2}
\]

the eigenfunctions must satisfy

\[
r^{l-n} \exp \left( -\frac{r^2}{2C} \right) L_n^{l-n} \left( \frac{r^2}{C} \right) \cos ((l-n)\theta) = \frac{1}{2} 2\pi A(\sigma AB)^2 \exp \left( -\frac{r^2}{2\alpha} \right) \int_0^\infty d\tilde{r} \exp \left( -\frac{\tilde{r}^2}{2\alpha} \right) \exp \left( -\frac{\tilde{r}^2}{2C} \right) L_n^{l-n} \left( \frac{\tilde{r}^2}{C} \right) I_{l-n}(\tilde{r}) \cos ((l-n)\theta)
\]

\[
= 2\pi A(\sigma AB)^2 \exp \left( -\frac{r^2}{2\alpha} \right) \int_0^\infty d\tilde{r} \exp \left( -\frac{\tilde{r}^2}{2} \left( \frac{\alpha + C}{\alpha C} \right) \right) \exp \left( -\frac{\tilde{r}^2}{2} \left( \frac{\alpha + C}{\alpha C} \right) \right) L_n^{l-n} \left( \frac{\tilde{r}^2}{C} \right) \cos ((l-n)\theta).
\]

Note the following integral, evaluated using Wolfram Research Inc. (2018):

\[
J_{n,l} = \int_0^\infty d\tilde{r} \exp \left( -\frac{\tilde{r}^2}{2B} \right) r^{l-n} I_{l-n}(\tilde{r}) L_n^{l-n} \left( \frac{\tilde{r}^2}{C} \right) = B^{l+1} \left( \frac{C - 2B}{BC} \right)^n \exp \left( \frac{B^2}{2} \right) r^{l-n} L_n^{l-n} \left( \frac{B^2 + r^2}{C - 2B} \right).
\]

Applying this integral to Eq. (27) gives,

\[
r^{l-n} \exp \left( -\frac{r^2}{2C} \right) L_n^{l-n} \left( \frac{r^2}{C} \right) \cos ((l-n)\theta)
\]

\[
= \frac{1}{2} 2\pi A(\sigma AB)^2 \exp \left( -\frac{r^2}{2\alpha} \right) \left( \frac{\alpha C}{\alpha + C} \right)^{l+1} \left( \frac{C - 2(\alpha + C)}{\alpha(\alpha + C)} \right)^n r^{l-n} \exp \left( \left( \frac{\alpha C}{\alpha + C} \right) \left( \frac{r^2}{2} \right) \right) L_n^{l-n} \left( \frac{(\alpha + C)^2}{2 - 2(\alpha + C)} \right) \frac{r^2}{2} \right) L_n^{l-n} \left( \frac{C \alpha^2 + r^2}{C^2 - \alpha^2} \right) \cos ((l-n)\theta).
\]

For this equivalence to be true, it is necessary to equate terms. After some simplification, it can be seen that equating both the exponential and Laguerre terms requires that,

\[
\frac{1}{C} = \frac{C \alpha^2}{C^2 - \alpha^2}
\]

\[
\rightarrow 0 = C(\alpha^2 - 1) + \alpha^2.
\]
Solving this quadratic in $C$ requires,

$$C = \frac{\alpha}{\sqrt{1 - \alpha^2}}, \quad (31)$$

from which condition we finally get,

$$r^{l-n}\exp \left( -\frac{r^2}{2C} \right) L^{l-n}_n \left( \frac{r^2}{C} \right) \cos((l-n)\theta)$$

$$= 2\pi A (\sigma^{AB})^2 \left( \frac{C\alpha}{\alpha + C} \right)^{l+n+1} r^{l-n}\exp \left( -\frac{r^2}{2C} \right) L^{l-n}_n \left( \frac{r^2}{C} \right) \cos((l-n)\theta). \quad (32)$$

Substituting the radial connection parameters back in using Eq. (26) finally gives,

$$C = \frac{(\sigma^{BC})^2}{2\sigma^{AB}\sqrt{(\sigma^{AB})^2 + (\sigma^{BC})^2}}. \quad (33)$$

Consequently, the eigenfunctions and eigenvalues for the learning equation can be expressed in polar coordinates as,

$$\lambda_{l,n} = 2\pi A \left( \frac{C(\sigma^{BC})^2}{C((\sigma^{AB})^2 + (\sigma^{BC})^2 + (\sigma^{BC})^2)} \right)^{l+n+1}$$

$$v_{l,n}(r, \theta) = N_{l,n} r^{l-n} \exp \left( -\frac{r^2}{2C} \right) L^{l-n}_n \left( \frac{r^2}{C} \right) \exp(i(l-n)\theta). \quad (34a)$$

$$v_{l,n}(r, \theta) = N_{l,n} r^{l-n} \exp \left( -\frac{r^2}{2C} \right) L^{l-n}_n \left( \frac{r^2}{C} \right) \exp(i(l-n)\theta). \quad (34b)$$

Eigenfunctions up to order 4 are shown in Fig. 2 in order of decreasing eigenvalue, $\lambda$. The eigenfunction with the largest eigenvalue has order $l + n = 0$, and is radially symmetric with all positive synaptic weights. Consequently, for the simplified learning equation described in Eq. (11), after learning for a sufficiently long period the synaptic weight structure of a layer $C$ postsynaptic neuron will be all excitatory connections with weights at the upper bound.

### 3.2 Radial eigenfunctions of the full learning equation

While covariance between the activity of layer $B$ input neurons primarily drives the structure of the layer $C$ cell, the $k_1$ and $k_2$ terms control the homeostatic equilibrium. MacKay and Miller [1990] empirically showed that the choice of $k_2^{BC}$ can change the structure of the dominant eigenfunction, and hence the resultant receptive field of a layer $C$ cell. As Fig. 2 shows, for the simplified system the leading eigenvalue has all synapses at the upper, or the lower, bound. For a negative value of $k_2^{BC}$, homeostasis can only be reached if some of the synapses are negative. To determine the impact of the learning constant, we find an analytical expression for the eigenfunctions of the full learning equation, Eq. (10), by conducting a perturbation analysis on the simplified learning equation, in Eq. (10).

If the simplified learning equation in Eq. (10) is denoted by $H^0(v_{l,n}(r, \theta))$, from the eigenfunctions derived for the simplified learning equation, we know that,

$$\lambda_{l,n} v_{l,n}(r, \theta) = H^0(v_{l,n}(r, \theta)). \quad (35)$$

If we perturb the simplified learning equation by adding a small $k_2^{BC}$, denote the perturbed system by $H^1(\cdot)$, and the eigenfunctions of the perturbed system by $v_{l,n}^1(r, \theta)$, so that

$$H^1(v_{l,n}^1(r, \theta)) = A \int_0^\infty \int_0^{2\pi} d\tilde{r} d\tilde{\theta} \left( \exp \left( -\frac{\tilde{r}^2 + \tilde{r}^2 - 2\tilde{r}\tilde{r}\cos(\theta - \tilde{\theta})}{2(\sigma^{AB})^2} \right) + k_2^{BC} \right) \exp \left( -\frac{\tilde{r}^2 + \tilde{r}^2}{(\sigma^{BC})^2} \right) w(\tilde{r}, \tilde{\theta}), \quad (36)$$

so that the perturbation on the integral operator is,

$$\delta H^1(v_{l,n}(r, \theta)) = A \int_0^\infty \int_0^{2\pi} d\tilde{r} d\tilde{\theta} k_2^{BC} \exp \left( -\frac{\tilde{r}^2 + \tilde{r}^2}{(\sigma^{BC})^2} \right) w(\tilde{r}, \tilde{\theta}), \quad (37)$$
and we require the new eigenfunctions to be similar to the eigenfunctions of the simplified learning equation, plus a small perturbation, so that the first order corrections to the eigenfunctions and eigenvalues can be defined as,

$$\delta v_{l,m}^1 (r, \theta) = v_{l,m} (r, \theta) + \delta v_{l,m}^1 (r, \theta), \quad \lambda_{l,m}^1 = \lambda_{l,m} v_{l,m} (r, \theta) + \delta \lambda_{l,m}^1. \quad (38)$$

For non-degenerate eigenfunctions, the first order corrections can be determined by (Kato, 1995)

$$\delta v_{l,m}^1 (r, \theta) = \sum_{l+n \neq m+p} \int_{-\infty}^{\infty} dr \int_{0}^{2\pi} d\theta (v_{l,m} (r, \theta))^* H^1 (v_{l,m} (r, \theta)) v_{m,p} (r, \theta) \frac{\lambda_{l,m} - \lambda_{m,p}}{\lambda_{l,m}^1 - \lambda_{m,p}^1}, \quad (39)$$

for non-degenerate eigenfunctions, i.e. \( l+n \neq m+p \). For degenerate eigenfunctions, the denominator of Eq. (39) is equal to zero. However, if \( W_{l,m}^{m,p} = \sum_{l+n \neq m+p} \int_{-\infty}^{\infty} dr \int_{0}^{2\pi} d\theta (v_{l,m} (r, \theta))^* H^1 (v_{l,m} (r, \theta)) v_{m,p} (r, \theta) \) then the first order correction of degenerate eigenfunctions of order \( l+n \), can be found as the eigenfunctions of the \((l+n) \times (l+n)\) matrix of \( W_{l,m}^{m,p} \) coefficients. Given that the degenerate eigenfunctions of order \( l+n \) have angular terms with different frequencies the off-diagonal terms of this matrix

Figure 2: Eigenvalues and eigenfunctions of the simplified learning equation, Eq. \( \text{(11)} \), given in Eq. \( \text{(34)} \) for pairs of indices, \((l, n) \in \lambda_{l,m} \). Eigenvalues are ordered by \( l+n \), with \( l+n = 0 \) giving the largest eigenvalue, and hence \((0, 0)\) being the leading eigenfunction. Eigenfunctions in the same row have the same eigenvalue and are therefore degenerate. Eigenfunctions are given for both the real part of Eq. \( \text{(34b)} \), i.e. the cosine angular component, and for the imaginary part, denoted by \( \Re \) and \( \Im \), respectively. From the figure it can be seen that when \( l = n \) the eigenfunction is radially symmetric, being fully determined by the radial component of the eigenfunction. White indicates a positive region of synaptic weights, while black indicates negative. The leading eigenfunction is all positive. As \( l-n \) increases, the frequency of the angular component increases.
are 0. Hence, the eigenfunctions of this matrix are simply the diagonal terms of $W_{l,n}^{m,p}$. Consequently, it is only necessary to evaluate the diagonal terms. The same logic applies to the non-degenerate eigenfunctions, meaning that it is only necessary to evaluate the diagonal terms, which are denoted by the single index pair, $W_{l,n}$, and can be evaluated as,

$$ W_{l,n} = 2\pi A N_{ln}^2 \int_0^\infty d\tilde{r} \tilde{r}^{2(l-n)} \exp \left( -\frac{\tilde{r}^2}{C} \right) \exp \left( -\frac{\tilde{r}^2 + r^2}{(\sigma BC)^2} \right) \left[ L_{l-n}^{l-n} \left( \frac{r^2}{C} \right) \right]^2, $$

where $C = (\sigma BC)^2 + C$. This integral on the right hand side can be evaluated as (Gradshteyn and Ryzhik, 2007),

$$ \int_0^\infty e^{-bx} x^a L_n^a(x) L_m^a(x) \, dx = \frac{\Gamma(m+n+a+1)(b-1)^{n+m}}{m!n!b^{m+n+a+1}} _2F_1 \left( -m, -n; -m-n-a; \frac{b(b-2)}{(b-1)^2} \right), $$

where $_2F_1()$ is the hypergeometric function, and hence,

$$ W_{l,n} = \pi C^{l+n+1} A N_{ln}^2 \Gamma(l+n+1) \alpha \left( \frac{\alpha}{\alpha-1} \right) ^2 \frac{\Gamma(n+1)\Gamma(l-n+2)}{n!} \frac{2F_1 \left( -n, l-n; \frac{\alpha(\alpha-2)}{(\alpha-1)^2} \right)}{\Gamma(l+n+1)}.$$

Since only the diagonal terms are non-zero, the shape of the perturbed eigenfunctions remains the same as those for the simplified learning equation, given in Eq. (24), but the eigenvalues change according to

$$ \lambda_{l,n}^1 = \lambda_{l,n} + W_{l,n}. $$

Inspection of Eq. (42) reveals that, for positive $k_2$, perturbation of the eigenvalues is positive and monotonically decreasing with $l+n$. Consequently, the order of the eigenvalues remains the same. For negative $k_2$ the perturbation on the eigenvalues is negative and monotonically increasing with eigenfunction order, $l+n$. Since these perturbations are being added to the original eigenvalues, which are positive, the result can be a change in the dominant eigenfunction. This result supports the empirical findings by MacKay and Miller (1990) that showed the emergence of a spatial opponent cell in $C$, where $l+n = 0$ for small values of $k_2$, and bilobed cells with $l+n = 1$, for larger values of $k_2$. 

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Figure 3: Effect upon eigenvalues $\lambda_{l,n}$ resulting from adding perturbation term $k_2$, represented by $W_{l,n}$ in Eq. (43): For positive $k_2$ the perturbation results in $W_{l,n}$ being positive, while for negative $k_2$ the perturbation causes $W_{l,n}$ to be negative.

4 Eigenfunctions in Cartesian coordinates

To characterise learning in terms of the eigenfunctions it is useful to approximate the system in Eq. (5) by its continuous limit, and initially simplify the system by assuming that $k_2 = 0$. In this case we need to solve the eigenvalue problem that integrates expected covariance over the layer, weighted by the probability of connection to the postsynaptic neuron, $i$, in layer $C$. That is, we need to solve the following eigenfunction equation,

$$\lambda \eta_w (x) = A \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} Q \left( f^B_j, f^B_i \right) \exp \left( -\frac{|x|^2}{2(\sigma_{AB}^2)} \right) \exp \left( -\frac{|x'|^2}{2(\sigma_{BC}^2)} \right) w(x') d^2 x'$$

$$= A \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \exp \left( -\frac{|x-x'|^2}{2(\sigma_{AB}^2)} \right) \exp \left( -\frac{|x|^2}{2(\sigma_{BC}^2)} \right) \exp \left( -\frac{|x'|^2}{2(\sigma_{BC}^2)} \right) w(x') d^2 x'$$

$$= A \exp \left( -(x^2 + y^2) \frac{2(\sigma_{AB}^2)^2 + (\sigma_{BC}^2)^2}{2(\sigma_{AB}^2)^2(\sigma_{BC}^2)^2} \right) \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \exp \left( -\frac{2(\sigma_{AB}^2)^2 + (\sigma_{BC}^2)^2}{2(\sigma_{AB}^2)^2(\sigma_{BC}^2)^2} x^2 + \frac{2(\sigma_{BC}^2)^2 y^2}{2(\sigma_{AB}^2)^2(\sigma_{BC}^2)^2} \right) \exp \left( -\frac{2(\sigma_{AB}^2)^2 + (\sigma_{BC}^2)^2}{2(\sigma_{AB}^2)^2(\sigma_{BC}^2)^2} y^2 \right) w(x') d\tilde{x} d\tilde{y},$$

where $w(\cdot)$ is the continuous time approximation to $w$, and neuron $m$ in layer $B$ is denoted by its position vector $x = (x, y)$, $x' = (\tilde{x}, \tilde{y})$, and subscripts have been omitted for readability. The coefficient, $A$, contains the constant terms from the synaptic connection probability (Eq. (1)), such that

$$A = \left( \frac{1}{\pi(\sigma_{AB}^2)^2} \right)^2.$$

Given the separability of the $x$ and $y$ dimensions, in conjunction with the exponential weight function, consider the Hermite polynomial as the form of the eigenfunction, such that the eigenfunctions are given by

$$v_{u,v} \left( \frac{x}{\sqrt{C}}, \frac{y}{\sqrt{C}} \right) = N_{u,v} H_u \left( \frac{x}{\sqrt{C}} \right) H_v \left( \frac{y}{\sqrt{C}} \right) \exp \left( -\frac{x^2 + y^2}{2C} \right),$$

where $N_{u,v}$ is the normalisation constant.
where $u$ and $v$ denote the order of the polynomial for each dimension, giving a two-dimensional eigenfunction of order $u + v$, and $N_{uv}$ is a normalization constant \( \frac{1}{\sqrt{\pi} \sigma_u \sqrt{\pi} \sigma_v} \). $C$ is a parameter that must be determined.

Consequently, when this expression is input into the eigenfunction equation from Eq. (44), the learning equation becomes,

$$
\eta \lambda_{uv} v_{uv} \left( \frac{x}{\sqrt{C}}, \frac{y}{\sqrt{C}} \right) = A \exp \left( - \left( x^2 + y^2 \right) \frac{2(\sigma^{AB})^2 + (\sigma^{BC})^2}{2(\sigma^{AB})^2 (\sigma^{BC})^2} \right) \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \exp \left( - \frac{2(\sigma^{AB})^2 + (\sigma^{BC})^2}{2(\sigma^{AB})^2 (\sigma^{BC})^2} \right) v_{uv} \left( \frac{x}{\sqrt{C}}, \frac{y}{\sqrt{C}} \right) d\tilde{x} d\tilde{y},
$$

(47)

which holds true only when

$$
C = \frac{(\sigma^{BC})^2}{2 \sqrt{1 + (\sigma^{BC})^2}}.
$$

(48)

Note that this result agrees with the result derived for the radial eigenfunctions, Eq. (33), once the scaling of the $r$ by $1/\sigma^{AB}$ is accounted for.

Due to the separability of the dimensions the eigenvalues for $x$ and $y$ can be derived independently. Therefore initially consider the problem in just one dimension.

In deriving the eigenvalues for the complete orthogonal set of Hermite polynomials, we follow the procedure used in [Wim-bauer et al., 1998], and make the ansatz that,

$$
\lambda_{uv} = \Lambda q^u.
$$

(49)

Using the generating function for one dimensional Hermite polynomials,

$$
\exp \left( -t^2 + 2t \frac{x}{\sqrt{C}} \right) = \sum_{l=0}^{\infty} \frac{t^l}{l!} H_l \left( \frac{x}{\sqrt{C}} \right),
$$

(50)

and the orthogonality of Hermite polynomials with respect to a Gaussian weight function, we know that,

$$
\exp \left( -t^2 + 2t \frac{x}{\sqrt{C}} \right) \exp \left( -\frac{x^2}{2C} \right) = \sum_{l=0}^{\infty} \frac{t^l}{l!} H_l \left( \frac{x}{\sqrt{C}} \right) \exp \left( -\frac{x^2}{2C} \right).
$$

(51)

Combining this with Eq. (47), considering a single dimension only, gives,

$$
\sum_{l=0}^{\infty} \lambda_l \frac{t^l}{l!} H_l \left( \frac{x}{\sqrt{C}} \right) \exp \left( -\frac{x^2}{2C} \right) = \sqrt{\Lambda} \exp \left( -x^2 \frac{2(\sigma^{AB})^2 + (\sigma^{BC})^2}{2(\sigma^{AB})^2 (\sigma^{BC})^2} \right) \int_{-\infty}^{\infty} \exp \left( - \frac{(2(\sigma^{AB})^2 + (\sigma^{BC})^2) x^2 + 2(\sigma^{BC})^2 \tilde{x} \tilde{y}}{2(\sigma^{AB})^2 (\sigma^{BC})^2} \right) \sum_{l=0}^{\infty} \frac{t^l}{l!} H_l \left( \frac{\tilde{x}}{\sqrt{C}} \right) \exp \left( -\frac{x^2}{2C} \right) d\tilde{x}
$$

$$
= \sqrt{\Lambda} \exp \left( -x^2 \frac{2(\sigma^{AB})^2 + (\sigma^{BC})^2}{2(\sigma^{AB})^2 (\sigma^{BC})^2} \right) \int_{-\infty}^{\infty} \exp \left( - \frac{(2(\sigma^{AB})^2 + (\sigma^{BC})^2) x^2 + 2(\sigma^{BC})^2 \tilde{x} \tilde{y}}{2(\sigma^{AB})^2 (\sigma^{BC})^2} \right) \exp \left( -t^2 + 2t \frac{\tilde{x}}{\sqrt{C}} \right) \exp \left( -\frac{x^2}{2C} \right) d\tilde{x}
$$

(52)
Evaluating the right hand side,

\[ \text{RHS} = \sqrt{\Lambda} \exp \left( -x^2 \left( \frac{2(\sigma^{AB})^2 + (\sigma^{BC})^2}{2(\sigma^{AB})^2(\sigma^{BC})^2} \right) \right) \]

\[ \int_{-\infty}^{\infty} \exp \left( -\frac{1}{2C} (\sigma^{AB})^2 + (\sigma^{BC})^2 + (\sigma^{AB})^2 - 2(\sigma^{BC})^2 \right) \exp \left( -t^2 + 2t \frac{x}{\sqrt{C}} \right) d\tilde{x} \]

\[ = \sqrt{\Lambda} \exp \left( -t^2 \right) \exp \left( -x^2 \left( \frac{2(\sigma^{AB})^2 + (\sigma^{BC})^2}{2(\sigma^{AB})^2(\sigma^{BC})^2} \right) \right) \]

\[ \int_{-\infty}^{\infty} \exp \left( -\frac{1}{2C(\sigma^{AB})^2(\sigma^{BC})^2} \left( 2C(\sigma^{AB})^2 + C(\sigma^{BC})^2 + (\sigma^{AB})^2 - 2(\sigma^{BC})^2 \right) \frac{\tilde{x}^2}{(2C(\sigma^{AB})^2 + (\sigma^{AB})^2(\sigma^{BC})^2)^2} \right) d\tilde{x} \]

\[ = \sqrt{\Lambda} \exp \left( -t^2 \right) \left( \frac{2\pi C(\sigma^{AB})^2(\sigma^{BC})^2}{2C(\sigma^{AB})^2 + C(\sigma^{BC})^2 + (\sigma^{AB})^2(\sigma^{BC})^2} \right) \exp \left( -x^2 \left( \frac{2(\sigma^{AB})^2 + (\sigma^{BC})^2}{2(\sigma^{AB})^2(\sigma^{BC})^2} \right) \right) \exp \left( \frac{-C(\sigma^{BC})^2t^2}{2C(\sigma^{AB})^2 + (\sigma^{AB})^2(\sigma^{BC})^2} \right) \]

\[ = \Lambda_0 \exp \left( -(qt)^2 + \frac{2q}{\sqrt{C}} xt \right) \exp \left( -x^2 \frac{2C}{2C} \right) \exp \left( -x^2 \frac{2C}{2C} \right). \quad (53) \]

Evaluating the left hand side of Eq. (52) gives

\[ \text{LHS} = \sum_{l=0}^{\infty} \Lambda_0 \frac{(qt)^l}{l!} H_l \left( \frac{x}{\sqrt{C}} \right) \exp \left( -\frac{x^2}{2C} \right) \]

\[ = \Lambda_0 \exp \left( -(qt)^2 + \frac{2q}{\sqrt{C}} xt \right) \exp \left( -x^2 \frac{2C}{2C} \right). \quad (54) \]

Comparing RHS and LHS requires that

\[ q = \frac{C(\sigma^{BC})^2}{2(\sigma^{AB})^2C + (\sigma^{BC})^2C + (\sigma^{AB})^2(\sigma^{BC})^2}; \quad \text{(55)} \]

and

\[ \Lambda_0 = \sqrt{\frac{2\pi C(\sigma^{AB})^2(\sigma^{BC})^2}{2C(\sigma^{AB})^2 + 2\sigma^{BC})^2C + (\sigma^{AB})^2(\sigma^{BC})^2}} \]

\[ = \sqrt{2\pi (\sigma^{AB})^2q} \quad \text{(56)} \]

so that

\[ \lambda_l = \Lambda_0 q^l \]

\[ = \sqrt{2\pi (\sigma^{AB})^2q^{l+\frac{1}{2}}} \quad \text{(57)} \]

For two dimensions, the final eigenfunctions and eigenvalue pairs, for order \( u \) and \( v \), for the \( x \) and \( y \) dimensions respectively, are given by,

\[ \lambda_{u,v} = 2\pi (\sigma^{AB})^2q^{u+v+1} \quad \text{(58a)} \]

\[ v_{u,v} \left( \frac{x}{\sqrt{C}}, \frac{y}{\sqrt{C}} \right) = \frac{1}{\sqrt{2}u!} \sqrt{2}v! H_u \left( \frac{x}{\sqrt{C}} \right) H_v \left( \frac{y}{\sqrt{C}} \right) \exp \left( -x^2 + y^2 \frac{2C}{2C} \right). \quad \text{(58b)} \]
Fig. 4 shows Cartesian eigenfunctions up to the fourth order, which is determined by $u + v$. The eigenfunctions are shown in order of decreasing eigenvalue, so that the eigenfunction with the largest eigenvalue is of order $u + v = 0$. This eigenfunction is radially symmetric, with all positive weights. Consequently, the Cartesian eigenfunctions of the simplified learning equation described in Eq. (44) give the same result as the radial eigenfunctions, shown in Fig. 2, after sustained learning the weight structure of neuron in layer $C$ will have all synapses at the upper bound.

Figure 4: Cartesian eigenfunctions of the simplified learning equation, Eq. (44), defined for index pairs $(u, v)$. Eigenvalues are determined by $u + v$, where $(0, 0)$ has the largest eigenvalue and therefore $v_{0,0} \left( \frac{x}{\sqrt{C}}, \frac{y}{\sqrt{C}} \right)$ is the leading eigenfunction. Eigenfunctions in the same row have the same eigenvalue and are therefore degenerate. Eigenvalues decrease with descending rows. Regions of white indicate positive synaptic weight, while black indicates negative. The leading eigenfunction has all positive synapse weights.
5 Discussion

In this paper we provide a general expression for the complete set of eigenfunctions for the three-layered feed-forward network proposed by Linsker (1986b). Initially the homeostatic parameters were set to zero to simplify the learning equation. This result was then extended via a perturbation analysis to provide the complete set of eigenfunctions for the network with non-zero homeostatic parameters.

Linsker’s (1986b) analysis was integral in revealing how neural learning occurred before the onset of structured environmental input, empirically demonstrating the emergence of spatial opponent cells in the third layer. MacKay and Miller (1990) provided a stability analysis of Linsker’s (1986b) network, noting the first six eigenfunctions, determined via an ansatz based on the results of Tang (1990). MacKay and Miller (1990) showed that the receptive field structure of cells in the third layer could be either spatial opponent cells or bilobed cells, depending upon the value of the homeostatic parameters. Similarly, Walton and Bissest (1992) extended Linsker’s (1986b) network to the auditory system, considering the morphology of the resulting cell based on the homeostatic parameters of the system. In this paper we provide the complete set of eigenvalues for the full learning equation, enabling an exact calculation of the homeostatic parameters required to induce this change, and a quantitative analysis on the parameter space.

Linsker (1986a) showed that augmenting the network with additional layers prompts the development of orientation selective cells. However, given the absence of a complete mathematical framework for the three layered network, there has been limited mathematical analysis provided for the development of orientation selective cells in Linsker’s (1986a) network. Yamauchi (2002) provided an analysis of deeper layers essentially based on an ansatz for the eigenfunctions for the three-layered network. The results in this paper provide the foundation for analysis of larger networks and hence the development of features other than spatial opponent cells. As the system is radially symmetric in connectivity distribution, radial eigenfunctions provide a natural coordinate system that will facilitate future work on more complex network and parameter regimes.

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A Expected number of shared inputs

To examine network dynamics, it is necessary to ascertain the expected number of shared connections between two neurons. The number of shared connections from a presynaptic layer to two neurons in the postsynaptic layer, say $i$ and $j$, depends on the radial distance between them since the synaptic connection density for each is a Gaussian function of distance (see Fig. 1). We assume for simplicity and without loss of generality that $i$ and $j$ differ only in their $x$ coordinate so that $d_{ij} = x_{mi} - x_{mj}$.

Center the Cartesian coordinates describing a neuron’s position in the laminar on one of the postsynaptic neurons, say $i$, so that the other postsynaptic neuron, say $j$, lies on the $x$ axis. From Eq. (1), neuron, $m$, in layer $A$, has a probability of connecting to neuron $i$ in layer $B$ of $p_N(x_{mi}, y_{mi}; \mathbf{0}, \Sigma^A)$ and a probability of connecting to neuron $j$ in layer $B$ of $p_N(x_{mj}, y_{mj}; \mathbf{0}, \Sigma^A) = p_N(x_{mi} - d_{ij}, y_{mj}; \mathbf{0}, \Sigma^A)$. The probability of the presynaptic neuron connecting to both postsynaptic neurons $i$ and $j$ is simply the product of the probability of each individual connection being made. The expected number of common connections can be determined by summing this joint probability over the layer or, in the continuous limit, integrating the joint probability over the layer of presynaptic neurons. If $N_{AB}$ denotes the number of synaptic connections from layer $A$ to a layer $B$ neuron and $N_{BB}(d)$ the number of shared connections between two postsynaptic neurons in layer $B$ separated by a distance of $d$, then in the continuous limit,

$$N_{BB}(d) = (N_{AB})^2 \iint_{xy} p_N(x, y; \mathbf{0}, \Sigma^A) p_N(x - d, y; \mathbf{0}, \Sigma^A) \, dx \, dy,$$

where the sub- and super-scripts on distance parameters have been dropped to aid readability. This can be expanded as

$$N_{BB}(d) = (N_{AB})^2 \iint_{xy} \frac{1}{(\pi(\sigma_{AB})^2)^2} \exp \left( -\frac{x^2 + y^2}{(\sigma_{AB})^2} \right) \exp \left( -\frac{(x-d)^2 + y^2}{(\sigma_{AB})^2} \right) \, dx \, dy$$

$$= \frac{(N_{AB})^2}{(\pi(\sigma_{AB})^2)^2} \iint_{xy} \exp \left( -\frac{2x^2 + 2y^2 + d^2 - 2xd}{(\sigma_{AB})^2} \right) \, dx \, dy$$

$$= \frac{(N_{AB})^2}{(\pi(\sigma_{AB})^2)^2} \iint_{xy} \exp \left( -\frac{2\left(\frac{(x-d)}{\frac{1}{2}}\right)^2 + y^2 + \frac{d^2}{\frac{4}{\pi}}} {(\sigma_{AB})^2} \right) \, dx \, dy.$$  \hspace{1cm} (60)

Introduce $x' = x - d/2$, so that

$$N_{BB}(d) = \exp \left( -\frac{d^2}{2(\sigma_{AB})^2} \right) \frac{(N_{AB})^2}{(\pi(\sigma_{AB})^2)^2} \iint_{xy} \exp \left( -\frac{2\left(x^2 + y^2\right)}{(\sigma_{AB})^2} \right) \, dx \, dy$$

$$= \exp \left( -\frac{d^2}{2(\sigma_{AB})^2} \right) \frac{(N_{AB})^2}{(\pi(\sigma_{AB})^2)^2} \sqrt{\frac{\pi(\sigma_{AB})^2}{2}} \sqrt{\frac{\pi(\sigma_{AB})^2}{2}}$$

$$= \frac{(N_{AB})^2}{2\pi(\sigma_{AB})^2} \exp \left( -\frac{d^2}{2(\sigma_{AB})^2} \right),$$  \hspace{1cm} (61)

using the identity $\int_{-\infty}^{\infty} \exp(-ax^2) = \sqrt{\pi/a}$.

This result demonstrates that the number of shared connections between two neurons with Gaussian synaptic connection densities is itself a Gaussian function of the radial distance between the neurons with a variance that is half the value of the synaptic connection density radius. This means that a postsynaptic neuron is expected to have the most common connections with itself, for which $d = 0$. Additionally, for small variance or connection radius, a postsynaptic neuron will share many connections with proximate neighbors, with the number of shared connections falling off quickly with distance. Since the expected number of synaptic inputs is constant, a large connection radius implies that the neuron will have shared connections with neurons comparatively distal to it, since nearby neurons will have comparatively fewer shared connections.
B Covariance of neural activity in layer B

Expressions for the covariance of layer B neurons are derived here. Sample covariance between two postsynaptic neuron rates in layer B, say $f_{i}^{B}$ and $f_{j}^{B}$, for neurons $i$ and $j$, respectively, is calculated as

$$
cov(f_{i}^{B}, f_{j}^{B}) = E[f_{i}^{B} f_{j}^{B}] - E[f_{i}^{B}] E[f_{j}^{B}].$$

(62)

For unitary weights from layer A to layer B, Eq. (4a), can be employed to give

$$
cov(f_{i}^{B}, f_{j}^{B}) = E \left[ (R_{i}^{B} + R_{A}^{B} \sum_{m} f_{m}^{A}) (R_{j}^{B} + R_{b}^{B} \sum_{n} f_{n}) - E[R_{i}^{B} + R_{A}^{B} \sum_{m} f_{m}^{A}] E[R_{j}^{B} + R_{b}^{B} \sum_{n} f_{n}] \right]
$$

$$
= (R_{i}^{B})^2 + 2R_{i}^{B} R_{A}^{B} \sum_{m} f_{m}^{A} + (R_{j}^{B})^2 \sum_{m} f_{m}^{A} - \left( (R_{i}^{B})^2 + 2R_{i}^{B} R_{b}^{B} \sum_{n} f_{n} + (N_{A}^{B} R_{A}^{B} R_{b}^{B})^2 \right)
$$

$$
= (R_{A}^{B})^2 \left( E[\sum_{m} f_{m}^{A} f_{m}^{A}] \right) - (N_{A}^{B})^2. \tag{63}
$$

Layer A neurons are uncorrelated so that the only non-zero contribution to this sum occurs when a layer A neuron has a synaptic connection to each of the layer B neurons under consideration. In this case the input rates are fully correlated, so that the contribution to covariance is proportional to the layer A firing rate.

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