Emergent organization of receptive fields in networks of excitatory and inhibitory neurons

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Abstract: Local patterns of excitation and inhibition that can generate neural waves are studied as a computational mechanism underlying the organization of neuronal tunings. Sparse coding algorithms based on networks of excitatory and inhibitory neurons are proposed that exhibit topographic maps as the receptive fields are adapted to input stimuli. Motivated by a leaky integrate-and-fire model of neural waves, we propose an activation model that is more typical of artificial neural networks. Computational experiments with the activation model using both natural images and natural language text are presented. In the case of images, familiar “pinwheel” patterns of oriented edge detectors emerge; in the case of text, the resulting topographic maps exhibit a 2-dimensional representation of granular word semantics. Experiments with a synthetic model of somatosensory input are used to investigate how the network dynamics may affect plasticity of neuronal maps under changes to the inputs.

1. Introduction

Recordings of neurons in retina, visual cortex, and other brain regions reveal spontaneous activity that resembles propagating waves (Ackman et al., 2012; Benucci et al., 2007; Han et al., 2008; Santos et al., 2014; Shadlen and Newsome, 1998). The waves can appear in the absence of outside stimuli (Gribizis et al., 2019), but can be disrupted in the presence of input (Churchland et al., 2010; Sato et al., 2012), and affect sensitivity of perception (Chemla et al., 2019; Davis et al., 2020; Muller et al., 2014). While the mechanisms and roles of neural waves are not fully understood, computational models have shown that spontaneous traveling waves can result from local patterns of inhibitory and excitatory recurrent connections, and that small changes to the relative balance of inhibition and excitation can have large effects on cortical activity (Bressloff, 2000; Brunel and Wang, 2003; Ermentrout and Kleinfeld, 2001; Gong and Van Leeuwen, 2009; Isaacson and Scanziani, 2011; Keane and Gong, 2015; Osan and Ermentrout, 2001; Rubin et al., 2017; Senk et al., 2020).

In this paper, local patterns of excitation and inhibition that can generate neural waves are studied as a computational mechanism underlying the organization of neuronal receptive fields. In early visual cortex (V1) in certain mammals, for example, the receptive fields are known to be edge detectors that are arranged topographically, with neighboring neurons coding for edges at similar
scales and orientations (Ackman and Crair, 2014; Bonhoeffer and Grinvald, 1991; Bonhoeffer and Grinvaldi, 1993; Crair et al., 1997). In the leaky integrate-and-fire (LIF) model proposed by Keane and Gong (2015), neurons are arranged in a regular grid or randomly throughout a 2-dimensional sheet. Each neuron receives input from excitatory neurons within a local neighborhood, and from inhibitory neurons within another, typically larger neighborhood. The relative proportions of excitatory to inhibitory neurons and the sizes of the neighborhoods are design parameters to the model and influence the properties of the emergent wave patterns. While previous investigations are focused on the wave characteristics as a function of network parameters (Brunel, 2000; Keane and Gong, 2015), here we study the emergent organization of the receptive fields when the neurons receive input stimuli.

We propose an abstraction of the leaky integrate-and-fire model as an activation model, where neurons do not have discrete firing events but rather are associated with a continuous level of activation, as is typical of artificial neural network models. The LIF and activation models use a similar local geometry of excitatory and inhibitory connections. The wave dynamics emerge in the activation model through an iterative thresholding operator, which solves a constrained optimization problem. Under the activation model, the wave patterns saturate and converge, while under the LIF model the waves are dynamic and typically do not converge. Mathematically, the activation model is viewed as a regularization scheme based on a graph Laplacian having both negative and positive weights. When the local geometry is repeated regularly throughout a 2-dimensional grid, the application of the Laplacian to a vector of inputs is equivalent to a convolution operator. The scale of the wave fluctuations, in the absence of input stimuli, is seen in the eigenspectrum of the Laplacian. The regularization can also be viewed as a reaction-diffusion system (Gilding and Kersner, 2004; Turing, 1952; Wooley et al., 2017), but where the reaction term appears as part of the diffusion operator, rather than as a separate potential.

We derive sparse coding algorithms based on this activation model and find emergent patterns in the receptive fields through a series of computational experiments, using both natural images and natural text. In the case of images, the resulting topographic maps resemble “pinwheel” patterns measured through neural recordings of the cat visual cortex (Bonhoeffer and Grinvald, 1991; Bonhoeffer and Grinvaldi, 1993; Crair et al., 1997; Issa et al., 2000). We also show how learning can take place in the LIF model, and report results with natural images in the supplement. We apply the same sparse coding algorithms used for images to distributed word representations obtained by training a language model on a large corpus of text. The resulting topographic maps exhibit a 2-dimensional representation of granular word semantics; the semantic units are thus analogous to visual edge detectors. We show through examples how the topographic map reveals elements of compositional semantics.

In a third computational experiment, we develop a model of somatosensory input. Specifically, we experiment with a simplified model of a hand with five digits, where neurons are tuned to input stimuli in an unsupervised manner. When one of the “fingers” stops receiving input stimulus, the resulting region of the topographic map gradually fails to be activated. Notably, when the same recurrent geometry is used in an artificial neural network in a supervised fashion, the topographic map is not well formed. These findings can be compared against actual measurements of neural maps for the hand in sensory cortex (Huber et al., 2020; Makin et al., 2015; Wesselink et al., 2020).
The main contributions of this work are the proposed activation model, its formulation as a convex optimization problem, associated algorithms for sparse coding, and experiments that demonstrate how this framework leads to emergent organization of receptive fields into topographic maps. The results presented here suggest that our framework for artificial neural networks has the potential to be used as a computational tool for better understanding the role of balanced excitation and inhibition in neuronal organization and plasticity, and as a biologically inspired building block for more complex neural network models. This approach is in line with a growing body of work on biologically constrained computational models for machine learning and neuroscience (Akrout et al., 2019; Bellec et al., 2019; Frenkel et al., 2021; Launay et al., 2020; Lillicrap et al., 2016; Nøkland, 2016; Song et al., 2021; Tanaka et al., 2019; Zhou et al., 2021).

2. Motivation and previous work

Our starting point is the model of Keane and Gong (2015), based on an $N \times N$ network of excitatory and inhibitory neurons whose dynamics are governed by a conductance-based integrate-and-fire model. The voltage $V_{ij}(t)$ of the neuron at position $(i,j)$ in the grid evolves according to the differential equation

$$C \frac{d}{dt} V_{ij}(t) = -g_L(V_{ij}(t) - V_L) - g^E_{ij}(t)(V_{ij}(t) - V_E) - g^I_{ij}(t)(V_{ij}(t) - V_I),$$

(2.1)

where $g_L$ is the “leak” conductance due to membrane resistance, and $g^E$ and $g^I$ are conductances determined by the neighboring excitatory and inhibitory neurons. Specifically, the excitatory and inhibitory conductances, $g^E_{ij}(t)$ and $g^I_{ij}(t)$, introduce a dependence on the firings of neighboring neurons according to

$$g^E_{ij}(t) = F^E + \sum_{(i',j') \in E(i,j)} W_E \exp(-d^2(i,j;i',j')/2\sigma^2_E) \sum_l G^E(t - T^E_{i',j'})$$

(2.2)

$$g^I_{ij}(t) = F^I + \sum_{(i',j') \in I(i,j)} W_I \sum_l G^I(t - T^I_{i',j'}).$$

Here $E(i,j)$ is the set of excitatory neurons connected to the neuron at $(i,j)$ and $I(i,j)$ is the set of inhibitory neurons connected to this neuron; $T^E_{i,j}$ denotes the $l$-th firing time of the neuron. Typical default parameters are $C = 1 \mu F$ for the capacitance, $g_L = 50 \mu S$ for the leak conductance, and $V_L = -70 mV$, $V_E = 0 mV$, and $V_I = -80 mV$ as the reversal potentials for the leak, excitatory, and inhibitory voltages, respectively.

If the voltage $V_{ij}(t)$ reaches the threshold potential $V_T = -55 mV$, the neuron fires and its voltage is reset to the potential $V_R = -70 mV$ for a refractory period of $\tau_{ref} = 5 ms$, in the default settings adopted in Keane and Gong (2015). We fix $F^I = 2 \mu S$ and let $F^E$ vary throughout learning based on the similarity between the neuron’s feedforward weights and the input stimulus, as described below. The kernels $G^E(t)$ and $G^I(t)$ describe the postsynaptic conductance of a neuron and are normalized to integrate to one.
While the focus of Keane and Gong (2015) is on understanding the emergence of propagating waves, here our goal is to study how the receptive fields of excitatory neurons might adapt to input stimuli. In the presence of an external stimulus \( X(t) \) the conductance of the excitatory term changes to \( F^E + \Phi^T X(t) \) where \( \Phi_{ij} \) denotes a vector of feedforward weights for the neuron at position \((i, j)\), if it is excitatory, acting as a linear filter. The system of differential equations (2.1) defines the neural dynamics of the network; it is not directly tied to an objective function or loss for learning the filters \( \Phi_{ij} \) from data. An example of the local geometry of excitation and inhibition we consider is given in Figure 1.

3. An activation model based on wave dynamics

The Euler dynamics of the differential equation (2.1) is given by the finite difference equations

\[
V_{ij}(t + dt) = V_{ij}(t) - \frac{dt}{C} \left( g_L(V_{ij}(t) - V_L) + g^E_{ij}(t)(V_{ij}(t) - V_E) + g^I_{ij}(t) (V_{ij}(t) - V_I) \right). \tag{3.1}
\]

As the voltage approaches the firing threshold, the potential differences satisfy \( V_{ij}(t) - V_E < 0 \) with \( V_{ij}(t) - V_I > 0 \) and \( V_{ij}(t) - V_L > 0 \). Thus, the excitatory term acts to increase the voltage, while the inhibitory and leak terms act to decrease the voltage. Our activation model abstracts the potential \( V_{ij} \) and firing times \( T^l_{ij} \) into a single scalar activation level \( a_{ij} \). An analogue of the Euler step (3.1) is then the iterative update

\[
a_{ij} \leftarrow \text{Soft}_\lambda \left( a_{ij} + \eta \left( \Phi^T_{ij} X - d_{ij} a_{ij} + \sum_{(i',j') \in E(i,j)} W^E_{ij;i',j'} a_{i'j'} - \sum_{(i',j') \in I(i,j)} W^I_{ij;i',j'} \right) \right) \tag{3.2}
\]

for a small step size \( \eta > 0 \). Just as in the LIF model, \( E(i,j) \) is the set of neurons within the excitatory radius \( d_E \) and \( I(i,j) \) is the set of neurons within the inhibitory radius \( d_I \); The constant \( W_I \) controls the strength of the inhibition, and the excitatory weights are given by

\[
W^E_{ij;i',j'} = W_E \exp \left( -(d^2(i, j; i', j'))/2\sigma^2_E \right).
\]
The constant $d_{ij} > 0$ incorporates the analogue of potential “leak,” and is specified below. In place of a firing threshold, we incorporate the soft-thresholding operator

$$\text{Soft}_\lambda(u) = \text{sign}(u) \max(|u| - \lambda, 0) = u \left(1 - \frac{\lambda}{|u|}\right)_+,$$

which can be thought of as a two-sided rectification.

It can now be seen that (3.2) is the “iterative soft thresholding algorithm” (ISTA) update for the optimization

$$\min_a \left\{ \frac{1}{2} \|\Phi^T X - a\|^2 + \frac{1}{2} a^T \Delta a + \lambda \|a\|_1 \right\}$$

(3.3)

where the matrix $\Delta$ is a Laplacian matrix associated with the excitatory and inhibitory weights. In vectorized form, the Laplacian is

$$\Delta_{i,j';j'} = \begin{cases} d_{i,j} & \text{if } (i, j) = (i', j') \\ -W_{i,j;i',j'} & \text{otherwise} \end{cases}$$

where the graph weights are defined by

$$W_{i,j;i',j'} \equiv W_{ij;i',j'}^E \mathbb{1}((i', j') \in E(i, j)) - W_I \mathbb{1}((i', j') \in I(i, j)).$$

The matrix $\Delta$ is positive semi-definite if it is diagonally dominant; that is, if

$$d_{i,j} \geq \sum_{(i', j') \in E(i, j)} W_{ij;i',j'}^E + \sum_{(i', j') \in I(i, j)} W_I.$$

(3.4)

Assuming condition (3.4), the optimization (3.3) is convex, and the set of minimizers is non-empty and convex. Moreover, for sufficiently small step size $\eta$ the iterative algorithm (3.2) will converge to a minimizer (Beck and Teboulle, 2008).

**3.1. Properties of the optimization**

The convex optimization (3.3) has three terms which are in tension with one another, each of which contributes different properties to the solutions.

**Response to the stimulus.** The squared error term $\frac{1}{2} \|\Phi^T X - a\|^2$ encourages the activations to respond to the stimulus. For an excitatory neuron at grid position $(i, j)$, the inner product $\Phi_{ij}^T X$ is large (in absolute value) if the neuron’s feedforward weights $\Phi_{ij}$, acting as a linear filter, matches the stimulus $X$. In the absence of any other terms in the optimization, the closed-form solution is

$$a_{ij} = \Phi_{ij}^T X.$$ 

**Sparsity.** The $\ell_1$ penalty $\lambda \|a\|_1$ encourages sparse solutions. In the absence of the Laplacian term, the optimization

$$\min_a \left\{ \frac{1}{2} \|\Phi^T X - a\|^2 + \lambda \|a\|_1 \right\}$$
also has a closed-form solution, given by

\[ a_{ij} = \text{Soft}_\lambda \left( \Phi_{ij}^T X \right). \]

In this way, if the neuron’s tuning only weakly matches the stimulus, with \( |\Phi_{ij}^T X| \leq \lambda \) then the activation would be zero, \( a_{ij} = 0 \), which corresponds to the voltage being below threshold in the firing model.

**Wave patterns.** The Laplacian regularization \( \frac{1}{2} a^T \Delta a \) encourages wave patterns in the solutions. This can be seen in the right two plots of Figure 1, which correspond to two eigenvectors of the Laplacian. Under condition (3.4), we have that \( a^T \Delta a \geq 0 \). The Laplacian regularization has three components, corresponding to excitation, inhibition, and “leak.” The excitatory weights encourage neighboring neurons to “fire together,” in the sense that neighboring neurons will tend to have similar activations. The inhibitory terms discourage the activation from spreading, playing the role of a reaction term in a reaction-diffusion system. And the diagonal term corresponds to voltage leak; setting the diagonal sufficiently large ensures that the optimization is well defined.

The optimization incorporates all three terms——stimulus, sparsity, and regularization—and the iterative soft thresholding algorithm (3.2) can be more succinctly written as

\[ a \leftarrow \text{Soft}_\lambda \left( a + \eta \left( \Phi_{ij}^T X - \Delta a \right) \right). \]

Our derivation of the activation model comes from the Euler method for integrating the LIF differential equations. The optimization (3.3) does not have an intrinsic time scale; rather, a time scale is implied by the iterative soft thresholding algorithm (3.2), and corresponds to the time scale of the Euler method. However, the soft-thresholding algorithm converges (under assumption (3.4)), while the Euler iterates need not converge. This is due to the refractory period after a neuron fires, which can lead to propagation of waves.

**Reconstruction error.** The optimization (3.3) is not directly targeting the error \( \| X - \Phi a \|^2 \) for reconstructing the stimulus from the activations. Under an \( \ell_1 \) sparsity penalty, the standard sparse coding procedure of Olshausen and Field (1996) is based on the lasso optimization \( \min_a \frac{1}{2} \| X - \Phi a \|^2 + \lambda \| a \|_1 \) with associated ISTA iterates

\[ a_{ij} \leftarrow \text{Soft}_\lambda \left( a_{ij} + \eta \left( \Phi_{ij}^T X - a_{ij} - \sum_{i',j' \neq i,j} a_{i'j'} \Phi_{ij} \Phi_{i'j'} \right) \right), \tag{3.5} \]

assuming the feedforward weights \( \Phi \) are normalized so that \( \| \Phi_{ij} \| = 1 \). The last term acts as a lateral inhibition effect (Rozell et al., 2008), but is non-local, coupling together the filters for neurons that are far apart. In a similar manner, Gregor and LeCun (2010) augment the reconstruction error with a structured lateral inhibition term. The approach of Hyvärinen and Hoyer (2001) learns topographic maps using a two-layer model of complex cells, based on reconstruction error through a likelihood function. Comparing (3.1) and (3.5), it is seen that our proposed activation model replaces lateral inhibition based on feedforward weights with lateral excitation and inhibition based on fixed, local connectivities.
3.2. Tuning the feedforward weights and receptive fields

When iteratively tuning the weights $\Phi$ as input stimuli are received, we update the weights using the gradient of the squared error objective:

$$\Phi_{ij} \leftarrow \Phi_{ij} + \gamma \sum_{k \in B} a_{ij}^{(k)} (X^{(k)} - \Phi a^{(k)})$$

(3.6)

where $B$ is a mini-batch of randomly selected inputs. Here $\gamma > 0$ is a small step size, and $a_{ij}^{(k)}$ is the activation for the excitatory neuron at location $(i, j)$ in the grid in response to the $k$th input in the mini-batch.

In each epoch of training, the activations over the mini-batch are iterated until convergence, and then a gradient step is made using the above update. A similar update can be used under the LIF model, where the Euler steps are made for a fixed number of iterations and the firing counts are used in the gradient step for the feedforward weights. Since neither the activations nor the firings are selected to minimize reconstruction error, this algorithm is not direct stochastic gradient descent; but we observe that it converges empirically.

We note that this update to the feedforward weights fields is non-local in the sense that the change in weight at neuron $(i, j)$ depends on the global residual $X^{(k)} - \Phi a^{(k)}$ involving all of the other activations. When the activations are very sparse, it is expected that this is well approximated by

$$\sum_{k \in B} a_{ij}^{(k)} (X^{(k)} - \Phi a^{(k)}) \approx \sum_{k \in B} a_{ij}^{(k)} X^{(k)} - \Phi_{ij} \sum_{k \in B} a_{ij}^{(k)} a_{ij}^{(k)}.$$  

(3.7)

This is the local update rule that is proposed by Zylberberg et al. (2011), and is a form of Oja’s rule for Hebbian learning (Oja, 1982). A justification of this approximation is that if each neuron fires with probability $p \ll 1$, then $\frac{1}{|B|} \sum_{k \in B} a_{ij}^{(k)} = O(p)$ while $\frac{1}{|B|} \sum_{k \in B} a_{ij}^{(k)} a_{ij}^{(k)} = O(p^2)$ for neurons at locations $(i, j)$ and $(i', j')$ that fire roughly independently. However, this local update rule is not effective when the neurons are organized topographically, since neighboring neurons are strongly correlated.

The receptive field of a neuron depends on the neuron’s feedforward weights as well as the responses of other neurons through lateral connections, both excitatory and inhibitory. Conceptually, the receptive field for a neuron at position $(i, j)$ in the grid can be thought of as the derivative $\frac{\partial a_{ij}(X)}{\partial X}$. To compute the receptive field we input delta functions having a spike in a given pixel position, and zeros elsewhere, and then standardize the stimulus to have mean zero and variance one. The receptive field for that pixel position is then the response of the neuron to that stimulus (Olshausen and Field, 1996). The resulting receptive fields are very similar to the feedforward weights, but sharpened and more selective, due to the sparsity imposed in the activations.

As seen in the following experiments, the receptive fields under this model naturally exhibit topographic maps as the weights are tuned to input stimuli. In contrast to other machine learning frameworks for sparse coding (Bell and Sejnowski, 1997; Olshausen and Field, 1996; Rozell et al.,
4. Organization of tunings to natural images

In this section we give examples of the topographic map that results from running the algorithm described above. Our setup consists of two coupled $40 \times 40$ grids of neurons; one grid is excitatory with each neuron receiving an input stimulus, and one grid is inhibitory. A neuron at a given grid point is connected to all excitatory neurons within a radius $d_E = 3$ and to all inhibitory neurons within a radius $d_I = 5$; the relative strengths of the excitatory and inhibitory neurons were determined by the parameters $W_E = 30$ and $W_I = 5$ in equation (3.2). The receptive fields of the excitatory neurons are tuned using stimuli that are random $16 \times 16$ patches from natural images; we use the original images from Olshausen and Field (1996) which are publicly available at http://www.rctn.org/bruno/sparsenet. The algorithm was run for 10,000 epochs with mini-batch size 128, where image patches are sampled randomly from the set of ten natural images. The patches are standardized to have unit standard deviation for each pixel. The activation threshold $\lambda$ is set to achieve a target sparsity of 20\%, meaning that 20\% of the neurons are active, on average, after the iterative soft-thresholding algorithm has converged. The diagonal terms, corresponding to
Figure 3. Tunings of a grid of 40 × 40 excitatory neurons from stimuli that are embedding vectors of words, sampled from the unigram distribution on a large corpus of text (Google 1-grams). Upper left: each neuron is mapped to a color by taking the top 3-principal components of the receptive fields as an RGB value. Lower left: The activations are high dimensional sparse vectors, arranged in a 2-dimensional sheet; a standard 2-dimensional t-SNE visualization distorts the embedding distances. Right: Neural activations for selected groups of words.

Voltage leak in the LIF model, are set to satisfy

\[ d_{i,j} = \sum_{(i',j') \in E(i,j)} W_{ij;i'j'}^E + \sum_{(i',j') \in I(i,j)} W_I \]  

so that the optimization is convex; the algorithm (3.2) converges in under 15 steps.

Figure 2 shows examples of the receptive fields that result. While the algorithm is not directly minimizing the reconstruction error, the error decreases and stabilizes. The tunings are organized into regions resembling “pinwheel” patterns with respect to the orientations of the edge detectors that have been measured experimentally (Crair et al., 1997). Figure 2 shows four image patches in a “saccade” along the edge of a piece of driftwood, and the neural responses.

5. Organization of tunings to natural language text

In this section, we describe the results of applying the same algorithm and network configuration to natural language text. For our experiments with images, the stimulus is a random image patch from natural images. In this new setting, the stimulus is a vector representation of a word sampled from the unigram distribution of a large corpus of natural language text. We consider two types
of vector representations, which are closely related. In the first, the vector is the 100-dimensional word embedding vector obtained by running the GloVe algorithm (Pennington et al., 2014). We limit the vocabulary to the top 55,529 words in frequency, which can be expected to reduce but not eliminate the well known societal biases that are present in large-scale word embeddings Bolukbasi et al. (2016). Sparse coding has previously been applied to word embeddings (Faruqui et al., 2015; Templeton, 2021; Yogatama et al., 2015); in this work we are focused on the topographic map of semantic meaning that emerges from the organization of the receptive fields. We also ran experiments where the vector is the first layer in a LSTM recurrent neural network trained to predict the sequence of words in a large corpus of text (Hochreiter and Schmidhuber, 1997; Ott et al., 2019); the results are similar and discussed further in the supplement. The structure of the excitatory and inhibitory network of neurons responding to these stimuli is the same as used above—a grid of 40 × 40 excitatory neurons is paired with a grid of 40 × 40 inhibitory neurons, with a neuron at a given grid point being connected to all excitatory neurons within a radius \( d_E = 3 \) and to all inhibitory neurons with a radius \( d_I = 5 \). The algorithm is run for 50,000 gradient steps.

Figure 3 illustrates the tunings in the grid of 40 × 40 excitatory neurons from stimuli as described above using the GloVe embeddings; the organization of receptive fields when the stimuli are embedding vectors from training an LSTM language model is qualitatively similar. To visualize the map, principal components analysis is carried out for the collection of 1,600 receptive fields. Each neuron is mapped to a color by taking the top 3-principal components as an RGB value. The map shows local regions where the color gradient changes slowly, implying a gradual change in the semantic meaning represented by the underlying neurons. The groups of similarly colored neurons correspond to edge detectors with similar spatial orientations and scales in the image model.

Figure 3 also illustrates how the organization of the neuronal tunings encodes these semantic differences. The activations for sets of related words are shown in columns. In the first column, for example, “algorithms” are semantically “equations for computers.” Several other semantic relations can be seen to be at play by inspecting the different groups of words and their activations. Such relations can be discovered by searching for words that have large components in specific semantic components. While direct neural recordings are not available for language regions of the human brain, fMRI studies suggest a distributed semantic map (Huth et al., 2016); in future work this might be compared with the emergent structure in our models.

6. A model of sensory perception

In our last computational experiment, we investigate a simple model of somatosensory perception in a toy computational model of a hand with five fingers. According to the model, in the default state the nerves in each of the five “fingers” generate random Gaussian outputs; when a finger is touched, uniformly distributed noise is added to the signal. The nerves across the fingers are rearranged according to a fixed, random permutation, resulting in a 256-dimensional signal received at the excitatory neurons. Seven possible input types are generated; either a single digit 1–5 is “touched” with equal probability, or digits 1 and 2 or 1 and 3 are simultaneously touched. Figure 4 shows an example where digit 3 is touched.
FIG 4. The nerves in each of the five “fingers” generate random Gaussian outputs in the baseline state; when a finger is touched, uniform noise is added to the signal. The nerves across the fingers are rearranged according to a fixed, random permutation, resulting in a 256-dimensional signal received at each excitatory neuron. Center: A signal generated when digit 3 is touched; Right: the stimulus received at the excitatory neurons.

FIG 5. Neuronal tunings to synthetic touch data. Upper left: Average of all activations, showing localized receptive fields for each digit. Right plots: Average activation (top row), activation for random stimulus (middle row) and standard deviation of activations (bottom row), when a stimulus is a touch to digit 1, 2, or 3, or to digits 1 and 3 simultaneously (last column). Lower left: Map after digit 3 is no longer touched, but the other digits are, showing diminished receptive field for that digit.

Similar to the image and text experiments, each excitatory neuron in a $40 \times 40$ grid receives these 256-dimensional stimuli. In this case, the network parameters are such that excitatory neurons are connected to each neuron within a radius of $d_E = 10$, and inhibitory neurons are connected to each neuron within a radius of $d_I = 13$. The resulting receptive fields are shown in Figure 5. The neurons that respond to the touch of each of the five digits are clearly localized in a coherent region, each being of roughly equal size. Note that this is an unsupervised learning algorithm. However, given the neuronal map, a supervised algorithm would learn to name the finger touches with just a handful of training examples. We find that when the same recurrent geometry is used in an artificial neural network in a purely supervised fashion, to predict which digit is touched, the topographic map is not well formed.

Next, the weights for the 1,600 neurons continue to be tuned, but we remove inputs corresponding to touches of digit 3 individually and digits 1 and 3 together, as if digit 3 were to be disabled.
As seen in Figure 5, the receptive fields for digits 1, 2, 4, and 5 remain stable. However, the size of the region that codes for signals from digit 3 begins to shrink, in a type of “use it or lose it” phenomenon, as those neurons are no longer activated. Notably, for this setting of network parameters the other digits do not recruit the neurons previously coding for digit 3. In this way, such activation models might serve as a computational tool to complement studies on reorganization of neural maps in the primary somatosensory cortex (Makin et al., 2015; Wesselink et al., 2020).

7. Discussion

This paper studied how the local patterns of excitation and inhibition that can generate spontaneous neural waves may also provide a computational mechanism for the emergent organization of receptive fields. Starting from a leaky integrate-and-fire model for modeling neural waves, we developed a new model where the firing of neurons is abstracted into a continuous level of activation. We formulated the neural dynamics of this model as an iterative procedure for solving a convex optimization, coupled with an algorithm for carrying out stochastic gradient descent over the feedforward weights. We found that the emergent receptive fields resemble known pinwheel patterns in V1 when trained on natural images, exhibit a type of compositional semantics when trained on word embeddings for large language models, and form a topographic map of the hand when trained on a simplified model of somatosensory input. For the image and text experiments, the entire training algorithm takes roughly 10 hours on a standard CPU machine. Since the Laplacian is based on a regular graph and can be expressed as a convolution, the computation could be accelerated with GPUs.

The neural activations in our model are driven by the local, lateral excitations and inhibitions, while the gradient update uses reconstruction error. We have observed empirically that the overall algorithm iteratively decreases the error. It is important to develop a mathematical analysis of this phenomenon in future work. Recent work has shown how convergence can be obtained in other contexts for two-layer networks that do not directly minimize a loss function (Song et al., 2021). Another interesting direction to explore is “pretraining” with internal stimuli from retinal waves, to shape the V1 receptive fields before they are tuned on natural, external stimuli.

While related work in machine learning has considered models of complex cells and structured inhibition (Gregor and LeCun, 2010; Hyvärinen and Hoyer, 2001) in the context of sparse coding of natural images, the framework developed here can be seen as more basic from a biological perspective. The sensory model explored here is limited; it would be of interest to build on these results with more realistic models. For text data, our experiments could in future work be compared with clustering-based models derived from fMRI studies of language perception, which have found that semantic representation of language is widely distributed (Huth et al., 2016). Finally, we note that while algorithms like t-SNE are commonly used to visualize vector representations of objects (van der Maaten and Hinton, 2008), the algorithms developed here provide an alternative way of interpreting and visualizing any such representation, separate from any motivation from neuroscience.
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References

Ackman, J. B., Burbridge, T. J., and Crair, M. C. (2012). Retinal waves coordinate patterned activity throughout the developing visual system. *Nature*, 490(7419):219–225.

Ackman, J. B. and Crair, M. C. (2014). Role of emergent neural activity in visual map development. *Current opinion in neurobiology*, 24:166–175.

Akrout, M., Wilson, C., Humphreys, P., Lillicrap, T., and Tweed, D. B. (2019). Deep learning without weight transport. In Wallach, H., Larochelle, H., Beygelzimer, A., d’Alché Buc, F., Fox, E., and Garnett, R., editors, *Advances in Neural Information Processing Systems*, volume 32. Curran Associates, Inc.

Beck, A. and Teboulle, M. (2008). A fast iterative shrinkage-thresholding algorithm for linear inverse problems. *SIAM J. Imaging Sciences*, 2(1):183–202.

Bell, A. J. and Sejnowski, T. J. (1997). The “independent components” of natural scenes are edge filters. *Vision Research*, 37(23):3327–3338.

Bellec, G., Scherr, F., Hajek, E., Salaj, D., Legenstein, R., and Maass, W. (2019). Biologically inspired alternatives to backpropagation through time for learning in recurrent neural nets.

Benucci, A., Frazor, R. A., and Carandini, M. (2007). Standing waves and traveling waves distinguish two circuits in visual cortex. *Neuron*, 55(1):103–117.

Bolukbasi, T., Chang, K.-W., Zou, J., Saligrama, V., and Kalai, A. (2016). Man is to computer programmer as woman is to homemaker? Debiasing word embeddings. In *Advances in Neural Information Processing Systems*, pages 4349–4357.

Bonhoeffer, T. and Grinvald, A. (1991). Iso-orientation domains in cat visual cortex are arranged in pinwheel-like patterns. *Nature*, 353(6343):429–431.

Bonhoeffer, T. and Grinvaldi, A. (1993). The layout of iso-orientation domains in area 18 of cat visual cortex: Optical imaging reveals a pinwheel-like organization. *The Journal of Neuroscience*, 13(10):4157–4180.

Bressloff, P. C. (2000). Traveling waves and pulses in a one-dimensional network of excitable integrate-and-fire neurons. *Journal of Mathematical Biology*, 40(2):169–198.

Brunel, N. (2000). Dynamics of sparsely connected networks of excitatory and inhibitory spiking neurons. *Journal of computational neuroscience*, 8(3):183–208.
Brunel, N. and Wang, X.-J. (2003). What determines the frequency of fast network oscillations with irregular neural discharges? I. Synaptic dynamics and excitation-inhibition balance. *Journal of neurophysiology*, 90(1):415–430.

Chemla, S., Reynaud, A., Di Volo, M., Zerlaut, Y., Perrinet, L., Destexhe, A., and Chavane, F. (2019). Suppressive traveling waves shape representations of illusory motion in primary visual cortex of awake primate. *Journal of Neuroscience*, 39(22):4282–4298.

Churchland, M. M., Byron, M. Y., Cunningham, J. P., Sugrue, L. P., Cohen, M. R., Corrado, G. S., Newsome, W. T., Clark, A. M., Hosseini, P., Scott, B. B., et al. (2010). Stimulus onset quenches neural variability: a widespread cortical phenomenon. *Nature neuroscience*, 13(3):369–378.

Crair, M. C., Ruthazer, E. S., Gillespie, D. C., and Stryker, M. P. (1997). Ocular dominance peaks at pinwheel center singularities of the orientation map in cat visual cortex. *Journal of Neurophysiology*, 77(6):3381–3385.

Davis, Z. W., Muller, L., Martinez-Trujillo, J., Sejnowski, T., and Reynolds, J. H. (2020). Spontaneous travelling cortical waves gate perception in behaving primates. *Nature*, 587(7834):432–436.

Ermentrout, G. B. and Kleinfeld, D. (2001). Traveling electrical waves in cortex: Insights from phase dynamics and speculation on a computational role. *Neuron*, 29(1):33–44.

Faruqui, M., Tsvetkov, Y., Yogatama, D., Dyer, C., and Smith, N. A. (2015). Sparse overcomplete word vector representations. In *ACL*.

Frenkel, C., Lefebvre, M., and Bol, D. (2021). Learning without feedback: Fixed random learning signals allow for feedforward training of deep neural networks. *Frontiers in neuroscience*, 15.

Gilding, B. H. and Kersner, R. (2004). *Travelling Waves in Nonlinear Diffusion-Convection Reaction*. Birkhäuser.

Gong, P. and Van Leeuwen, C. (2009). Distributed dynamical computation in neural circuits with propagating coherent activity patterns. *PLoS Computational Biology*, 5(12):e1000611.

Gregor, K. and LeCun, Y. (2010). Emergence of complex-like cells in a temporal product network with local receptive fields.

Gribizis, A., Ge, X., Daigle, T. L., Ackman, J. B., Zeng, H., Lee, D., and Crair, M. C. (2019). Visual cortex gains independence from peripheral drive before eye opening. *Neuron*, 104(4):711–723.

Han, F., Caporale, N., and Dan, Y. (2008). Reverberation of recent visual experience in spontaneous cortical waves. *Neuron*, 60(2):321–327.

Hochreiter, S. and Schmidhuber, J. (1997). Long short-term memory. *Neural computation*, 9(8):1735–1780.

Huber, L., Finn, E., Handwerker, D., Boenstrup, M., Glen, D., Kashyap, S., Ivanov, D., Petridou,
N., Marrett, S., Goense, J., Poser, B., and Bandettini, P. (2020). Sub-millimeter fmri reveals multiple topographical digit representations that form action maps in human motor cortex. *NeuroImage*, 208.

Huth, A., De Heer, W., Griffiths, T., Theunissen, F., and Gallant, J. (2016). Natural speech reveals the semantic maps that tile human cerebral cortex. *Nature*, 532(7600):453–458.

Hyvärinen, A. and Hoyer, P. O. (2001). A two-layer sparse coding model learns simple and complex cell receptive fields and topography from natural images. *Vision Research*, 41(18):2413–2423.

Isaacson, J. S. and Scanziani, M. (2011). How inhibition shapes cortical activity. *Neuron*, 72(2):231–243.

Issa, N. P., Trepel, C., and Stryker, M. P. (2000). Spatial frequency maps in cat visual cortex. *Journal of Neuroscience*, 20(22):8504–8514.

Keane, A. and Gong, P. (2015). Propagating waves can explain irregular neural dynamics. *Journal of Neuroscience*, 35(4):1591–1605.

Launay, J., Poli, I., Boniface, F., and Krzakala, F. (2020). Direct feedback alignment scales to modern deep learning tasks and architectures. *arXiv preprint arXiv:2006.12878*.

Lillicrap, T. P., Cownden, D., Tweed, D. B., and Akerman, C. J. (2016). Random synaptic feedback weights support error backpropagation for deep learning. *Nature communications*, 7(1):1–10.

Makin, T. R., Scholz, J., Henderson Slater, D., Johansen-Berg, H., and Tracey, I. (2015). Reassessing cortical reorganization in the primary sensorimotor cortex following arm amputation. *Brain*, 138(8):2140–2146.

Muller, L., Reynaud, A., Chavane, F., and Destexhe, A. (2014). The stimulus-evoked population response in visual cortex of awake monkey is a propagating wave. *Nature communications*, 5(1):1–14.

Nøkland, A. (2016). Direct feedback alignment provides learning in deep neural networks. *arXiv preprint arXiv:1609.01596*.

Oja, E. (1982). A simplified neuron model as a principal component analyzer. *J. Mathematical Biology*, 15:267–273.

Olshausen, B. A. and Field, D. J. (1996). Emergence of simple-cell receptive field properties by learning a sparse code for natural images. *Nature*, 381:607–609.

Osan, R. and Ermentrout, B. (2001). Two dimensional synaptically generated traveling waves in a theta-neuron neural network. *Neurocomputing*, 38:789–795.

Ott, M., Edunov, S., Baevski, A., Fan, A., Gross, S., Ng, N., Grangier, D., and Auli, M. (2019). fairseq: A fast, extensible toolkit for sequence modeling.
Pennington, J., Socher, R., and Manning, C. D. (2014). Glove: Global vectors for word representation. In *Proceedings of the 2014 conference on empirical methods in natural language processing (EMNLP)*, pages 1532–1543.

Rozell, C. J., Johnson, D. H., Baraniuk, R. G., and Olshausen, B. A. (2008). Sparse coding via thresholding and local competition in neural circuits. *Neural Comput.*, 20(10):2526–2563.

Rubin, R., Abbott, L. F., and Sompolinsky, H. (2017). Balanced excitation and inhibition are required for high-capacity, noise-robust neuronal selectivity. *Proc. Nat. Acac. Science*, 114(44):9366–9375.

Rubino, D., Robbins, K. A., and Hatsopoulos, N. G. (2006). Propagating waves mediate information transfer in the motor cortex. *Nature neuroscience*, 9(12):1549–1557.

Santos, E., Schöll, M., Sánchez-Porras, R., Dahlem, M. A., Silos, H., Unterberg, A., Dickhaus, H., and Sakowitz, O. W. (2014). Radial, spiral and reverberating waves of spreading depolarization occur in the gyrencephalic brain. *Neuroimage*, 99:244–255.

Sato, T. K., Nauhaus, I., and Carandini, M. (2012). Traveling waves in visual cortex. *Neuron*, 75(2):218–229.

Senk, J., Korvasová, K., Schuecker, J., Hagen, E., Tetzlaff, T., Diesmann, M., and Helias, M. (2020). Conditions for wave trains in spiking neural networks. *Physical review research*, 2(2):023174.

Shadlen, M. N. and Newsome, W. T. (1998). The variable discharge of cortical neurons: Implications for connectivity, computation, and information coding. *Journal of Neuroscience*, 18:3870–3896.

Song, G., Xu, R., and Lafferty, J. (2021). Convergence and alignment of gradient descent with random backpropagation weights. *CoRR*, abs/2106.06044.

Tanaka, H., Nayebi, A., Maheswaranathan, N., McIntosh, L., Baccus, S. A., and Ganguli, S. (2019). From deep learning to mechanistic understanding in neuroscience: The structure of retinal prediction. In *Advances in Neural Information Processing Systems*.

Templeton, A. (2021). Word equations: Inherently interpretable sparse word embeddings through sparse coding. *Proceedings of the Fourth BlackboxNLP Workshop on Analyzing and Interpreting Neural Networks for NLP*.

Turing, A. (1952). The chemical basis of morphogenesis. *Phil. Trans. Royal Society of London*, 237(641):37–72.

van der Maaten, L. and Hinton, G. (2008). Visualizing data using t-SNE. *Journal of Machine Learning Research*, 9:2579–2605.

Wesselinck, D. B., Sanders, Z.-B., Edmondson, L. R., Dempsey-Jones, H., Kieliba, P., Kikkert, S., Themistocleous, A. C., Emir, U., Diedrichsen, J., Saal, H. P., and Makin, T. R. (2020). Malleability of the cortical hand map following a finger nerve block. *bioRxiv*.
Wooley, T. E., Baker, R. E., and Maini, P. K. (2017). Turing’s theory of morphogenesis. In Copeland, B. J., Bowen, J. P., Wilson, R., and Sprevak, M., editors, *The Turing Guide*. Oxford University Press.

Yogatama, D., Faruqui, M., Dyer, C., and Smith, N. (2015). Learning word representations with hierarchical sparse coding. In Bach, F. and Blei, D., editors, *Proceedings of the 32nd International Conference on Machine Learning*, volume 37 of *Proceedings of Machine Learning Research*, pages 87–96, Lille, France. PMLR.

Zanos, T. P., Mineault, P. J., Nasiotis, K. T., Guitton, D., and Pack, C. C. (2015). A sensorimotor role for traveling waves in primate visual cortex. *Neuron*, 85(3):615–627.

Zhou, B., Li, Z., Kim, S. S. Y., Lafferty, J., and Clark, D. A. (2021). Shallow neural networks trained to detect collisions recover features of visual loom-selective neurons. *bioRxiv*.

Zylberberg, J., Murphy, J. T., and DeWeese, M. R. (2011). A sparse coding model with synaptically local plasticity and spiking neurons can account for the diverse shapes of V1 simple cell receptive fields. *PLOS Computational Biology*, 7:1–12.