

# Can Single Neurons Solve MNIST? The Computational Power of Biological Dendritic Trees

Ilena Simone Jones<sup>1</sup> and Konrad Kording<sup>2</sup>

<sup>1</sup>Department of Neuroscience, University of Pennsylvania

<sup>2</sup>Departments of Neuroscience and Bioengineering, University of Pennsylvania

September 4, 2020

## Abstract

Physiological experiments have highlighted how the dendrites of biological neurons can nonlinearly process distributed synaptic inputs. This is in stark contrast to units in artificial neural networks that are generally linear apart from an output nonlinearity. If dendritic trees can be nonlinear, biological neurons may have far more computational power than their artificial counterparts. Here we use a simple model where the dendrite is implemented as a sequence of thresholded linear units. We find that such dendrites can readily solve machine learning problems, such as MNIST or CIFAR-10, and that they benefit from having the same input onto several branches of the dendritic tree. This dendrite model is a special case of sparse network. This work suggests that popular neuron models may severely underestimate the computational power enabled by the biological fact of nonlinear dendrites and multiple synapses per pair of neurons. The next generation of artificial neural networks may significantly benefit from these biologically inspired dendritic architectures.

# 1 Introduction

## 1.1 Dendritic Nonlinearities

Though the role of biological neurons as the mediators of sensory integration and behavioral output is clear, the computations performed within neurons has been a point of investigation for decades (McCulloch and Pitts, 1943; Hodgkin and Huxley, 1952; FitzHugh, 1961; Poirazi et al., 2003a; Mel, 2016). For example, the McCulloch and Pitts (M&P) neuron model is based on an approximation that a neuron linearly sums its input and maps this through a nonlinear threshold function, allowing it to carry out a selection of logic-gate-like functions, which can be expanded to create logic-based circuits (McCulloch and Pitts, 1943). The M&P neuron also sets the foundation for modern day neurons in artificial neural networks (ANNs), where each neuron in the network linearly sums its input and maps this through a nonlinear activation function (Goodfellow et al., 2016; Lecun et al., 2015). ANNs, made up of often millions of these neurons, are demonstrably powerful algorithms that can be trained to solve complex problems, from reinforcement learning to natural language processing to computer vision (Lecun et al., 2015; Krizhevsky et al., 2006; Mnih et al., 2015; Devlin et al., 2018; Huval et al., 2015). However, M&P neurons and neurons of ANNs are point-neuron models that rely on linear sums of their inputs, whereas the observed physiology of biological neurons shows that dendrites impose nonlinearities on their synaptic inputs before summation at the soma (London and Häusser, 2005; Poirazi et al., 2003b; Antic et al., 2010; Agmon-Snir et al., 1998). This indicates that M&P and ANN neurons may radically underestimate what individual neurons can do.

Although many models of single neuron activity use linear point neurons (Ujfalussy et al., 2015), it is known that dendritic nonlinearities are responsible for a variety of neuronal dynamics and can be used to mechanistically explain the roles of biological neurons in a variety of behaviorally significant circuits (London and Häusser, 2005; Agmon-Snir et al., 1998; Barlow and Levick, 1965). For example, passive properties of dendrites lead to attenuation of current along the dendrite, allowing for low-pass filtering of inputs (London and Häusser, 2005; Rall, 1959). Active properties of dendrites allow for synaptic clustering to result in super-linear summation of voltage inputs upon reaching the soma (Antic et al., 2010; Schiller et al., 2000; Branco and Häusser, 2011). These properties allow for important functions such as auditory coincidence

detection and even logical operations within dendrites (Mel, 2016; London and Häusser, 2005; Agmon-Snir et al., 1998; Koch et al., 1983). To fully explore the scope of biological neuron function it is then important to model more sophisticated computations within dendritic trees.

Models for individual neurons with meaningful dendrites have been proposed to better understand neuron computation (Mel, 2016; Gerstner and Naud, 2009). Biologically detailed approaches, such as employing the multi-compartmental biophysical model (Hines and Carnevale, 1997), have been fitted to empirical data in order to study dendritic dynamics such as backpropagating action potentials and nonlinear calcium spikes (London and Häusser, 2005; Hay et al., 2011; Wilson et al., 2016). Poirazi et al. (Poirazi et al., 2003a) pioneered a more abstracted approach of modelling single neurons that isolates the impacts of including dendritic sigmoidal nonlinearities on predicting neural firing rates produced by dendrite-complete biophysical models. This novel approach used a sparsely connected two-layer ANN whose structure is analogous to that of a dendritic tree, showing it is possible to model individual neurons with ANNs.

## 1.2 Repetition of synaptic inputs

While the morphology of a dendritic tree is key to modelling its computational capabilities (Mel, 2016; London and Häusser, 2005; Mel, 1993; Segev, 2006; Wilson et al., 2016), it may also be important to consider the role of repeated synaptic inputs to the same postsynaptic neuron. Complex computation in ANNs depends on dense connection, which repeats inputs to each node in each layer (Lecun et al., 2015). Empirically, electron microscopy studies have shown that a presynaptic axon synapses approximately 4 times per postsynaptic neuron (Kincaid et al., 1998). Also, these studies show evidence of a certain kind of repeated synapses called multi-synaptic boutons (MSBs) (Jones et al., 1997). MSBs have shown to occur 11.5% of the time in rats living in enriched environments (Jones et al., 1997). Additionally, it has been shown that an *in vitro* long-term potentiation (LTP) induction protocol can also increase the number of MSBs of the same dendrite 6-fold (Jones et al., 1997). LTP, involved in learning and memory (Bliss and Lomo, 1973; Stuchlik, 2014), can then lead to the replication of synapses between two neurons. This suggests that repeated synapses may be important for changing the computations a single neuron can do.

### 1.3 Contribution

By training and testing ANNs on complex tasks, the field of machine learning gains computational clarity (Goodfellow et al., 2016; Lecun et al., 2015). At the moment the field of neuroscience does not have this kind of in-depth computational clarity with individual, dendrite-complete neurons, despite the fact that we can describe the different behaviorally significant functions individual neurons are able to fulfill (London and Häusser, 2005; Agmon-Snir et al., 1998; Barlow and Levick, 1965; Gidon et al., 2020). If we are to consider a neuron as an input/output device with a binary tree as its dendritic tree, we may be able to test its ability to learn to perform complex tasks and gain insight on how dendritic trees may impact the computation of a defined task.

Here we design a trainable, dendrite-complete neuron model in order to test its performance on binary classification tasks taken from the field of machine learning. The model comprises a sparse ANN: a binary tree in which each nonlinear unit receives only 2 inputs. The nonlinearities and structural constraints of this ANN can be compared to a linear point-neuron model, allowing us to test the impacts of nonlinearities in a dendrite-like tree. The model also allows us to test the impact of repeated inputs on task performance. We found that our binary tree model, representing a *single biological neuron*, performs better than a comparable linear classifier. Furthermore, when repeated inputs are incorporated into our model, it approximately matches the performance of a comparable 2-layer fully connected ANN. These results demonstrate that complex tasks, for which it has been assumed that an ensemble of multiple relatively simple neuron models are required, can in fact be computed by a singular, dendrite-complete neuron model.

## 2 Results

One of the classical questions in neuroscience is how dendrite structure and the various synaptic inputs to the dendritic tree affect computation (London and Häusser, 2005; Mel, 2016; Rall, 1959). Traditional neuron models are designed to best match observed neural dynamics (Poirazi et al., 2003a; Gerstner and Naud, 2009; Brette et al., 2011; Gouwens et al., 2018; Hay et al., 2011; Ahrens et al., 2006), however, with exceptions (Poirazi et al., 2003a; Ujfalussy et al., 2015; Gidon et al., 2020; Zador et al., 1992; Zador and Pearlmutter, 1996; Legenstein and Maass, 2011), the impacts of nonlinearities and, especially,

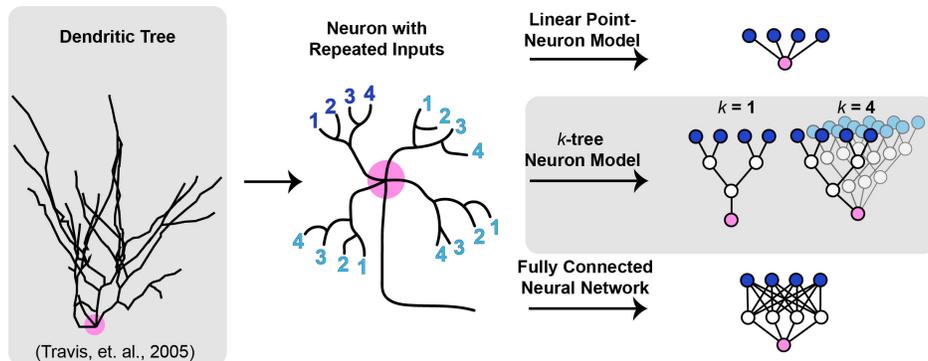


Figure 1: Novel ANN neuron model with repeated inputs. Left: Traced morphology of the dendrite of a human BA18 (occipital) cell (Travis et al., 2005). Soma location is marked in pink. Middle: A representation of a hypothetical neuron. Inputs in dark blue at the terminal ends of one subtree are repeated in light blue in 3 other subtrees. Upper right: Representation of a M&P-like linear point neuron model. Middle right:  $k$ -tree neuron model, where  $k$  = number of subtrees. Each input and hidden node has leaky ReLU activation function, and the output node has a sigmoid activation function. Bottom right: Representation of a 2-layer fully connected neural network (FCNN). Each input and hidden node has leaky ReLU activation function and the output node has a sigmoid activation function.

the impacts of repeated inputs on the computational capabilities of neurons have yet to be quantified in the way we suggest. The computational abilities of ANNs can be judged by their performance on various complex tasks (Goodfellow et al., 2016; Lecun et al., 2015). Following this lead, we imposed dendritic binary tree structural constraints (Figure 1) on a trainable nonlinear ANN, resulting in a special case of sparsely connected ANN. We call this a 1-tree because it is similar to the structure of a single soma-connected subtree of a dendritic tree. (Figure 1) By repeating this subtree structure multiple times and feeding each the exact same input, we create what we call a  $k$ -tree, where  $k$  is the number of repeated trees connected to a soma node. By using a trainable  $k$ -tree that has a biological structure constraint and repeated inputs, we can quantitatively judge the computational performance of this neuron model on performing complex tasks.

Neurons, arguably, produce binary outputs (presence or absence of an action potential) (Hodgkin and Huxley, 1952). Therefore, to fairly judge

$k$	<b>256 inputs</b>		<b>1024 inputs</b>		<b>3072 inputs</b>	
	k-tree	FCNN	k-tree	FCNN	k-tree	FCNN
1	511	514	2,047	2050	6,143	6,146
2	1,022	1,028	4,094	4,100	12,286	12,292
4	2,044	2,056	8,188	8,200	24,572	24,584
8	4,088	4,112	16,376	16,400	49,144	49,168
16	8,176	8,224	32,752	32,800	98,288	98,336
32	16,352	16,448	65,504	65,600	196,576	196,336

Table 1: ANN Parameter Size Comparison. Fully connected neural network (FCNN) architectures are matched in parameter size to the  $k$ -tree architectures.

an individual neuron model’s performance on a complex task, we will use a binary classification task. The complexity in the tasks can come from high-dimensional vector inputs from images taken from classic computer vision datasets used in the field of machine learning (Figure 2).

As controls for performance comparison, we used a linear discriminant analysis (LDA) linear classifier to approximate the performance of a linear point neuron model, and a fully connected neural network (FCNN) that is comparable in size to the  $k$ -tree. The linear classifier model is relatively simple compared to the more parameter-complex  $k$ -tree and FCNN, and we expect it to be able to learn fewer functions (Dreiseitl and Ohno-Machado, 2002); therefore, its performance sets an expected lower-bound. The FCNN is densely connected and consists of 2-layers. With its nonlinearities, we expect it to learn to express a greater variety of functions, therefore its performance sets an expected upper bound. To compare the two ANNs, let us say that  $n$  is the number of pixel inputs to each classifier, determining the number of parameters,  $P$ , needed in each network, and  $h$  is the number of nodes in the hidden layer of the FCNN. Based on the constraints of each network, the FCNN will then have  $P = h(n + 1)$  and the  $k$ -tree will have  $P = k(2n - 1)$ . To match the number of parameters of the FCNN to that of the  $k$ -tree, we assert that  $h = 2k$ . (Table 1).

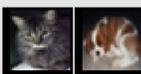
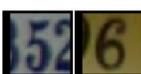
Binary Classification across tasks			
Dataset	Classes	Examples	1-D Input Size
MNIST	3, 5		32x32 = 1024
Fashion-MNIST (FMNIST)	0, 6		32x32 = 1024
EMNIST	14, 17		32x32 = 1024
Kuzushiji-MNIST (KMNIST)	2, 6		32x32 = 1024
CIFAR-10	3, 5		3x32x32 = 3072
Street View House Numbers (SVHN)	5, 6		3x32x32 = 3072
USPS	3, 5		16x16 = 256

Figure 2: Classification task datasets. We considered seven machine learning datasets of varying content and size, each with ten classes. For each dataset, two of the classes were chosen by selecting the least linearly separable pair using a linear discriminant analysis (LDA) linear classifier. Each image was vectorized in order to be compatibly presented to each model.

## 2.1 Nonlinear tree neuron model performs better than a linear classifier

Classical models of neurons have been of linear point neurons that do not take into consideration dendritic nonlinearities (McCulloch and Pitts, 1943; Hodgkin and Huxley, 1952; FitzHugh, 1961). By considering dendritic non-linearity and structure, we designed a new neuron model: a nonlinear ANN with the structural constraints of a dendritic tree called a 1-tree. We then compared the performance of this new model against a proxy for a point neuron, an LDA linear classifier. Focusing on one simple image classification task of a binary dataset of handwritten numbers, MNIST, we compare the computational performance of the 1-tree and the linear classifier and the nonlinear, structurally dendritic 1-tree. Significantly, the performance of the

	<b>MNIST</b>	<b>FMNIST</b>	<b>EMNIST</b>	<b>KMNIST</b>
1-tree	0.9220 $\pm$ 0.0179	0.7900 $\pm$ 0.0202	0.8524 $\pm$ 0.1520	0.8035 $\pm$ 0.0488
32-tree	0.9635 $\pm$ 0.0043	0.8300 $\pm$ 0.0063	0.9851 $\pm$ 0.0029	0.8791 $\pm$ 0.0113
LDA	0.8753 $\pm$ 0.0120	0.6750 $\pm$ 0.0108	0.5821 $\pm$ 0.0180	0.6790 $\pm$ 0.0164
1-FCNN	0.9546 $\pm$ 0.0053	0.8262 $\pm$ 0.00063	0.9779 $\pm$ 0.0046	0.8674 $\pm$ 0.0188
32-FCNN	0.9696 $\pm$ 0.0053	0.8290 $\pm$ 0.0075	0.9846 $\pm$ 0.0034	0.9088 $\pm$ 0.0080
1-tree vs LDA	$p < 0.0001$	$p < 0.0001$	$p < 0.0001$	$p < 0.0001$
1-tree vs 1-FCNN	$p = 0.0001$	$p = 0.0001$	$p = 0.0235$	$p = 0.0018$
32-tree vs 32-FCNN	$p = 0.0156$	$p = 0.7516$	$p = 0.7357$	$p < 0.0001$

	<b>CIFAR10</b>	<b>SVHN</b>	<b>USPS</b>
1-tree	0.5605 $\pm$ 0.0140	0.5811 $\pm$ 0.0412	0.8221 $\pm$ 0.0465
32-tree	0.5784 $\pm$ 0.0111	0.6036 $\pm$ 0.0661	0.8981 $\pm$ 0.0080
LDA	0.5254 $\pm$ 0.0069	0.5186 $\pm$ 0.0102	0.8362 $\pm$ 0.0306
1-FCNN	0.5592 $\pm$ 0.0148	0.6117 $\pm$ 0.0844	0.8971 $\pm$ 0.0199
32-FCNN	0.5654 $\pm$ 0.0104	0.7794 $\pm$ 0.0301	0.9067 $\pm$ 0.0169
1-tree vs LDA	$p < 0.0001$	$p = 0.0005$	$p = 0.4897$
1-tree vs 1-FCNN	$p = 0.8736$	$p = 0.4024$	$p = 0.0012$
32-tree vs 32-FCNN	$p = 0.0344$	$p < 0.0001$	$p = 0.2031$

Table 2:  $k$ -tree Mean Performance Comparison to FCNN and LDA. Performance accuracy is listed as mean  $\pm$  standard error for a set of 10 trials.  $p$ -Values calculated using student’s t-test. LDA and FCNN are used as lower and upper bounds that the  $k$ -tree is compared to.

1-tree is greater than that of the linear classifier with  $p < 0.0001$  (Figure 3A, Table 2). Repeating this test with 6 more datasets, we find that for most of these datasets, regardless of the size of the input dimensionality in each dataset, the 1-tree performs consistently above the linear classifier (FMNIST, EMNIST, KMNIST, CIFAR10:  $p < 0.0001$ ; SVHN:  $p = 0.0005$ ) (Figure 3B-F, Table 2). Exceptionally, the performance of the 1-tree on the USPS dataset had no significant difference of performance compared to the linear classifier. The USPS dataset has the smallest input dimensionality (256 pixels) and leads to a 1-tree with the fewest parameters ( $P = 511$ , Table 1). It could be the network was not complex enough to perform better than the

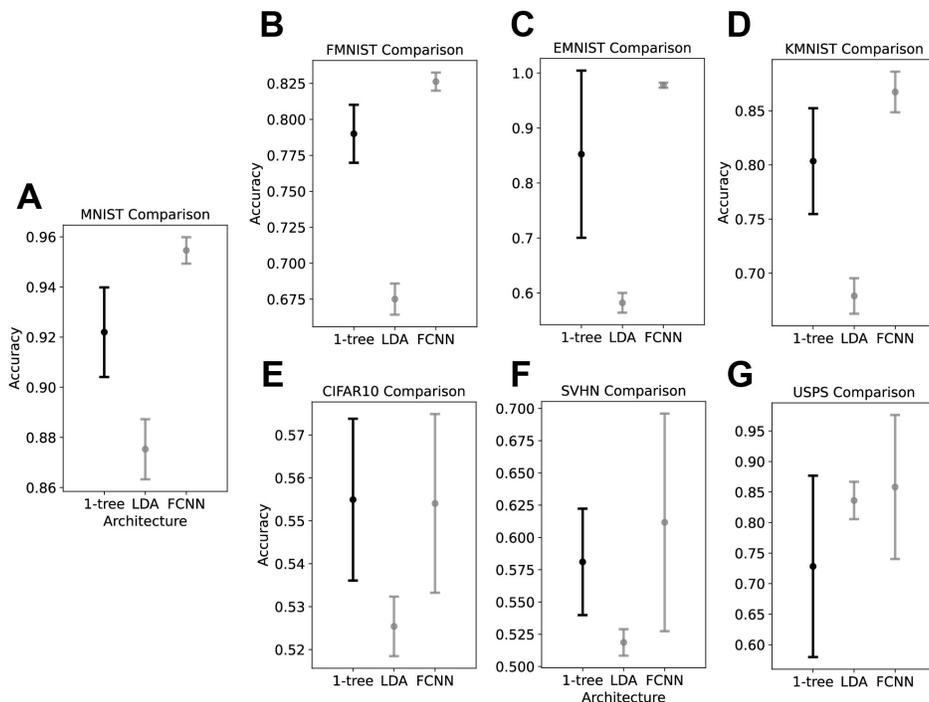


Figure 3: Performance of 1-tree compared to linear classifier and FCNN. 1-tree performance is compared to that of a lower bound, LDA, and an upper bound, FCNN. For most tasks, the 1-tree performs better than LDA, and FCNN performs better than the 1-tree.

linear classifier. Barring this exception, not only do dendrites have nonlinear properties, nonlinearities in a dendrite-like neuron model generally improves its computational performance compared to that of a linear classifier.

For comparison to the 1-tree, we tested a 2-layer fully connected neural network (FCNN) matched in parameter size to the 1-tree. In the MNIST task, the FCNN performed significantly better than the 1-tree with a  $p = 0.0001$  (Figure 3A, Table 2). We then tested the 6 additional datasets, resulting in differently sized 1-trees and FCNNs due to differences in input sizes. The similarly sized FMNIST, EMNIST, and KMNIST dataset networks maintained the significant difference between the 1-tree and FCNN (Figure 3B-D, Table 2). The USPS dataset also maintained a significant difference (Figure 3G). The CIFAR10 and SVHN datasets did not have a significant difference in performance (Figure 3E-F, Table 2). The high variance in the

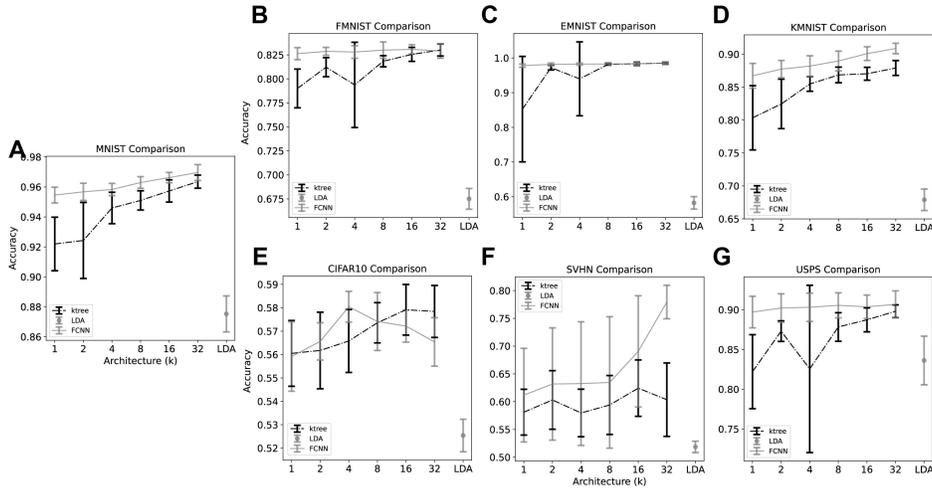


Figure 4: Performance of  $k$ -tree compared to a linear classifier and FCNN.  $k$ -tree performance is compared to that of a lower bound, LDA, and an upper bound, FCNN. The  $k$  is doubled 5 times, resulting in tests of  $k = 1, 2, 4, 8, 16, 32$ . In all cases, as  $k$  (the number of repeated dendritic subtrees) increases, so does the performance accuracy of the  $k$ -tree, approaching the upper bound.

FCNN performance for CIFAR10 and SVHN (Figure 3E-F, Table 2) may be due to the FCNN’s failure to train in some trials, resulting in performances close to 50%. For most tasks we tried, the FCNN performed much better than the 1-tree.

## 2.2 Repeating inputs to tree model increases performance comparable to FCNN with a small fraction of the parameters

The computational impact of repeated inputs to a dendritic tree is not clear, however studies have shown increased repetition of inputs as a result of plasticity events (Toni et al., 1999), which has implications for learning and memory. By modifying the 1-tree by repeating the tree structure and input to the model  $k$  times, we can then achieve a  $k$ -tree neuron model (Figure 1). This can be a proxy for seeing how repeated inputs might impact computational performance on various binary image classification tasks. Returning to the MNIST dataset, we tested  $k = 1, 2, 4, 8, 16, 32$  and observed how increasing

$k$  can gradually improve performance. For example, compare the performance of a 1-tree to that of a 32-tree in the MNIST binary classification task ( $p = 0.0000$ ) (Figure 4A). Remarkably, the performance of the 32-tree ( $96.35 \pm 0.43\%$ ) is very close to the performance of the FCNN ( $96.96 \pm 0.53\%$ ), yet still different with  $p = 0.0156$  (Figure 4A, Table 2). Increasing the number of repeats to a  $k$ -tree neuron model improves its performance on the MNIST binary classification task, nearly meeting the performance of a comparable FCNN.

In order to see if this result generalizes, we tested the  $k$ -tree on 6 additional binary image classification datasets. All tasks see an increase in performance as the number of subtrees in the  $k$ -tree increases up to  $k = 32$  (Figure 4B-G). The 32-tree has meets the performance of the FCNN in the FMNIST ( $p = 0.7516$ ), EMNIST ( $p = 0.7357$ ), and USPS ( $p = 0.2031$ ) tasks (Figure 4B,C,G, Table 2). For the CIFAR10 dataset, FCNN performance peaks at  $k = 4$ , then decreases, resulting in the 32-tree surpassing the 32-FCNN (Figure 4E, Table 2). We can then say that increasing the number of repeats to a  $k$ -tree neuron model improves its computational performance in all tasks such that it approaches the performance of a comparable FCNN.

## 3 Methods

### 3.1 Computational Tasks

Knowing that the output of a neuron is binary (presence or absence of an action potential), we chose to train our neuron model on a binary classification task. Using standard, high-dimensional, computer vision datasets, we used linear discriminant analysis (LDA) linear classifier to determine which 2 classes within each dataset were least linearly separable through training the LDA linear classifier and testing it on pairs of classes (Figure 2). We used MNIST (Lecun et al., 1998), Fashion-MNIST (Xiao et al., 2017), EMNIST (Cohen et al., 2017), Kuzushiji-MNIST (Clanuwat et al., 2018), CIFAR-10 (Krizhevsky, 2009), Street View House Numbers (SVHN) (Goodfellow et al., 2014), and USPS (Hastie et al., 2001) datasets.

## 3.2 Controls

The controls we use are the LDA linear classifier and a fully connected neural network (FCNN). The linear classifier sets a baseline performance for linear separability of each of the two classes per dataset, in addition to acting as a proxy for a linear point neuron model. The 2-layer FCNN is a comparable reference to see if  $k$ -tree performance meets or exceeds that of a densely connected network. The hidden layer of the FCNN is equal to twice the number of trees ( $2k$ ) in the  $k$ -tree it is compared to and its output layer has 1 node.

## 3.3 Data Preprocessing

We used datasets from the torchvision (version 0.5.0) python package. We then padded the 28 by 28 resolution images with zeros so that they were 32 x 32, and flattened the images to 1-D vectors. We then split the shuffled training set into training and validation sets (for MNIST, the ratio was 1:5 so as to let the validation set size match the test set), Then we split the resultant shuffled training set and validation set into 10 independent subsets. Each set was used for a different cross-validation trial.

## 3.4 Model Architecture

Using PyTorch (version 1.4.0), we designed the  $k$ -tree model architecture to be a feed forward neural network with sparse binary-tree connections. The weight matrices, which were dense tensors, of each layer were sparsified such that each node receives 2 inputs and produces 1 output. For example, the 1024 pixel-size images were fed to a 1-tree with 10 layers: the input layer is 1024 by 512, the 2nd layer 512 by 256 etc. until the penultimate layer is reached with dimensions 2 by 1. The final layer is  $k$  by 1 where  $k$  is the number of subtrees in the  $k$ -tree; in this case it would be 1 by 1. In the special case of the 3072 pixel size images, inputs were fed into a 1-tree with 11 layers, the input layer is 3072 by 1024, the 2nd layer is 1024 by 512, etc.

To account for the sparsification, we altered the initialization of the weight matrices: we used standard “Kaiming normal” initialization with a gain of  $1/\text{density}$  of sparsified dense tensor weight matrices. We also created a “freeze mask” that recorded which weights were set to 0 in order to freeze those weights during training later. For the forward step, we used leaky ReLU with

a slope of 0.01 for nodes between layers, and sigmoid nonlinearity at the final output node which kept output values between 0 and 1.

### 3.5 Model Training

The model, inputs, and labels were loaded onto a Nvidia GeForce 1080 GPU using CUDA version 10.1. The batch size was 256. Early stopping was used such that after 60 epochs where no decrease in the loss is observed, training is stopped. Loss was calculated using binary cross entropy loss. We used an Adam optimizer with a learning rate of 0.001. Within the training loop immediately after the backward step and before updating the weights using the gradients, we zeroed out the gradients indicated by the freeze mask so as to keep the model sparsely connected. Each train-test loop was run for 10 trials with a different training subset each trial and the same test set every trial. Trial averages and standard deviation were then calculated and p-values were calculated using student t-test.

## 4 Discussion

Here we quantify the potential computational capabilities of an abstracted neuron model with dendritic features and repeated inputs. We designed a trainable neuron model: a sparse ANN with binary dendritic tree constraints made up of nonlinear nodes (Figure 1). The tree that resulted from this constraint was repeated  $k$  times with identical inputs in order to explore the impacts of repeated inputs. We judged the model by determining its performance on 7 high-dimensional binary image classification tasks (Figure 2), and compared its performance to a linear classifier, a lower bound, and a comparable FCNN, an upper bound. The 1-tree, with its nonlinear nodes and dendritic structure constraint, performed better than the linear classifier in almost all tasks (Figure 3). When we increased  $k$  of the  $k$ -tree from  $k = 1$  to  $k = 32$ , we saw a consistent increase in  $k$ -tree performance across all tasks (Figure 4). In the case of the MNIST task, the performance of the 32-tree was close to the comparable FCNN performance. Surprisingly, the 32-tree in the FMNIST, EMNIST, and USPS tasks met that of the comparable FCNN. These findings emphasize the importance for modelers to consider both dendrites and synaptic input repetitions.

A limitation of this study is the relevance of our computational tasks.

Although it is hard to know exactly what kind of input a neuron receives from its presynaptic connections, we do not believe the 1-dimensional vectorized input we provide our neuron model is biologically plausible. Ordering the pixel input to these models randomly overall decreases  $k$ -tree performance, implying that the order of the input impacts performance (see Figure S1 in the Supplementary Material). Further investigation may be needed to explore how the ordering of the 1-D pixel input might impact performance.

The binary tree structure we chose to constrain an ANN to make the  $k$ -tree makes several assumptions. Each node of the tree is analogous to a compartment in a dendritic tree, and in biological dendritic trees each compartment will receive an exclusive set of inputs. Therefore, we chose not to use convolution or any kind of weight sharing in our model. In addition, the synaptic weights and inter-node weights are real-valued free parameters, however the weights analogous to inter-compartmental axial resistances (Rall, 1959; Huys et al., 2006) could only be positive scalar values if biologically plausible. Future work to address this would be to constrain the free parameter ranges to be completely positive.

In this study we used an abstracted model to give us insights into the impacts of biological constraints and properties. After all, these kinds of optimizations are not currently doable in more realistic models of neurons. Using this model, we see how nonlinear dendrites increase a neuron model’s task performance above that of a linear classifier, which serves as a proxy for models following the point-neuron assumption. Importantly, we see how by repeating the inputs to this dendrite model we can observe a consistent increase in task performance. These findings emphasize the importance for modelers to consider both dendrites and synaptic input repetitions.

Our results may also be relevant for the field of deep learning. The  $k$ -trees we consider are special cases of sparse ANN, wherein there are only 2 inputs to all nodes after the first layer. These contrast with randomly-made sparse networks or pruned sparse networks (Frankle and Carbin, 2019), because they have very severe constraints. It is then surprising that a  $k$ -tree could perform at the level of a comparable FCNN. We would be interested in future work comparing the performance of binary tree structures, inspired by biological dendrites, against the performance of less structured sparse ANNs with comparable edge density.

This study tests the classification performance of a dendrite-complete neuron model and compares it to a model that follows the point-neuron assumption, highlighting the importance of considering branching dendrite

structure and nonlinearities when modeling neurons. We expand this test to consider the possibility of repeated synaptic inputs in our model, showing that the model consistently performs better with more repeated inputs to additional subtrees. We also see that the sparse network neuron model we designed can reach similar performance to a comparable densely connected network. Fundamentally, this study is a foray into directly considering a neuron’s computational capability by training the model to perform complex tasks using deep learning methodology, which promises to further our insights into single neuron computation.

## 5 Acknowledgements

I would like to thank the members of the Kording Lab, specifically Roozbeh Farhooi, Ari Benjamin, and David Rolnick for their help over the development of this project.

## 6 Code

The code for this project can be found at the following github repository: <https://github.com/ilennaj/ktree>

## References

- H. Agmon-Snir, C. E. Carr, and J. Rinzel. The role of dendrites in auditory coincidence detection. *Nature*, 393:268–272, 1998.
- M. B. Ahrens, Q. J. M. Huys, and L. Paninski. Large-scale biophysical parameter estimation in single neurons via constrained linear regression. *Advances in Neural Information Processing Systems*, 2006. ISSN 10495258. doi: 10.1007/s00439-005-0104-y. URL <http://citeseerx.ist.psu.edu/viewdoc/download?doi=10.1.1.184.2712&rep=rep1&type=pdf>.
- S. D. Antic, W. L. Zhou, A. R. Moore, S. M. Short, and K. D. Ikonomu. The decade of the dendritic NMDA spike. *Journal of Neuroscience Research*, 88(14):2991–3001, 2010. ISSN 03604012. doi: 10.1002/jnr.22444.
- H. B. Barlow and W. R. Levick. The mechanism of directionally selective units in rabbit’s retina. *The Journal of Physiology*, 178(3):477–504, 1965. ISSN 14697793. doi: 10.1113/jphysiol.1965.sp007638.
- T. V. P. Bliss and T. Lomo. Long-lasting potentiation of synaptic transmission in the dentate area of the unanaesthetized rabbit following stimulation of the perforant path. *The Journal of Physiology*, 232(2):357–374, 1973. ISSN 14697793. doi: 10.1113/jphysiol.1973.sp010274.
- T. Branco and M. Häusser. Synaptic Integration Gradients in Single Cortical Pyramidal Cell Dendrites. *Neuron*, 69(5):885–892, 2011. ISSN 08966273. doi: 10.1016/j.neuron.2011.02.006.
- R. Brette, B. Fontaine, A. K. Magnusson, C. Rossant, J. Platkiewicz, and D. F. M. Goodman. Fitting Neuron Models to Spike Trains. *Frontiers in Neuroscience*, 5 (February):1–8, 2011. doi: 10.3389/fnins.2011.00009.
- T. Clanuwat, M. Bober-Irizar, A. Kitamoto, A. Lamb, K. Yamamoto, and D. Ha. Deep Learning for Classical Japanese Literature. *Advances in Neural Information Processing Systems*, pages 1–8, 2018. doi: 10.20676/00000341. URL <http://arxiv.org/abs/1812.01718><http://dx.doi.org/10.20676/00000341>.
- G. Cohen, S. Afshar, J. Tapson, and A. Van Schaik. EMNIST: Extending MNIST to handwritten letters. *Proceedings of the International Joint Conference on Neural Networks*, 2017-May:2921–2926, 2017. doi: 10.1109/IJCNN.2017.7966217.
- J. Devlin, M.-W. Chang, K. Lee, and K. Toutanova. BERT: Pre-training of Deep Bidirectional Transformers for Language Understanding. *arXiv preprint*, 2018. URL <http://arxiv.org/abs/1810.04805>.

- S. Dreiseitl and L. Ohno-Machado. Logistic regression and artificial neural network classification models: A methodology review. *Journal of Biomedical Informatics*, 35(5-6):352–359, 2002. ISSN 15320464. doi: 10.1016/S1532-0464(03)00034-0.
- R. FitzHugh. Impulses and Physiological States in Theoretical Models of Nerve Membrane. *Biophysical Journal*, 1(6):445–466, 1961. ISSN 00063495. doi: 10.1016/S0006-3495(61)86902-6. URL [http://dx.doi.org/10.1016/S0006-3495\(61\)86902-6](http://dx.doi.org/10.1016/S0006-3495(61)86902-6).
- J. Frankle and M. Carbin. The lottery ticket hypothesis: Finding sparse, trainable neural networks. *7th International Conference on Learning Representations, ICLR 2019*, pages 1–42, 2019.
- W. Gerstner and R. Naud. How good are neuron models? *Science*, 326(5951):379–380, 2009. ISSN 00368075. doi: 10.1126/science.1181936.
- A. Gidon, T. A. Zolnik, P. Fidzinski, F. Bolduan, A. Papoutsi, P. Poirazi, M. Holtkamp, I. Vida, and M. E. Larkum. Dendritic action potentials and computation in human layer 2/3 cortical neurons. *Science (New York, N.Y.)*, 367(6473):83–87, 2020. ISSN 1095-9203. doi: 10.1126/science.aax6239. URL <http://www.ncbi.nlm.nih.gov/pubmed/31896716>.
- I. Goodfellow, Y. Bengio, and A. Courville. *Deep Learning*. MIT Press, 2016. URL [www.deeplearningbook.org](http://www.deeplearningbook.org).
- I. J. Goodfellow, Y. Bulatov, J. Ibarz, S. Arnoud, and V. Shet. Multi-digit number recognition from street view imagery using deep convolutional neural networks. *2nd International Conference on Learning Representations, ICLR 2014 - Conference Track Proceedings*, pages 1–13, 2014.
- N. W. Gouwens, J. Berg, D. Feng, S. A. Sorensen, H. Zeng, M. J. Hawrylycz, C. Koch, and A. Arkhipov. Systematic generation of biophysically detailed models for diverse cortical neuron types. *Nature Communications*, 9(1), 2018. ISSN 20411723. doi: 10.1038/s41467-017-02718-3. URL <http://dx.doi.org/10.1038/s41467-017-02718-3>.
- T. Hastie, R. Tibshirani, and J. Friedman. *The elements of statistical learning*. Springer-Verlag, 2001.
- E. Hay, S. Hill, F. Schürmann, H. Markram, and I. Segev. Models of neocortical layer 5b pyramidal cells capturing a wide range of dendritic and perisomatic active properties. *PLoS Computational Biology*, 7(7), 2011. ISSN 1553734X. doi: 10.1371/journal.pcbi.1002107.

- M. L. Hines and N. T. Carnevale. The NEURON simulation environment. *Neural computation*, 9(6):1179–209, 1997. ISSN 0899-7667. URL <http://www.ncbi.nlm.nih.gov/pubmed/9248061>.
- Hodgkin and Huxley. A quantitative description of membrane current and its application to conduction and excitation in nerve. *J Physiology*, 1117:500–544, 1952. ISSN 09237984. doi: 10.1080/00062278.1939.10600645.
- B. Huval, T. Wang, S. Tandon, J. Kiske, W. Song, J. Pazhayampallil, M. Andriluka, P. Rajpurkar, T. Migimatsu, R. Cheng-Yue, F. Mujica, A. Coates, and A. Y. Ng. An Empirical Evaluation of Deep Learning on Highway Driving. *arXiv preprint*, pages 1–7, 2015. URL <http://arxiv.org/abs/1504.01716>.
- Q. J. M. Huys, M. B. Ahrens, and L. Paninski. Efficient Estimation of Detailed Single-Neuron Models. *Journal of Neurophysiology*, 96(2):872–890, 2006. ISSN 0022-3077. doi: 10.1152/jn.00079.2006.
- T. A. Jones, A. Y. Klintsova, V. L. Kilman, A. M. Sirevaag, and W. T. Greenough. Induction of multiple synapses by experience in the visual cortex of adult rats. *Neurobiology of Learning and Memory*, 68(1):13–20, 1997. ISSN 10747427. doi: 10.1006/nlme.1997.3774.
- A. E. Kincaid, T. Zheng, and C. J. Wilson. Connectivity and convergence of single corticostriatal axons. *Journal of Neuroscience*, 18(12):4722–4731, 1998. ISSN 02706474. doi: 10.1523/jneurosci.18-12-04722.1998.
- C. Koch, T. Poggio, and V. Torre. Nonlinear interactions in a dendritic tree: Localization, timing, and role in information processing. *Proceedings of the National Academy of Sciences of the United States of America*, 80(May):2799–2802, 1983.
- A. Krizhevsky. Learning multiple layers of features from tiny images. *ArXiv*, 2009. ISSN 00012475.
- A. Krizhevsky, I. Sutskever, and G. E. Hinton. ImageNet Classification with Deep Convolutional Neural Networks. *Advances in Neural Information Processing Systems*, 8:713–772, 2006. doi: 10.1016/B978-008046518-0.00119-7.
- Y. Lecun, L. Bottou, Y. Bengio, and P. Haffner. Gradient-based learning applied to document recognition. *proc. of the IEEE*, 1998. URL <http://ieeexplore.ieee.org/document/726791/{#}full-text-section>.

- Y. Lecun, Y. Bengio, and G. Hinton. Deep learning. *Nature*, 521(7553):436–444, 2015. ISSN 14764687. doi: 10.1038/nature14539.
- R. Legenstein and W. Maass. Branch-specific plasticity enables self-organization of nonlinear computation in single neurons. *Journal of Neuroscience*, 31(30):10787–10802, 2011. ISSN 02706474. doi: 10.1523/JNEUROSCI.5684-10.2011.
- M. London and M. Häusser. Dendritic Computation. *Annual Review of Neuroscience*, 28(1):503–532, 2005. ISSN 0147-006X. doi: 10.1146/annurev.neuro.28.061604.135703. URL <http://www.annualreviews.org/doi/10.1146/annurev.neuro.28.061604.135703>.
- W. S. McCulloch and W. Pitts. A logical calculus of the ideas immanent in nervous activity. *The Bulletin of Mathematical Biophysics*, 5(4):115–133, 1943. ISSN 00074985. doi: 10.1007/BF02478259.
- B. Mel. Toward a simplified model of an active dendritic tree. In G. J. Stuart, N. Spruston, and M. Häusser, editors, *Dendrites*. Oxford Scholarship Online, 2016. ISBN 9780199682676. doi: 10.1093/acprof.
- B. W. Mel. Synaptic integration in an excitable dendritic tree. *Journal of neurophysiology*, 70(3):1086–101, 1993. ISSN 0022-3077. doi: 10.1152/jn.1993.70.3.1086. URL <http://www.ncbi.nlm.nih.gov/pubmed/8229160>.
- V. Mnih, K. Kavukcuoglu, D. Silver, A. A. Rusu, J. Veness, M. G. Bellemare, A. Graves, M. Riedmiller, A. K. Fidjeland, G. Ostrovski, S. Petersen, C. Beattie, A. Sadik, I. Antonoglou, H. King, D. Kumaran, D. Wierstra, S. Legg, and D. Hassabis. Human-level control through deep reinforcement learning. *Nature*, 518(7540):529–533, 2015. ISSN 14764687. doi: 10.1038/nature14236. URL <http://dx.doi.org/10.1038/nature14236>.
- P. Poirazi, T. Brannon, and B. W. Mel. Pyramidal neuron as two-layer neural network. *Neuron*, 37(6):989–999, 2003a. ISSN 08966273. doi: 10.1016/S0896-6273(03)00149-1.
- P. Poirazi, T. Brannon, and B. W. Mel. Arithmetic of subthreshold synaptic summation in a model CA1 pyramidal cell. *Neuron*, 37(6):977–987, 2003b. ISSN 08966273. doi: 10.1016/S0896-6273(03)00148-X.
- W. Rall. Physiological Properties of Dendrites. *Annals of the New York Academy of Sciences*, 96(4):1071–1092, 1959.

- J. Schiller, G. Major, H. J. Koester, and Y. Schiller. NMDA spikes in basal dendrites. *Nature*, 1261(1997):285–289, 2000. ISSN 1863-9135. doi: 10.1127/1863-9135/2007/0169-0223.
- I. Segev. What do dendrites and their synapses tell the neuron? *Journal of Neurophysiology*, 95(3):1295–1297, 2006. ISSN 0022-3077. doi: 10.1152/classicessays.00039.2005. URL <http://jn.physiology.org/cgi/doi/10.1152/classicessays.00039.2005>.
- A. Stuchlik. Dynamic learning and memory, synaptic plasticity and neurogenesis: An update. *Frontiers in Behavioral Neuroscience*, 8(APR):1–6, 2014. ISSN 16625153. doi: 10.3389/fnbeh.2014.00106.
- N. Toni, P. Buchs, I. Nikonenko, C. R. Bron, and D. Muller. LTP promotes formation of multiple spine synapses between a single axon terminal and a dendrite. *Nature*, 402(November):421–425, 1999.
- K. Travis, K. Ford, and B. Jacobs. Regional dendritic variation in neonatal human cortex: a quantitative golgi study. *Developmental neuroscience*, 27(5):277–287, 2005.
- B. B. Ujfalussy, J. K. Makara, T. Branco, and M. Lengyel. Dendritic nonlinearities are tuned for efficient spike-based computations in cortical circuits. *eLife*, 4(DECEMBER2015):1–51, 2015. ISSN 2050084X. doi: 10.7554/eLife.10056.
- D. E. Wilson, D. E. Whitney, B. Scholl, and D. Fitzpatrick. Orientation selectivity and the functional clustering of synaptic inputs in primary visual cortex. *Nature Neuroscience*, 19(8):1003–1009, 2016. ISSN 15461726. doi: 10.1038/nn.4323.
- H. Xiao, K. Rasul, and R. Vollgraf. Fashion-MNIST: a Novel Image Dataset for Benchmarking Machine Learning Algorithms. *arXiv preprint*, pages 1–6, 2017. URL <http://arxiv.org/abs/1708.07747>.
- A. M. Zador and B. A. Pearlmutter. VC Dimension of an Integrate-and-Fire Neuron Model. *Proceedings of the ninth annual conference on Computational learning theory*, pages 10–18, 1996.
- A. M. Zador, B. J. Claiborne, and T. H. Brown. Nonlinear pattern separation in single hippocampal neurons with active dendritic membrane. *Advances in Neural Information Processing Systems*, pages 51–58, 1992.

## 7 Supplementary Material

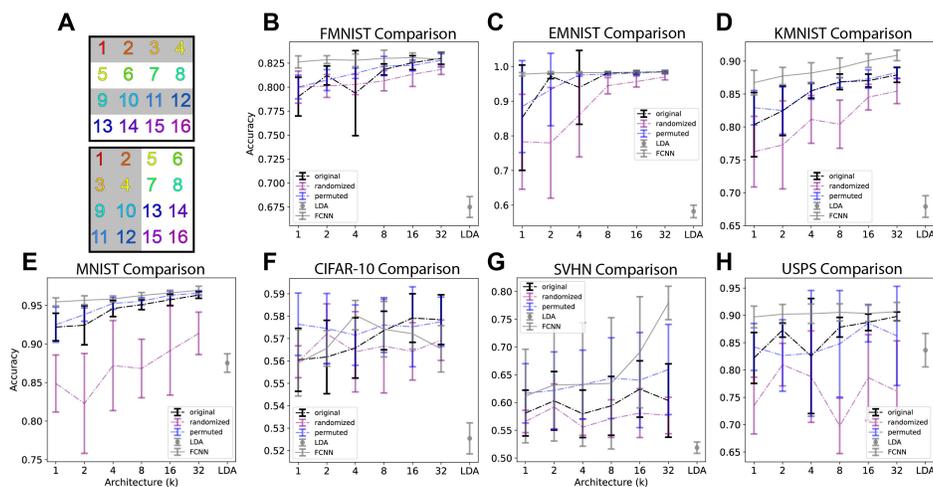


Figure S1: Permuted and randomized input trials.  $k$ -tree performance is compared to that of a lower bound, LDA, and an upper bound, FCNN. A: Example of original input setting (top) and permuted input setting (bottom). B-H: Original input is in black, permuted is in blue, randomized is in purple, FCNN and LDA are in gray. Randomized input tends to perform lower than original and permuted input.