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BIOLOGY



Background

While individual neurons are complex entities that can process inputs and encode outputs of their own, the truly interesting behavior of neurons arises when many are linked together in a network. Networks of neurons increase the amount and complexity of the information that can be encoded, transmitted or stored. However, with the increase in information power comes practical complications for the network. While the amount of information that can be transmitted is maximized when the neurons are completely decorrelated and entropy is maximized, a network of this form is unable or inefficient at actually transmitting information since firing between different neurons is largely randomized. Instead, the neurons in a network must form correlations between each other in their firing patterns. A balance must be struck between the amount and diversity of information that can be transmitted and the efficiency with which that information can be encoded by the network and later decoded by the system receiving the information.

To form these correlations, the neurons in this network must learn to communicate in specific manners, for instance learning to fire in conjunction with certain neurons but not with others or responding to certain firing patterns but not others. There are many theoretical paradigms for how these neurons learn to communicate; one prominently used method is Hebbian learning. In this method, the connection between the postsynaptic and presynaptic neurons strengthens as the presynaptic neuron repeatedly stimulates the postsynaptic neuron (Gerstner & Sjöström 2010).

However, this method only considers simultaneously firing neurons but does not contain information on how differences in firing times between the postsynaptic and presynaptic neurons can affect the strength of their connection. Hebbian learning can be extended to include this, which leads to the method of spike-timing-dependent plasticity (STDP). STDP modulates the connection strength between two pairs of neurons based on the average timing of the spikes produced by both neurons. Generally, if a presynaptic neuron tends to fire right before the postsynaptic neuron fires, then the synapse will be strengthened, but if on average it fires right after the postsynaptic neuron, the synapse will be weakened (Dan & Poo 2004). This has the effect of reinforcing excitatory inputs to the postsynaptic neuron and disregarding or lessening inputs that do not contribute to postsynaptic firing. This process results in a network of equally connected neurons that are refined to neuron subsets of the network, which are highly correlated in time and synaptically independent of the other irrelevant components. This project will investigate the functionality of STDP as a valid method for learning between neurons and within networks of neurons.

Significance

Our project will explore the ability of neurons to learn to respond to a particular signal in a predictable way. Our first proposal involves a “teacher” neuron teaching a “student” neuron to imitate the input of neuron A while ignoring the signal of neuron B. The question of whether it is possible for the weight of B to decay while maximizing the weight of A will be explored across different parameters of the model.

Our model greatly simplifies the processes that occur *in vivo* as learning occurs, but incorporates the fundamental importance of timing and causality in learning, which is left out of

the purely Hebbian model (Caporale & Dan 2008). In classical conditioning, for example, there are limits on when a reward (unconditioned stimulus) is effective for conditioning a particular response to an unconditioned stimulus. We will not create models on the timescale of classical conditioning, but the principle of the importance of timing in learning is effectively the same.

Although there is compelling evidence for its existence, the exact mechanism of STDP is not well understood (Caporale & Dan 2008). For the timing of the spike to determine the probability that the postsynaptic neuron will fire, it is possible that the timing of the spike has an effect on the external conductance of the postsynaptic membrane, as has been modeled in literature (Song et al. 2000). One could then use an integrate-and-fire model to determine what the firing pattern of the postsynaptic neuron will look like given some input. Due to the increased complexity of such a model, we will model the effect of the presynaptic neuron as a current input to the postsynaptic neuron rather than a change in conductance.

However, we will add complexity to our model by examining a model for birdsong learning. It has been shown that STDP is involved in the learning of birdsong, though it is not enough by itself to allow for learning of long sequences (Fiete et al. 2010). Thus, we will investigate a greatly simplified, short model of birdsong that can be learned with STDP alone, given a particular sequence of inputs.

Methods

Teacher/student

Neurons A and B have particular stimulus sequences associated with them, which are fed into the student. These stimulus sequences consist of randomly timed spikes, drawn from a Poisson process. Initially, the student fires based on a constant external current, incorporating spikes in current from A and B with equal weighting. The stimulus coming from A and B creates a rise in current that depends on the synaptic weight, and this current extra then decays exponentially over time. The student is an integrate-and-fire neuron that fires after enough external current has gone into it. The teacher exists to tune the student to a particular presynaptic neuron (i.e. A or B); in this experiment, our aim is to tune the student to A and to teach the student to disregard B. Critically, neuron A is also connected to the teacher, which therefore knows what A is sending to the student. When neuron A sends a spike to the student, the teacher follows through by sending its own spike that reaches the student neuron simultaneously, hence providing a feedforward stimulus for the student. This network is shown in Figure 1.

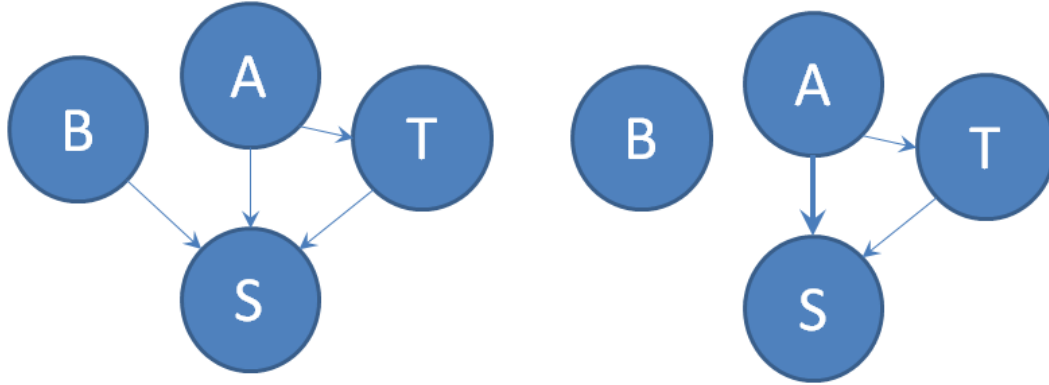
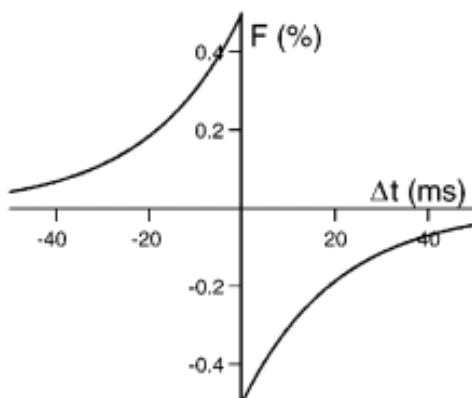


Figure 1. The network on the left shows neurons B and A feeding current into the student (S), with A connected to the teacher (T) such that their current inputs reach S simultaneously. The network on the right shows what we will teach the student neuron: to respond strongly to A and ignore B.

Now consider two cases. In one, the student fires after it receives a stimulus from A, and the following feedforward stimulus from the teacher. According to Figure 2 below, both of these input stimuli correspond to negative Δt , with $|\Delta t_A| = |\Delta t_{teacher}|$, so they both contribute a positive change in weighting, $F(\Delta t)$. In this case, the teacher's stimulus provides an even more positive change in weighting than the stimulus from A alone. In the second case, the student fires before it receives the stimuli from A and the teacher. Hence, both A and the teacher contribute negative change in weighting for the synaptic strength between A and the student. The synaptic weight change for a negative Δt will be greater in magnitude than a positive strengthening, so if the presynaptic neuron fires just as much before the student neuron as after, its synapse will eventually decay away. Unless stated otherwise, our ratio of the inhibition coefficient to the strengthening coefficient, labeled A_- and A_+ respectively, is 1.05, which was found in the literature (Song et al. 2000).

The same changes in weighting occur for the synapse between B and S. The difference between B and A is that A fires concurrently with the teacher, whose weighting does not change with regard to current input to the student. The net effect of repeated instances of these cases is that the weightings associated with A increase over time, despite the negative changes resulting from the student occasionally firing before A. This is due to the fact that since A and the teacher fire together and therefore generate more current in the student than B, they are more likely to cause the student to spike than just B. Hence, the connection between the student and A is strengthened due to the increased weighting, which increases the correlation between A firing and the student firing. The synapse with B, on the other hand, is weakened over time.



$$F(\Delta t) = \begin{cases} A_+ \exp(\Delta t / \tau_+) & \text{if } \Delta t < 0 \\ -A_- \exp(-\Delta t / \tau_-) & \text{if } \Delta t \geq 0 \end{cases}$$

Figure 2. A form of the STDP weighting change plot is shown above, as are the equations that are used to create it. The constant before the inhibition equation is larger in magnitude than that of the strengthening equation in our model, which should cause stimuli that are about as likely to come before a spike as after to decay.

Our STDP function is shown below in Figure 3. However, we need to determine what quantity the y-axis changes. If the values represent a change in the weighting of the synapse, that could lead to an infinitely strong synaptic connection, which does not make physical sense. Therefore, we create a nonlinear function that saturates at high and low x-values, making the y-axis on the STDP correspond to a change in the position on the x-axis of this nonlinearity. We use a sigmoidal function for the nonlinear weighting function (Figure 4). The result is that the synaptic weight can never be higher than 10 and never lower than 0, which makes our model much more realistic.

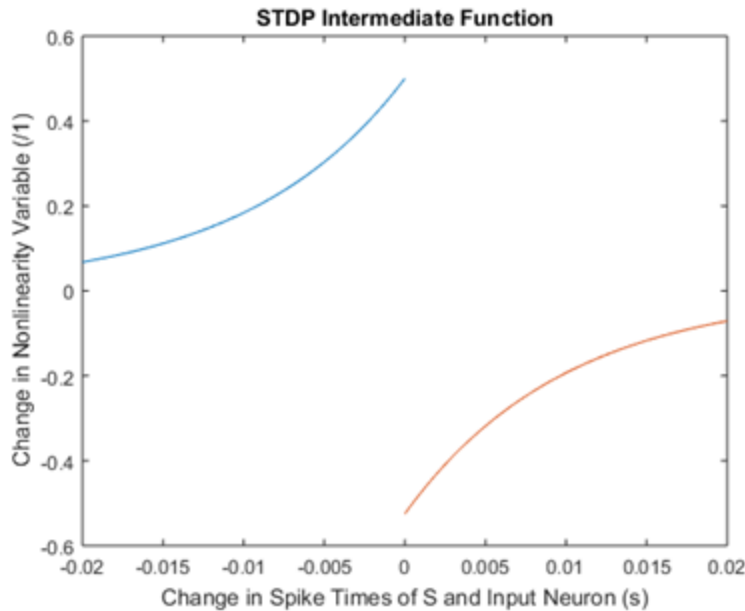


Figure 3. Our STDP function. The blue line corresponds to an increase in the x-axis in Figure 4, while the red line corresponds to a decrease. The origin represents the time when the student neuron spiked, with the x-axis represents the difference in time between that spike and a spike from A or B.

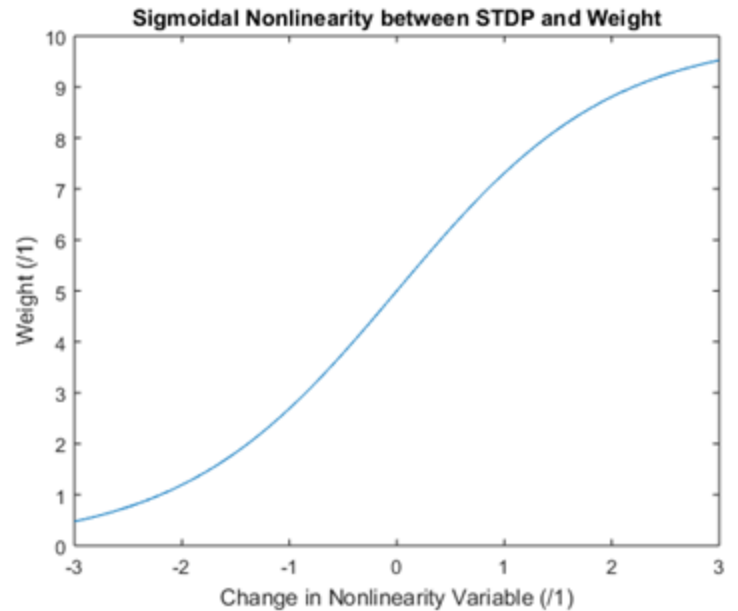


Figure 4. This function shows how the STDP function causes a change in weights. The synaptic weights are initialized at some point on the x-axis, and this is what changes due to the STDP function. Thus, the weights saturate at either zero or ten.

The next step is to introduce the inputs to the student cell. We use functions in MATLAB to draw the space between spikes from a Poisson distribution, making neurons A and B Poisson-process neurons. We then code differential equations for the current input to the student as well as for the membrane voltage of the student. We can plot each of these values against time to see how current inputs from A gradually cause a sharper rise in current, and therefore voltage, while input from B decays. Additionally, we create differential equations for the synaptic weights between A and S as well as B and S. Plotting these quantities over time would give us the most accurate view of whether the neuron had learned: if at long times the synaptic weight between A and S saturates at the maximum, and if the weight between B and S saturates at 0, then we can say that the student learned. In our experiment, we use the conditions that the weight of A is greater than 9 and the weight of B is below 1 to define learning.

With a working model, we can adjust parameters of the model to increase the rate of learning, investigating which are most relevant. We test different values of the exponent in the sigmoidal weighting curve, making it either steeper or more gently sloped. We also test different

values of the inhibition strength in the STDP exponential function, using the optimum steepness of the sigmoid as calculated in the above optimization procedure. We run 100 trials for each value of a parameter to find the probability that the neuron learns.

Having optimized parameters, we then create a function to decrease the synaptic weight of the teacher over time. Once the student learns to respond strongly to A, we want to know whether this connection will stay strong if the teacher neuron's signal decays away. Biologically, this represents a more efficient network in the brain, as the three presynaptic neurons are pruned down to one. For this, we use a sigmoidal function that changes the synaptic weight from some maximum value to zero over time.

Birdsong Model

Once we have a complete STDP model, we can then use STDP to implement a model for birdsong learning. The network for that is shown in Figure 5. We assume that there are three input neurons, each firing at the same rate but offset so that they fire at fixed intervals.

Our goal is to use STDP to train the post-synaptic neurons 1, 2, and 3 to respond to the desired stimulus. In this case, we want A to induce neurons 1 and 2 to fire, B to induce 2 and 3, and C to induce 3 and 1. Biologically, this represents the bird hearing a note, causing one of the presynaptic neurons to fire, and the bird reproducing the note by using muscles controlled by the appropriate two postsynaptic neurons.

Accomplishing this task requires a set-up similar to the STDP learning of a single neuron connection. The postsynaptic neurons are all integrate-and-fire neurons, using a constant current in addition to injections of current from the presynaptic neurons. The addition of the teacher strengthens the synaptic connections by inducing the postsynaptic neurons to fire after the correct presynaptic neurons with an extra increase in current. For computational simplicity, the weight of the teacher stays constant throughout the duration of a trial. We run 100 trials for different values of inhibition strength using a steep sigmoid. The similarity to single-neuron STDP procedure leads us to expect that learning will occur in these neurons as well.

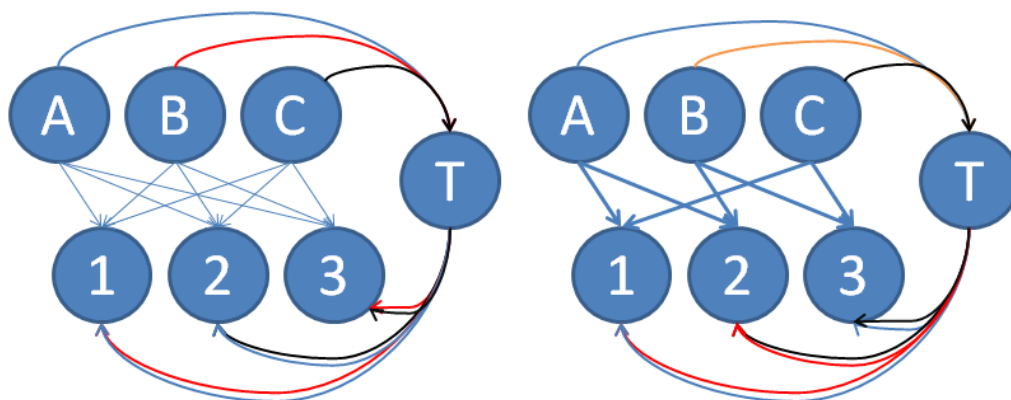


Figure 5. The network on the left shows the initial conditions, where all neurons are connected in a feedforward network. The teacher neuron's color-coded connections demonstrate what connections it strengthens. For example, the blue line coming from A means that the teacher contributes to current in neurons 1 and 2 when A fires. On the right, the network has learned the correct synaptic connections from the teacher.

Results

Single-Neuron STDP

Our implementation of STDP for a single student neuron was successful, and we were able to experiment with parameter optimization. Resulting plots of voltage and weights for an example trial of STDP learning are shown in Figure 6 and Figure 7.

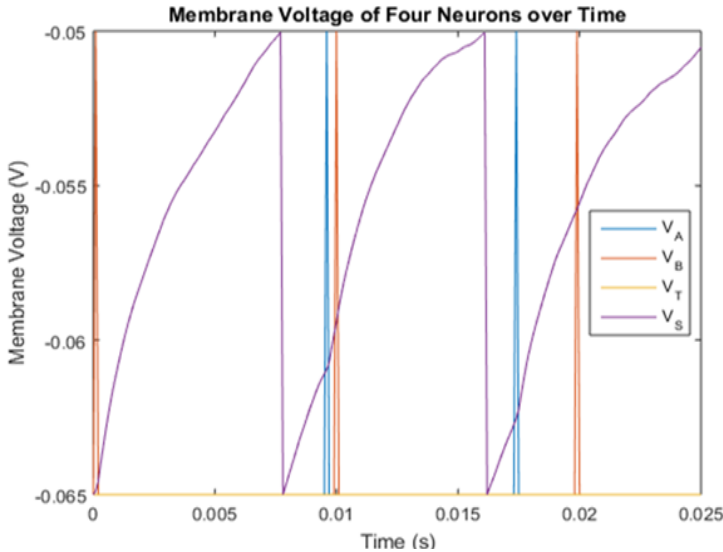


Figure 6. This plot shows the beginning of a trial. The purple line represents the membrane voltage of the student neuron, which peaks as the result of a constant current. The spikes represent the firing of A and B. Following those spikes, one can observe an increase in voltage for the student due to current contributions from those spikes.

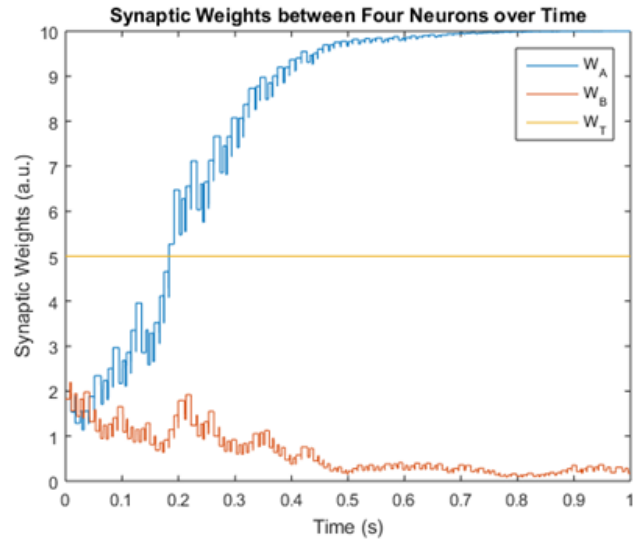


Figure 7. The synaptic weights of neuron A (blue), neuron B (red), and the teacher (yellow) are shown. Over time, the neuron learns to weight the input current from neuron A, and mostly ignores the current coming from neuron B.

Parameter Optimization: Steepness of A, B Weight Sigmoid

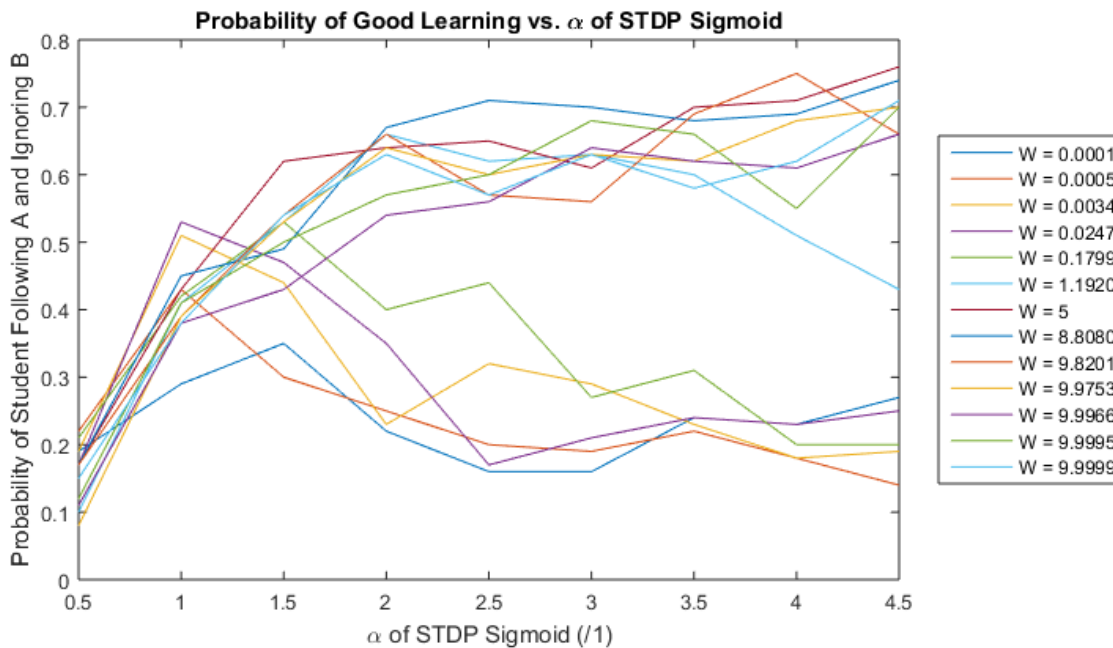


Figure 8. The probability of learning given different parameters. The x-axis represents the steepness of the sigmoid function used to convert the STDP function to a change in weight, and the different traces represent different initial weights.

For shallow sigmoids (lower alphas), the weights of A and B are subject to more variability initially, since the sigmoid is not flat in the regime near the initial weights of A and B. This allows the weight of B to experience occasional significant increases, which prevent the weight from decaying. Therefore, learning probability is low for shallow sigmoids across all teacher weights.

A steep sigmoid and high teacher weight result high probability of learning. This setup ensures that the stimulus from A that the student feels is always strong, thus forcing a spike from the student soon afterwards. This allows the weight of A to reach a high value quickly. In addition, a steep sigmoid prevents the weight of B from increasing significantly. Spikes from B are not followed by a reinforcement from the teacher, so the changes in the weight of B are minimal, since the sigmoid is flat near the initial weight of B. Therefore, the weight of A increases, and the weight of B decreases, resulting in a high probability of learning, as evident in the plot. The probabilities follow a saturating exponential, roughly of the form $1 - c * e^{-\alpha}$.

A steep sigmoid and a low teacher weight result in reduced probability of learning. Since the teacher's stimulus is weaker, the total stimulus from A that the student feels is not significantly greater than the stimulus exclusively from A. This results in smaller changes in the weight of A, which may not be enough to push the weight of A over the sigmoid. Therefore, the probability of learning is reduced.

Interestingly, the probability of learning for lower teacher weights is optimum for alpha between 1 and 1.5. The low teacher weight is too weak to push the weight of A over a steep sigmoid, but it is potentially strong enough to increase the weight of A for a shallow sigmoid. The probability is not very large since the shallow sigmoid also allows the weight of B to increase, which hinders proper learning.

Parameter Optimization: Strength of STDP Inhibition

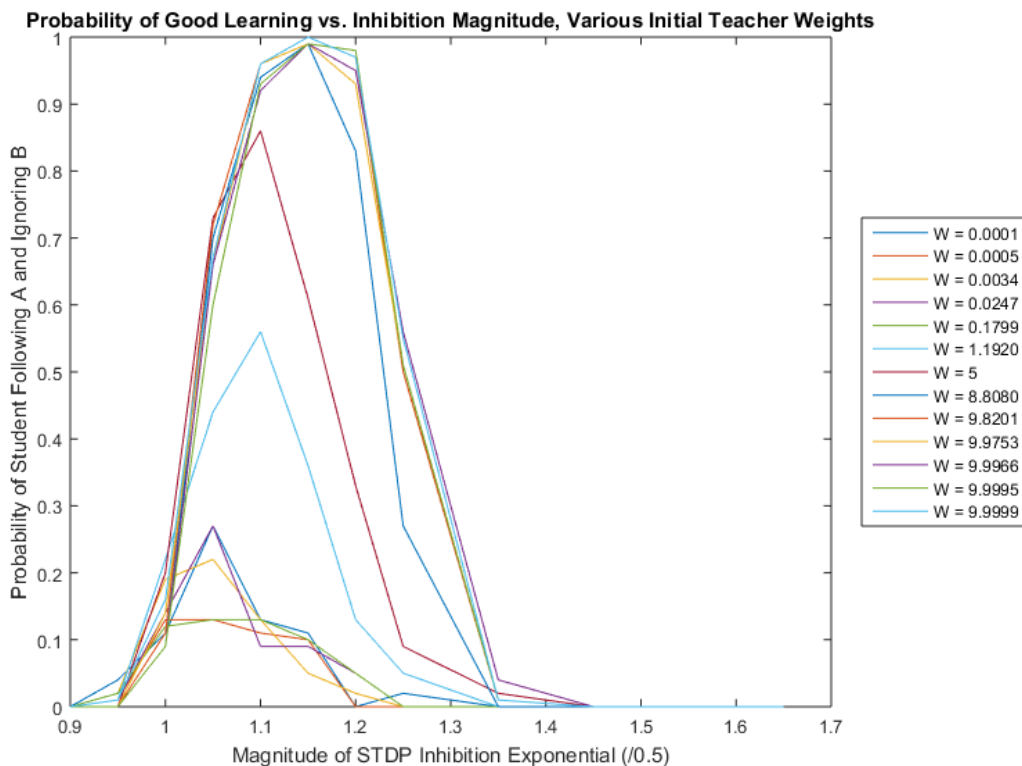


Figure 9. The x-axis of this plot represents the ratio of the coefficient of the STDP inhibition function to the coefficient of the STDP strengthening function (labeled A_- and A_+ respectively in Figure 2). The differently colored lines, as in Figure 8, represent different initial weights.

This plot displays the balancing act between teacher weight and inhibition of spikes from A or B that occur after a spike from the student. If the inhibition is too strong, no teacher weight can provide a strong enough stimulus to the student to counter the decrease in weights of A and B due to random spiking after the student, thus preventing proper learning. If the inhibition is too weak, the weights of both A and B increase over time, which also prevents proper learning. However, each teacher weight has a particular range of alphas over which learning is not suppressed. Notably, as teacher weight increases, the strength of the inhibition that results in strongest learning increases as well.

Atrophy of Teacher Weight

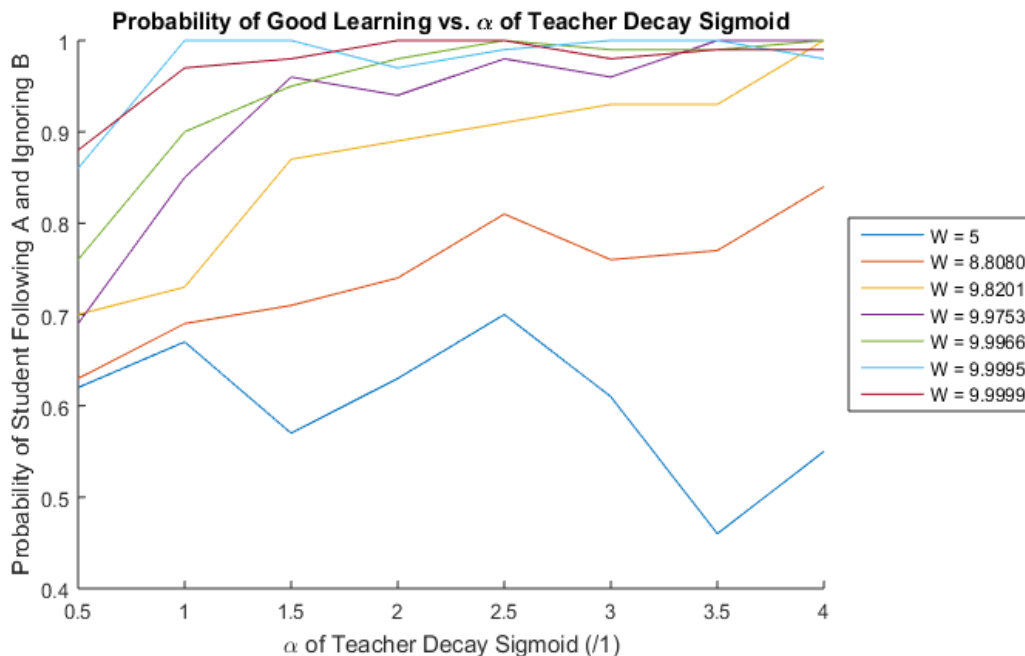


Figure 10. The atrophy of the teacher weight follows a sigmoidal function with decay parameter alpha. Larger values of alpha signify steeper sigmoidal functions. Each trace represents a different initial value of the teacher weight. We choose teacher weights of value five or greater because the initial value must be large enough to undergo a significant decay.

We characterize the decay of the teacher weight by a sigmoidal function with an initial value and a steepness parameter, alpha (note that this sigmoid and alpha are independent from the sigmoid and alpha employed in the STDP model for the weights of A and B).

For high initial weight of the teacher and a steep sigmoid, the weight of the teacher remains close to its initial value for a significant duration of the trial. This allows the teacher to increase the weight of A while the teacher's weight is high; once the teacher's weight decays, the weight of A will have already peaked. This setup used a steep sigmoid to model the weights of A and B, so the weight of B is naturally suppressed. Therefore, this setup results in high probability of learning, as is evident in the figure.

Low initial teacher weights result in reduced probability of learning since the teacher is not strong enough to consistently send the weight of A to a peak value. As a result, the steepness of the sigmoid cannot significantly affect the probability of learning. This is evident in the probability of the lowest initial weight; although the trace does increase and decrease for certain alphas, it does not increase as a whole from low alpha to high alpha.

Birdsong Model

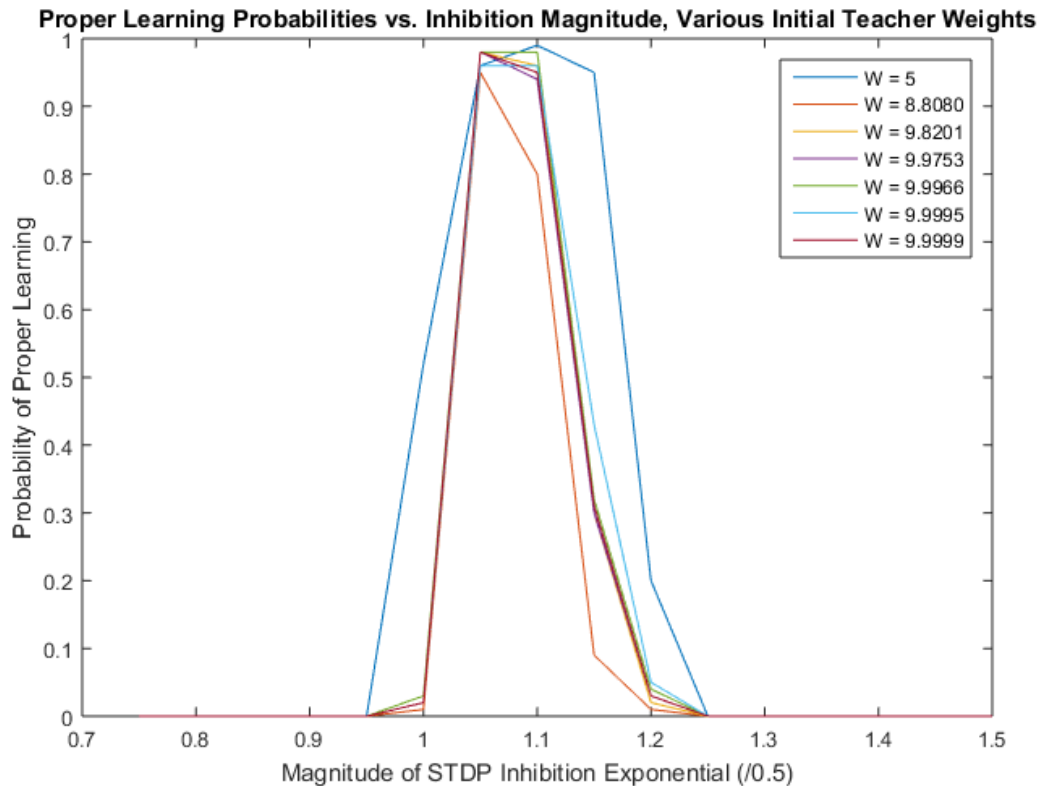


Figure 11. Results for running the birdsong model with various STDP inhibition strengths. Each trace represents a different value of the teacher weight. The x-axis represents the ratio of the coefficient of the STDP inhibition function to the coefficient of the STDP strengthening function.

As in our model of single-cell STDP, our model of birdsong learning includes a parameter governing the strength of STDP inhibition. For teacher weights below 5, the probability of learning is either zero or negligible for all values of inhibition strength. The probability of learning peaks at an inhibition strength of either 1.05 or 1.10 for all teacher weights. Notably, the peaks are approximately symmetric in most cases.

Conclusions

STDP is a powerful theoretical framework for modeling neuronal learning and synaptic plasticity that incorporates the time differences between presynaptic and postsynaptic neuron firing to modulate the synaptic connection strengths. With the influence of a teacher neuron, this causes the correct neuronal connections to be strengthened and the incorrect ones to atrophy over time. STDP has been found to greatly improve on traditional Hebbian learning methods in modeling neuronal learning and has been used to study birdsong learning. A basic model of STDP was implemented as a proof of concept. This model was used to optimize different parameters, including the steepness of the weight sigmoid nonlinear transformation and the strength of STDP inhibition. Optimization of the nonlinearity found that steeper sigmoids produced bifurcated behavior, where stronger initial teacher strengths increased learning efficiency while lower weaker strengths decreased the probability of learning. Optimizing STDP inhibition found that learning was maximized with an inhibition slightly larger than the excitatory

STDP and varied around this maximum in a distribution that qualitatively appeared Gaussian or Poisson. Notably, peak learning occurred at higher inhibition values for higher teaching strengths. Decay of the teacher synapse was implemented through a sigmoidal function and the rate of this decay was varied. This found that steeper sigmoids produced improved learning for higher teacher strengths but had little effect for weaker strengths. The STDP model of birdsong learning was implemented and the STDP inhibition was varied. It was found that no or little learning occurred below a certain level of teacher strength, but above that level a highly similar distribution of learning probability was produced. This distribution peaked at a magnitude slightly larger than the excitatory STDP and qualitatively appeared Gaussian. These results show that with the correct parameters, STDP is a valid and powerful model for studying neuronal systems of learning, especially the phenomenon of birdsong learning.

In the future, a more accurate model of STDP can be found by investigating the exact biomolecular mechanism by which it occurs. Once the full function of STDP is better understood, it might become possible to create better models for higher cognitive functions such as memory (Dan & Poo 2004). It is likely that rules other than STDP are involved in the learning of longer or more complex sequences of behaviors, as has been shown in the case of birdsong, which also requires heterosynaptic competition to fully develop (Fiete et al. 2010). Closer examination of how individual neuron behavior results in STDP as well as other emergent network properties is therefore crucial to creating more effective learning models.

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