

# STDP Produces Well Behaved Oscillations and Synchrony

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**Abstract**— It has been demonstrated that, in a network of excitatory and inhibitory neurons, a synchronous response gradually emerges due to spike timing dependant plasticity acting upon an external spatio-temporal stimulus that is repeatedly applied. This paper builds on these findings by addressing two questions relating to STDP and network dynamics. Firstly, how does the choice of neuron model affect the learning of oscillation through STDP? Our experiments suggest that the earlier results hinge on the selection of a simple, biologically less realistic neuron model. Secondly, how do neural oscillators that have learned to oscillate only in response to a particular stimulus behave when connected to other such neural oscillators? We investigate this question by emulating the results of a classic experiment by Kuramoto.

## Introduction

Spike Timing Dependent Plasticity (STDP) is a refinement of the Hebbian learning principle for spiking neural networks, and has been reported in many experimental studies [1]. STDP has further been studied in relation to oscillations. Hosaka *et al* [2] demonstrate oscillatory dynamics in a network of excitatory and inhibitory neurons that has been trained using STDP with an external spatio-temporal stimulus that was repeatedly applied. They found that a synchronous response gradually emerges, and the synchrony becomes sharp as learning proceeds. The authors state that the generation of synchrony itself does not depend on the length of the cycle of external input, however they found that synchrony emerges once per cycle of the length of the external stimulus trained upon.

This paper addresses two issues relating to STDP and network dynamics. Firstly, how does the choice of neuron model affect the learning of oscillation through STDP? Secondly, how do neural oscillators that have learned to only oscillate in response to a particular stimulus behave when connected to other neural oscillators?

## Methods

### A: Quadratic integrate-and-fire neurons

The Quadratic Integrate and Fire (QIF) model [3] displays Type I neuron dynamics [4] with a saddle node bifurcation. The time evolution of the neuron membrane potential is given by:

$$\frac{dV}{dt} = \frac{1}{\tau} (V - V_r)(V - V_t) + \frac{I}{C}$$

where  $V$  is the membrane potential, with  $V_r$  and  $V_t$  being the resting and threshold values respectively.  $C$  is the capacitance of the cell membrane.  $\tau$  is the membrane time constant such that  $\tau = RC$  with  $R$  being the resistance.  $I$  represents a depolarizing input current to the neuron.

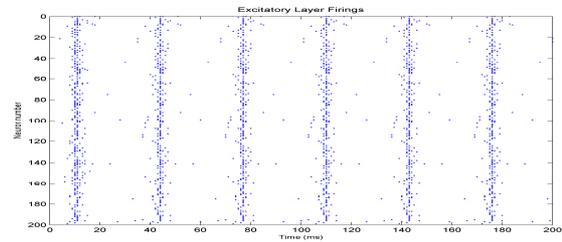


Fig. 1. Raster plot of neuron firings from the excitatory layer of a QIF PING node that has learnt to oscillate at 30 Hz.

### B: Izhikevich neurons

The Izhikevich (IZ) neuron model [5] is a two variable system that can model both Type I and Type II neurons depending upon how it is parameterized. The time evolution of the model is defined as follows:

$$\frac{dV}{dt} = 0.04V^2 + 5v + 140 - U + I$$

$$\frac{dU}{dt} = a(bV - U)$$

$$\text{if } V > 30, \text{ then } \{ V \leftarrow c, U \leftarrow U + d$$

$I$  is the input to the neuron.  $V$  and  $U$  are the voltage and recovery variable respectively, and  $a$ ,  $b$ ,  $c$  and  $d$  are dimensionless parameters. The chosen parameter values dictate that the Izhikevich neurons used in this paper are Type II neurons with a saddle node bifurcation.

### C: Hodgkin-Huxley neurons

The Hodgkin-Huxley (HH) model [6] is a Type II neuron with an Andronov-Hopf bifurcation. Hodgkin and Huxley found three different types of ion current: sodium ( $\text{Na}^+$ ), potassium ( $\text{K}^+$ ), and a leak current that consists mainly of chloride ( $\text{Cl}^-$ ) ions. From their experiments, Hodgkin and Huxley formulated the following equation defining the time evolution of the model:

$$C \frac{dV}{dt} = g_K n^4 (V - E_K) - g_{Na} m^3 h (V - E_{Na}) - g_L (V - E_L)$$

$C$  is the capacitance and  $n$ ,  $m$  and  $h$  describe the voltage dependence opening and closing dynamics of the ion channels. The standard parameterisation and rate functions for each chemical and channel are used and can be found in Hodgkin and Huxley's book [6].

### D: Synaptic model

A conductance synaptic model is used for experiments using the QIF and IZ models model, whereas the HH model uses synaptic reversal potentials to further scale incoming spikes. The latter model is as follows:

$$I_j(t) = \sum_i w_{ij} t_i (Rev - V_j)$$

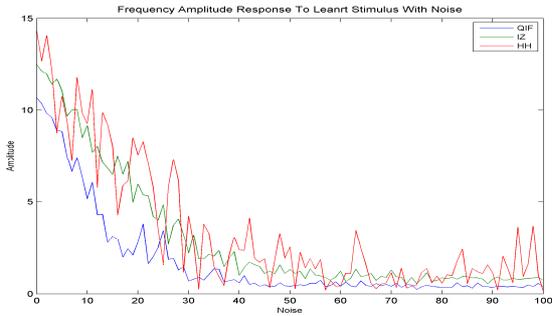


Fig. 2. Amplitude of desired 30 Hz frequency response for QIF, IZ and HH models with 0%-100% noise added to stimulus.

where  $I_j(t)$  is the input to neuron  $j$  at time  $t$ ,  $t_i$  is the spike from neuron  $i$  arriving at time  $t$ , and  $w_{ij}$  is the weight of the synapse connecting the two neurons.  $Rev$  is the reversal potential and  $V_j$  is the voltage of the target neuron.

#### E: Spike timing dependent plasticity

The STDP update method used in this paper is an 'additive nearest neighbour' scheme. A pre-synaptic spike followed by a post-synaptic spike potentiates the synaptic weight, where as a post-synaptic spike followed by a pre-synaptic spike depresses the weight. The change in weight ( $\Delta w$ ) is affected by the exponential of the time difference ( $\Delta t$ ) and the learning rate constant ( $\lambda$ ):

$$\Delta w = \lambda e^{\frac{-|\Delta t|}{\tau}}$$

For potentiation, the learning rate value  $\lambda$  is 0.3, and the window  $\tau$  is 20 ms. For depression, the learning rate value  $\lambda$  is 0.3105 and the window  $\tau$  is 10 ms.

#### F: Evolution of oscillatory nodes

The neural architecture for generating oscillations used in this paper is pyramidal inter-neuronal gamma (PING), and can give rise to both faster gamma oscillations, as well as slower oscillations such as theta in the cortex and the hippocampus [7].

Whilst the general PING architecture is well understood, the specific details required for both particular oscillatory frequencies and neuron model varies and involves a large space of parameter values within the general PING framework. In order to obtain these values we used a genetic algorithm. In the present work, all neural populations used an excitatory layer of 200 neurons and an inhibitory layer of 50 neurons. The excitatory layer drives the entire network and so is the only one to receive external input. The networks were wired up with connections between excitatory neurons, between inhibitory neurons, from excitatory to inhibitory neurons, and from inhibitory to excitatory neurons.

The parameters that were evolved were the length in milliseconds of the external stimulus presentation, the synaptic weights and delays, as well as the number of synaptic connections between source and target neurons in each pathway. The amount of time trained for was also an evolved parameter for networks that learnt. Two types of PING architecture networks were investigated. The first learnt a stimulus and then after learning would only oscillate to the learnt stimulus. The second did not use learning and so would oscillate to any input stimuli.

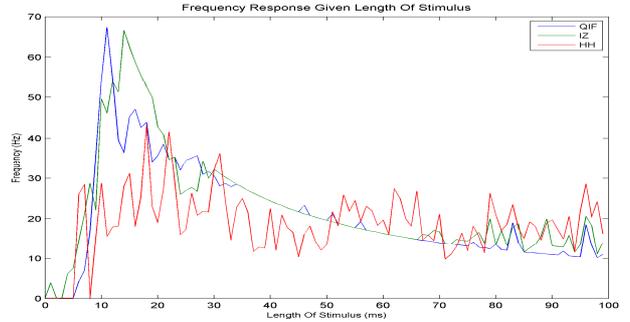


Fig. 3. Frequency response for QIF, IZ and HH models after learning with varying stimulus lengths.

#### G: Synchronisation metric

The Kuramoto inspired critical coupling experiment simulations in this work consisted of 64 neural PING oscillators connected together. We only calculated synchrony amongst the excitatory neuron layers. The spikes of each neuron in each excitatory layer were binned over time, and then a Gaussian smoothing filter was passed over the binned data to produce a continuous time varying signal. Following this, we performed a Hilbert transform on the mean-centred filtered signal in order to identify its phase. The synchrony at time  $t$  was then calculated as follows:

$$\varphi = \frac{1}{t_{\max}} \sum_t \left| \frac{1}{N} \sum_j e^{i\theta_j(t)} \right|$$

where  $\theta_j(t)$  is the phase at time  $t$  of oscillatory population  $j$ .  $i$  is the square root of  $-1$ .  $N$  is the number of oscillators, and  $t_{\max}$  is the length of time of the simulation.

#### Results

##### A: Neuron model and the learning of oscillation

Our first investigation explored how the neuron model affects the ability of a cluster of neurons to learn to oscillate. In order to explore this we evolved neural learning PING oscillators to oscillate at 30 Hz for QIF, IZ and HH neuron models. Figure 1 shows a raster plot of the firings of the excitatory layer from the evolved QIF solution when it has been presented with a learnt stimulus after training. In accord with the finding of Hosaka *et al* [2], the network fires regularly at the stimulus presentation, and has narrow and pronounced periodic bands. These thin bands appear approximately every 33 milliseconds giving the 30 Hz oscillation desired.

Figure 2 shows how the networks respond to between 0% to 100% noise in the stimulus averaged over 10 runs. The aim of this study is to ascertain if the network only responds by oscillating to the learnt stimulus and no other. The QIF network performs the best, showing a gradual decline in the amplitude of the frequency response until it reaches a minimal response at 40% noise. Less than 0.5 amplitude implies that only a few neurons are firing hence no response is really being produced, hence it is highly selective to only its learnt stimulus. The IZ model performs almost as well. The HH model performs poorest with a less pronounced frequency amplitude decline as noise rises, and also a less stable re-

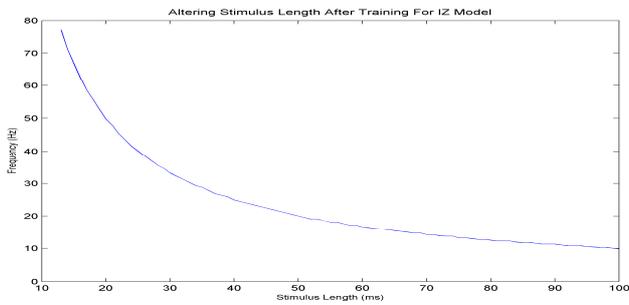


Fig. 4. IZ model after learning with stimulus. Frequency response for varying stimulus lengths presented after learning .

sponse throughout. The less stable response is due to a high variance in the amplitude over the 10 sample runs, and is indicative of the fact that the network is inherently more volatile.

Figure 3 shows the effect of changing the length in milliseconds of the stimulus trained upon (averaged over 10 runs). All learning stages for all stimulus lengths  $t$  had the same learning time. We located the frequency with the highest amplitude only. From the figure we can see that none of the models respond significantly to stimuli less than 10 ms long. Beyond this, the figure shows that for both QIF and IZ models, the length of the stimulus is roughly proportional to the frequency ( $f$ ), with  $f=1000/t$ . This cannot be said of the HH model, which is unable to use the same network architecture to learn to oscillate at different frequencies, given only a change in the stimulus length. Having found a dependency on stimulus length, we removed the inhibitory layer from the networks and found it made no difference to the performance of QIF, IZ and HH models. We conclude that, regular repetition of a stimulus to a network that has been trained using STDP will cause oscillation at the frequency of presentation. For the HH model this further means that whilst stimulus length is important in achieving the result, the tuning of other variables is necessary to achieve the desired oscillation.

The fact that oscillatory frequency is dependent upon the length of the presentation can be elucidated by the work of Masquelier *et al* [8]. They report that, ‘*Each time the neuron discharges in the pattern, it [STDP] reinforces the connections with the presynaptic neurons that fired slightly before in the pattern. As a result next time the pattern is presented the neuron is not only more likely to discharge to it, but it will also tend to discharge earlier*’ [8]. The fact that neurons learn to always respond to a particular stimulus implies that the regular repetition of a stimulus to a recurrent network would cause the network to fire regularly at the stimulus presentation, and that this firing would become earlier and sharper, in the sense of producing narrower and more pronounced periodic bands, as learning proceeds. Hence, the resulting synchrony.

It follows from this that after an appropriate period of learning the frequency of the oscillation can be adjusted by simply altering the length of the stimulus, as it is only the beginning of the stimulus that is required to induce firing. To test this hypothesis we generated a stimulus of 100 ms, trained the network on it repeatedly until a satisfactory amplitude response was attained. We then tested the network only using the first  $t$  milliseconds repeatedly.

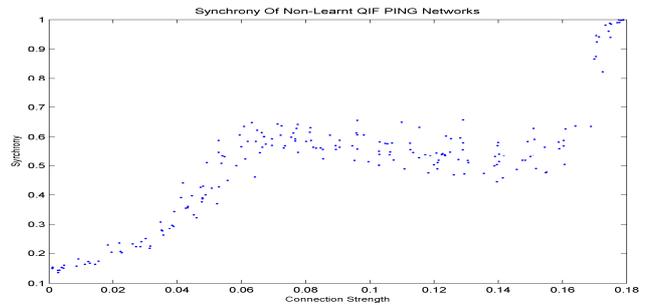


Fig. 5. Synchrony of QIF models that have not used STDP to train to respond to a particular stimulus and therefore responds to any stimuli.

We did this for every value of  $t$  between 13 and 100 ms. As can be seen by the results for the IZ model shown in figure 4, the hypothesis is correct. Hosaka *et al* [2] state that in a network of excitatory and inhibitory neurons, STDP transforms a spatiotemporal pattern to temporal information. However, from the evidence above we conclude that the resultant temporality is not due to the network dynamics that result from the PING architecture, but is an artifact of repeated *periodic presentation* of a learnt stimulus. The network will respond “synchronously” whenever the stimulus is presented.

### B: Critical coupling experiment

Our next investigation explored the critical coupling experiment [9] in which synchrony increases smoothly but rapidly as connection strength increases in a uniformly connected network of oscillators. We compare the results to neural oscillators that respond to any stimulus to with those that only respond to a learnt stimulus. We generated every frequency of oscillation between 10 Hz and 50 Hz for both types of architecture using QIF neurons.

In all our experiments we used 64 neural oscillator nodes to form a network, with frequencies selected using a Gaussian distribution with a mean of 30 HZ and a variance of 10 Hz. The phase of each oscillator was determined by the time at which external input to the oscillator was started, which varied from 0 ms to 100 ms. The slowest oscillator was 10 Hz and therefore a random start point ranging from 0 ms to 100 ms allowed for 10 Hz oscillators (as well as all oscillators of higher frequency) to be completely out of phase with each other. The neurons in the excitatory layers of each node were synaptically connected to the neurons in the excitatory layers of each other node with a connection ratio of 0.2. The experiments involved a sweep of 200 synaptic weights for all inter-node connections. Weights were set to the same value within each iteration in the parameter sweep, but with each different iteration having a different synaptic weight. On each sweep the overall synchrony of the network was measured. The networks were simulated for 2000 ms for each iteration of the sweep. Each network comprised 16000 neurons and 36,256,000 synapses.

Figure 5 shows the synchrony results for the evolved PING architectures that **do not use learning**. At 0 connection strength there is a synchrony of around 0.2, which indicates no synchrony at all except for coincidental alignments in phase. Synchrony rises with connection strength but so too does the spread of the dots, indicating some variation in behaviour with these systems. The

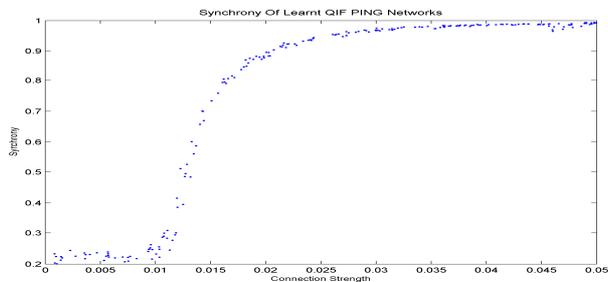


Fig. 6. Synchrony of QIF models that have used STDP to train to respond only to a particular.

synchrony levels off at 0.07 connection strength and remains the same until there is a major discontinuity at 0.17 connection strength.

By contrast figure 6 show the synchrony for the neural oscillators **that had learnt to oscillate**. Within a critical region of connection strengths, synchrony can be seen to increase smoothly but rapidly as connection strength increases, in accord with Kuramoto's findings. The connection strength is effective at different levels from the non-learning PING model due to different sensitivities in the different architectures, Poisson process parameters, and scaling factors. However the behaviour is the key difference to note. There is a very tight sinusoidal increase, indicating little variation in behaviour with these learnt systems, unlike those in figure 5. There are also no discontinuities.

On reaching 100% synchrony both types of architecture exhibited saturation, by which we mean all neurons were firing all the time. Figure 7 shows a 200 ms snippet of the pairwise synchrony between oscillator nodes at their respective maximal synchronies before saturation. The non-learning oscillator networks show deviations from full synchrony in which the network separates into sub-groups, which although they diverge, show similar phase movements indicating mutual influence between the groups. The learning architectures show little group separation behaviour but instead single oscillators seem to separate into their own phases away from full synchrony. The same behaviours are manifest at lower global synchrony levels albeit that the deviations are greater. The behaviour may be intuitively explained by the fact that in the non-learning architectures the individual intrinsic oscillatory frequencies of the nodes as well as the interaction between them are generated by the network architecture which forms a complete system, whereas in the learning architectures the individual intrinsic oscillatory frequencies are created by an external stimulus that is separate from the network system and as such is unable to receive dynamic feedback and therefore facilitates more individual rather than group behaviour.

## Discussion

It has been shown that STDP generates robust synchronous responses. After learning, the networks are highly selective for their learnt stimulus, responding at the beginning of each repeated stimulus presentation, and do not respond to other stimuli. We can conclude that repeated post-learning presentation of the stimulus overrides or interferes with the oscillations that would otherwise be caused by the delays in the PING architecture. A fast EI/IE loop will feed back and subside before the next

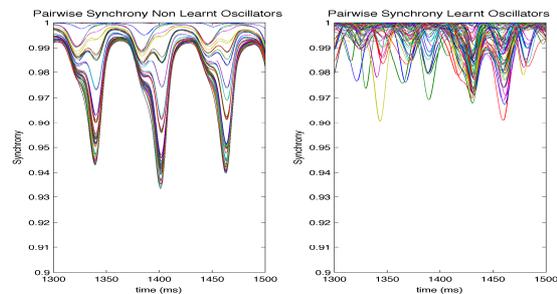


Fig. 7. Pairwise synchrony of QIF models at maximal synchrony before saturation. 200 ms shown only.

learnt stimulus response. In this case oscillations from the periodic stimulus will take precedence over PING oscillations. Using neurons of either Type I or Type II classification produces equivalent results with STDP. However, the HH model does not perform in the same manner. The difference in the HH model is the Andronov-Hopf bifurcation and the neuron's synaptic reversal potential. The result is a less robust network that is also unable to use the same architecture to learn to respond to stimuli that have a variety of presentation times. Further to this, the critical coupling experiment demonstrates that the collective behaviour of oscillatory architectures that have been pre-trained using STDP is well defined and precise, in contrast to those that have not been trained. However, the internal dynamical behaviour differs between the two architectures.

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