Computational Neurophysiology - Final Project

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Introduction

The role of synchronization in the binding of perception has slowly come into appreciation over the last couple decades. That synchronization is a widespread and fundamental aspect of neural behavior is not disputed [2]. What is disputed is what exactly the role of synchronization is. One proposal is that synchronization binds together otherwise independent perceptual features, symbolizing in a way that these features "belong" together in the current perceptual landscape [4].

The physical mechanism for consciousness is still unknown, but that has not stopped several researchers from searching for what they call "neuronal correlates to consciousness", or NCC [5]. Regardless of whether they can explain what exactly is happening, they can say that when a subject claims to experience a conscious percept, there is a corresponding and measurable activity of some variety in the nervous system. One of the most compelling NCC is that of transient synchronization of neural assemblies in the cortex. One question from all this is: why synchronization? How does synchronization in particular help the cortex to perceive whole things, when these perceptions are composed of more or less atomic features?

One way to approach this problem is to start with basic models of synchronization. How can synchronization be usefully modeled in a way that is applicable to neural dynamics? We explore a simple model of synchronization, the Kuramoto model, and then one of its applications to the connectivity and function of the primary visual cortex, given by Sompolinsky [6]. Ultimately we will elaborate on the Sompolinsky model by providing a

means of differing connection topologies between receptive fields, and varying dimensions of sensory stimuli.

Models of Synchronization

Kuramoto Model

One of the most successful models of general mathematical synchronization is the Kuramoto model [1] [3]. The N elements in the Kuramoto model are simple phase oscillators with a single phase variable θ and a preferred frequency ω. In addition, there is a connection matrix K whose elements K_{ij} express the strength of the coupling between the ith element to the jth element. The equation as a whole is given by a differential equation for a given element i:

$$\frac{\mathrm{d}\theta_i}{\mathrm{d}t} = \omega_i + \sum_{j=1}^{N} K_{ij} \sin(\theta_j - \theta_i)$$

where $i = 1, ..., N$. So basically, this equation is a sum over the sine of all of the differences between a particular element and all of the other elements, scaled by the connection matrix. The sine plays the functional role of emphasizing the differences between the phases. The more different are the phases of each of the oscillators to the one in question, the more that element's phase θ_i will be adjusted. If all of the elements happen to be in the same phase then the summing term would vanish and we would be left with the ω_i, which is the element's natural frequency. Left entirely to its own devices, the phase θ_i would be adjusted by its natural frequency ω_i each time step, and the phase would march merrily along a constant cycle.

The Kuramoto model displays remarkable robustness of synchronization, and if no other factors come into play the elements will be swiftly phase-locked. This model is straightforward to implement. Here is the python code for a basic implementation of the Kuramoto model:

```python
from pylab import *
tau = 2 * pi

class Kuramoto:
    def __init__(self, N, K=0.1, order=0.1):
        self.N = N
```

```python
        self.K = K
        self.order = order
        self.scale = K / N
        self.reset()

    def reset(self):
        self.phase = random(self.N) * tau
        self.intrinsic = random(self.N) * self.order
        self.spikes = zeros(self.N)
        self.phases = self.phase

    def deltax(self, x):
        differences = sum(sin(self.phase - self.phase[x]))
        return self.intrinsic[x] + self.scale * differences

    def delta(self):
        return array(map(lambda x: self.deltax(x), range(self.N)))

    def step(self):
        self.phase += self.delta()
        spiking = (self.phase >= tau)
        self.spikes = vstack([self.spikes, where(spiking, 1, 0)])
        self.phase = where(spiking, self.phase - tau, self.phase)
        self.phases = vstack([self.phases, self.phase])

    def run(self, steps):
        self.reset()
        for step in range(steps):
            self.step()
```

To use this code it is necessary to have a working installation of python with pylab (python's open source incarnation of matlab), then for $N = 50$ elements running for 100 time steps invoke:

```python
from kuramoto import *
model = Kuramoto(50)
model.run(100)
plot(model.phases)
```

This is a direct implementation of the above equations for the Kuramoto model. N is the number of elements and K is a universal connection factor (all elements are coupled equally to one another). For this simulation the intrinsic frequencies are generated as random variables between 0.0 and 0.1, and the initial phase for each oscillator is somewhere between 0 and 2π. The behavior is striking:

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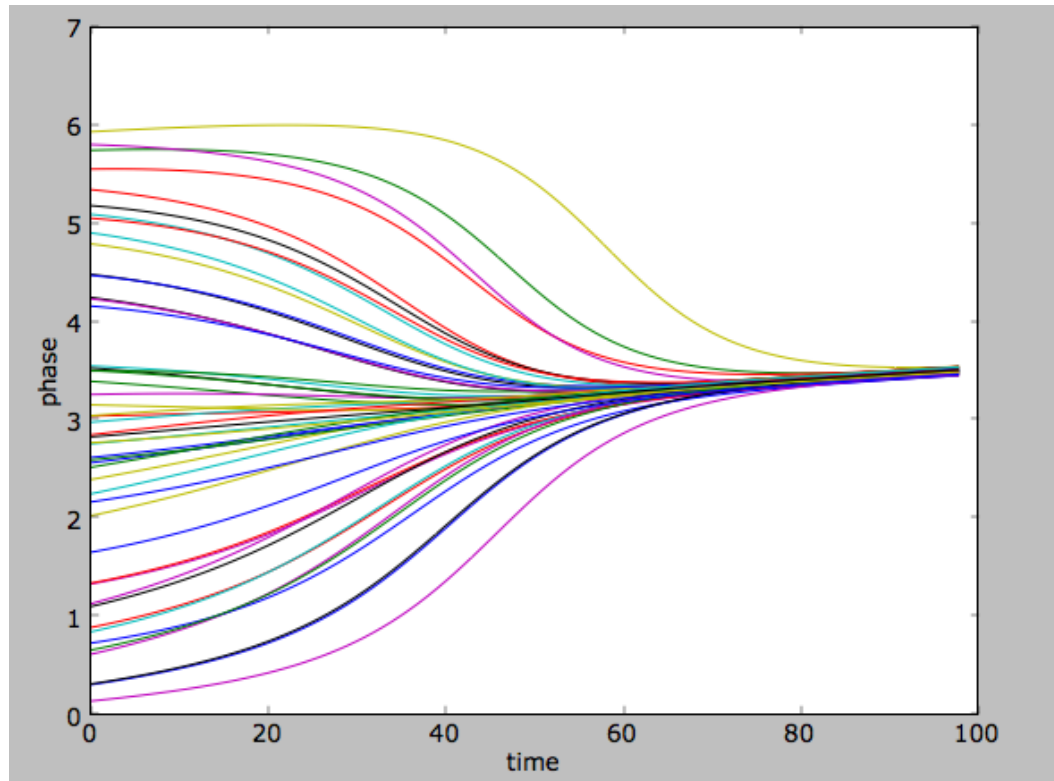
This is a plot of the phase of each element against time. In the space of about 100 time steps the model was completely synchronized. It can synchronize even more quickly if K (the coupling) is raised. What else is remarkable is that each of these oscillators has a different innate phase, and the system seeks a common frequency that is a balance of all of the elements at once. Here is the same model at 300 time steps to emphasize the strengh of the synchronization.
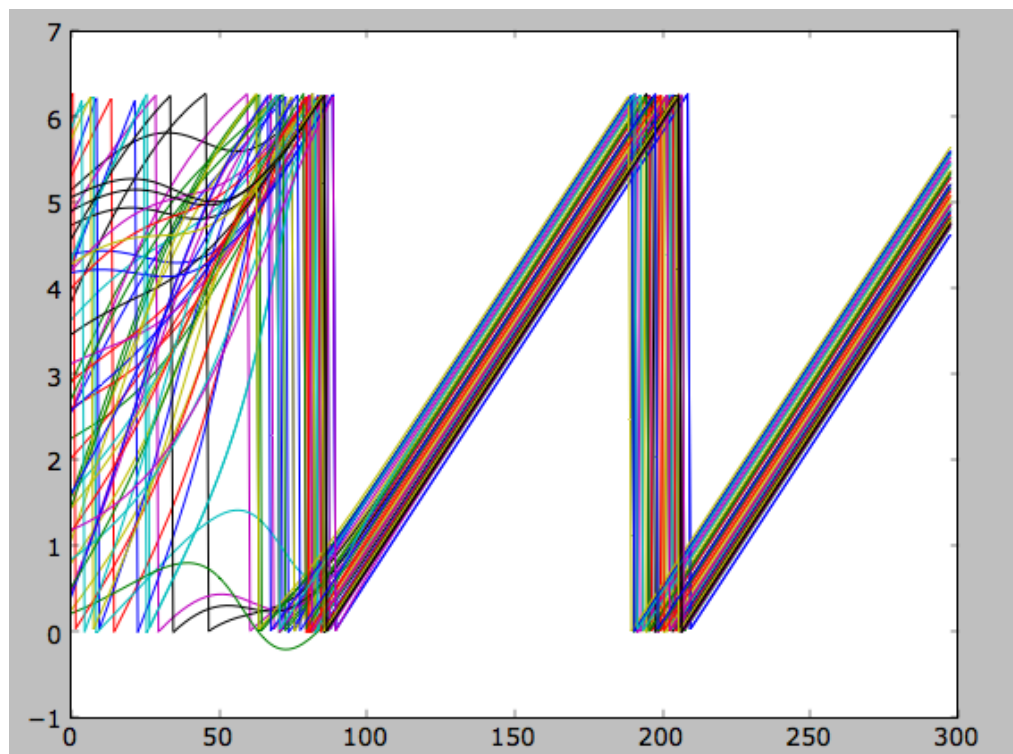
Synchronization and the Visual System

One of the neural systems we know quite a bit about is the primary visual cortex, the initial gateway of direct visual information into the cortex [7]. There are findings that reveal potential mechanisms for perception based on synchronization between populations of coordinating neural groups. Some of these findings are nicely summarized by [6]. The subject of Sompolinsky's work is the orientation of bars that span a receptive field and the responsiveness of various neural assemblies in the presence of these bars. A receptive field Sompolinsky defines to be a set of neurons that discriminate different features of the same spatial area. These receptive regions are spatially vaguely defined, but are mostly circular and include much overlap with neighboring regions. Within a receptive field the neurons each respond to a different stimulus. One responds to horizontal bars say, and others vertical ones, with a spectrum of various angles in between. Some code for red, some for green. Some are responsive to motion in one direction, some motion in another (motion alone can be decomposed into direction, speed, rotation

or expansion/contraction). All of these neurons belonging to a common receptive field are clustered together, each firing fairly specifically to a single modality and a single flavor of that modality, but interacting with each other through synaptic coupling. If there is a vertical bar that is green for example, the neurons that fire when there is only a vertical bar will synchronize with the neurons that fire in response to green. This synchrony between mutually activated neurons is characteristic of activity within a receptive field.

In addition to this action *within* a receptive field, there is also action *between* receptive fields. This takes the character of synchronization between neurons which discriminate the same feature, but in neighboring receptive fields. If the same vertical bar is detected in the neighboring field both vertical bar neurons will synchronize. If the bar is broken, each vertical bar neuron will fire, but they may not synchronize. Synchronization between receptive fields is accomplished through a system of weak coupling between corresponding neurons of similar sensitivity, whereas the coupling between neurons within a field are strongly coupled.

All of this points to the functional role of synchronization in neural and cortical bases of perception. Now that we know that synchronization is an important mechanism in the generation of experience, this leads to the question: how can synchronization be modeled?

Sompolinsky's Model

The Kuramoto model is impressive due to its strength of synchronization and its ultimate simplicity. It is the perfect ingredient to more complex models, as is amply displayed in [1]. One of the intriguing applications of the Kuramoto model is Sompolinsky's work on the primary visual cortex [6]. This model attempts to capture the notion of interacting receptive fields discussed earlier. Each neuron in the receptive field responds strongly to a single variety of a single type of stimulus, ignoring all others. All of the neurons within a receptive field code for a different stimulus, but this pattern of selectivity is repeated in each neighboring receptive field, so that there is in a sense a mirror image, or tiling, of the selectivities in each field. The neurons which respond to a particular feature are weakly coupled between receptive fields.

To model this Sompolinsky used a system based on the simplified Kuramoto model above, but with variable coupling strengths between neurons to represent the different receptive fields, and the notion of a stimulus and a

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tuning curve for each neuron representing its responsiveness to that stimulus. Neurons within a cluster each respond to a different stimulus according to a tuning curve, and activated neurons are coupled strongly and can be considered to reduce to the simple Kuramoto model. Neurons between clusters are coupled if they respond to the *same* stimulus.

Another addition is that the firing of a neuron is taken to be a probabilistic event. In concrete terms, the firing probability P of a neuron is given by

$$P(\mathbf{r}, t) = V(\mathbf{r})(1 + \lambda \cos \Phi(\mathbf{r}, t))$$

where $\Phi(\mathbf{r}, t)$ is the phase of neuron $\mathbf{r}$ at time t, λ is the strength of the contribution of the other neurons to a particular neuron's phase, and $V(\mathbf{r})$ is that neuron's response to the stimulus presented:

$$V(\mathbf{r}) = V(\theta_0(\mathbf{r}) - \theta(\mathbf{r}))$$

Here, $\theta_0(\mathbf{r})$ is an angle representation of the stimulus at neuron $\mathbf{r}$, and $\theta(\mathbf{r})$ is that neurons own preferred angle. The tuning curve used is

$$V(\theta_0(\mathbf{r}) - \theta(\mathbf{r})) = e^{-|\theta_0(\mathbf{r}) - \theta(\mathbf{r})|/\sigma}$$

where σ is some scaling constant. This tuning curve is a sharp point at the selectivity orientation with exponential decay in both directions from that point. The behavior of the phases Φ of the system is almost exactly that of the Kuramoto model (with an extra noise term η added):

$$\tau_0 \frac{\mathrm{d}\Phi(\mathbf{r}, t)}{\mathrm{d}t} = \omega \tau_0 + \eta(\mathbf{r}, t) - \sum_{r'} J(\mathbf{r}, \mathbf{r}') \sin(\Phi(\mathbf{r}, t) - \Phi(\mathbf{r}', t))$$

The θs in the original model have been replaced with the phase function Φ and the noise term η has been introduced, which is governed by white noise with variance proportional to τ_0. The function $J(\mathbf{r}, \mathbf{r}')$ has replaced the matrix K to represent the connectivity of the neurons to each other. This function $J(\mathbf{r}, \mathbf{r}')$ is crafted in such a way as to express the connectivity scheme as outlined above, namely, neurons are strongly coupled to other neurons in their same receptive field, and weakly coupled to neurons in other receptive fields that display the same selectivity as themselves.

Officially, the form of $J(\mathbf{r}, \mathbf{r}')$ is

$$J(\mathbf{r}, \mathbf{r}') = V(\mathbf{r})W(\mathbf{r}, \mathbf{r}')V(\mathbf{r}')$$

where the V terms represent the activity of each neuron and W is the connections matrix. This means that if either of the neurons are inactive the effect will be greatly reduced. For any real effect to take place, both neurons must be active at the same time.

The function $W_{RR}(\theta, \theta')$ is different depending on whether the neurons occupy the same receptive field or different ones. For neurons in the same field, W is simply

$$W_{RR}(\theta, \theta') = \frac{W_S}{N}$$

where W_S is the weighting constant for short range. For neurons coding the same features in different receptive fields the relationship is

$$W_{RR'}(\theta, \theta') = \frac{W_L}{N^2}F(\theta - \theta')$$

where $F(\theta - \theta')$ is a function which ensures that the difference between the selectivities of coupled neurons is small. At the limit, $F(\theta - \theta')$ is exactly 1 when the selectivities are identical, and 0 otherwise.

Simulation

For the simulation, some simplifications and some enhancements were made. The first simplification is that rather than firing stochastically based on the phase value we do away with the firing entirely, and retain only the phase. The second is that no noise term is added. Sompolinsky claims that the noise is vital for the synchronizing and desynchronizing dynamics, but I saw no evidence for this. In all cases the model behaved identically and as expected, noise or not. I see this more to mean that the system is noise-tolerant, and functions in the face of noise, but does not inherently require noise to function.

Some enhancements to the model that were not in the original is the ability to add any number of sensory dimensions and the ability to specify and arbitrary receptive field topology. In a real receptive field there are clusters of disjoint sensory perceptors, each responding to both a specific kind of stimulus and a specific variety of that kind. This is seen most clearly

in the distinction between orientation and color responsive cells. Beyond responding to entirely different modalities, there are a number of neurons within a modality devoted to different qualities within that modality. So for orientation there are an array of perceptors for each angle of orientation. For color, there is a different neuron or neuronal group for each hue, brightness and saturation. In the simulation developed here, the number of dimensions of stimuli can be specified, and stimuli take the form of a vector for each receptive field of the size given by the dimension of the model. The stimuli ranges within a dimension are subdivided by a given granularity. This model assumes all stimulus modalities are cyclic in value, ie, that there is no greatest or smallest but just an angle around a circle, but other stimulus dynamics could be included if desired.

In Sompolinsky's model, all connections within a receptive field were identical and all connections between similar discriminators in other fields were identical. In the simulation here, any connection graph between fields can be specified. Strong connections are always assumed between neurons in the same field, but weak connections can be given or withheld at will. In the configuration provided there are three fields, one of which is connected to the other two, acting as a "bridge" between them. It is my aim to see whether synchronization can occur between the two fields that are otherwise unconnected, through a synchronization with the bridge between them.

In the trials that follow there are three dimensions with a granularity of four levels of distinction. I provided constant stimulus of a variety of orientations to the three different fields. The stimuli used were

$$S_1 = [\pi, 0, \pi]$$
$$S_2 = [0, 0, \pi]$$
$$S_3 = [\pi, \pi, \pi]$$

These were selected because they represent different kinds of relationships between the three sensory dimensions. In this simulation, the second field acts as the bridge between the first and the third. The first dimension (the first column, if you look at the three stimuli for the three different receptive fields as a matrix) represents a broken band of π (whatever the dimension actually encodes is left unspecified, as the scheme could work with any generalized sensory apparatus). It would be expected that the neurons responding to the first π would not synchronize with the neurons in the third field even

though they are both responsive to the same stimulus, because the stimulus at the bridge is 0. In the third sensory dimension all of the values are π, so we would expect all of these neurons to synchronize (signifying the unity of the band of π for this modality).

Here is the total activity of the model, including neurons both responding to and indifferent to the given stimulus.
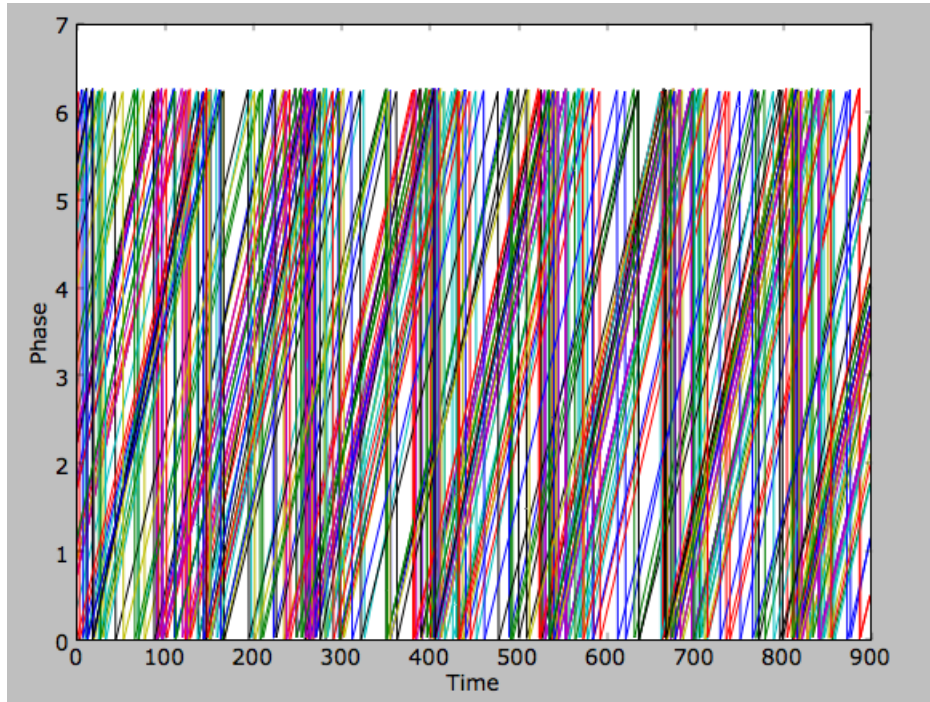

The spread of phase is fairly heterogenous, as would be expected from a population of oscillators provided a random intrinsic frequency and random initial phase. However, there is a band which is thicker that the background. As we will discover, this is the synchronizing component of the model, representing the neurons that happen to respond to the stimuli as presented.

Here is the behavior of neurons within a field that all respond to the given stimulus:
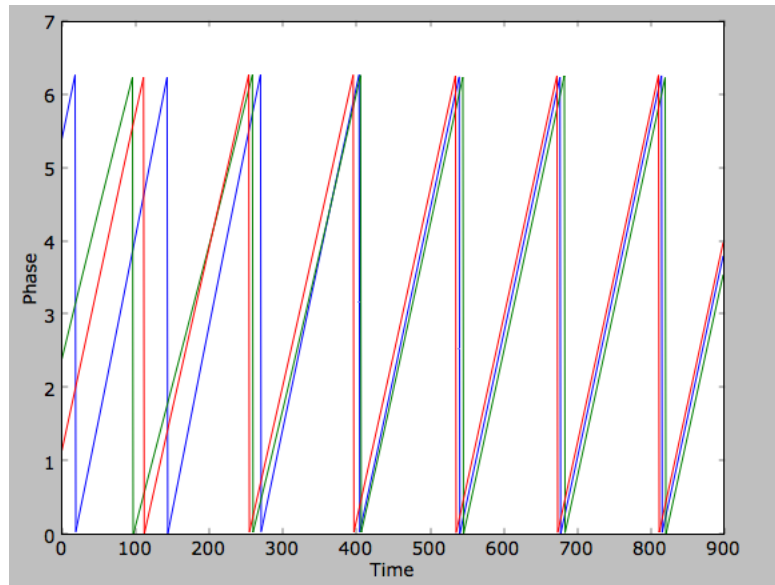
The phases start out all over the cycle, but quickly converge as these neurons synchronize in the face of common stimuli. The strong connections between neurons in the same receptive field make this an inevitability. However, synchronization only occurs between neurons that are activated by the stimulus. Inspection of the total activity of a receptive field reveal a general lack of coherency:

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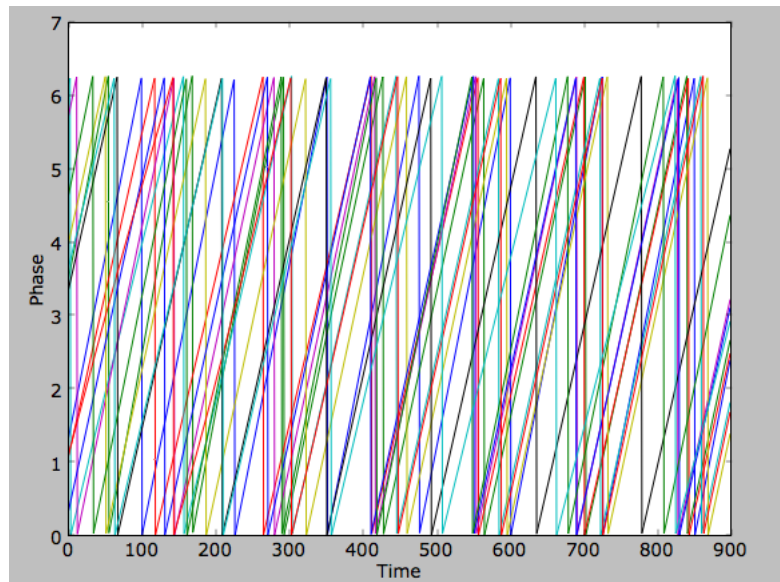
Between fields it is harder to synchronize, since the effect within the field is so strong. However, if the two opposing forces are balanced the common features between receptive fields are able to synchronize these neurons too. Here is some behavior of neurons between fields that all respond to the same stimulus. Notice this does not synchronize so tightly as there are so many other forces pulling them in other directions, but still the synchronization is unmistakable.
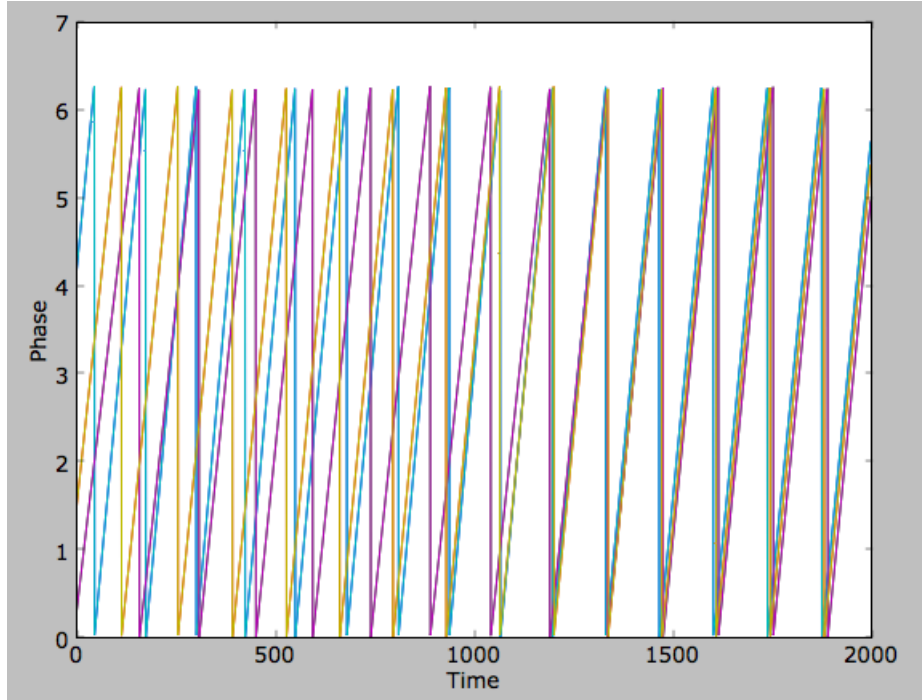
Since these are all neurons in different receptive fields, this shows that the neural groups are able to synchronize even without being directly connected.

The next step is to examine the behavior with a changing stimulus. In the next trials the same constant stimulus is provided as before for the first 900 time steps, and then switched to another stimulus for 900 more time steps.

$$S_4 = [\frac{\pi}{2}, \pi, \frac{3\pi}{2}]$$
$$S_5 = [\pi, 0, \pi]$$
$$S_6 = [0, \pi, \frac{\pi}{2}]$$

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Here is the behavior of the model from the perspective of all neurons receptive to the original stimulus, regardless of field:
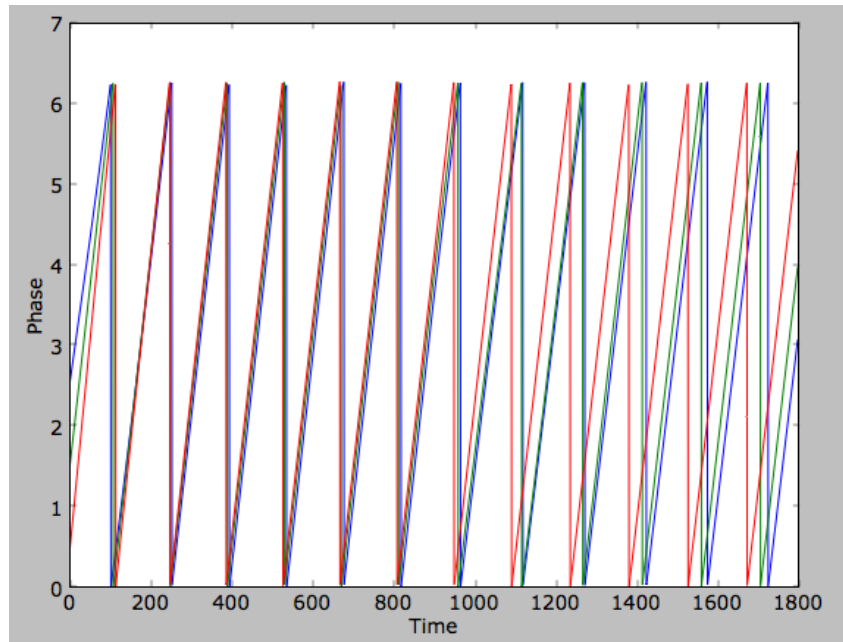
The neurons are highly synchronized for the first 900 time steps, and quickly drift due to variances in intrinsic frequency when there is no longer an external force compelling them to synchronize.

Discussion

References

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