An Agent-Based Model of Neural Field, A Survey

Ramón Heberto Martínez Erasmus Mundus Masters in Complex Systems Science École Polytechnique, Paris

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Instructor: René Doursat

Abstract

In this work we present an agent-based model of neural fields. The agents in this model are Integrate and Fire neurons and the interactions are inspired by Mexican Hat connectivity patterns. Spatio-temporal patterns have been found and we present them in this work. Alongside we present and discuss the possible ways of making sense of the diversity of the emergent patterns we found. Finally studies of the space of parameters with first and second order metrics were carried out in order to classify such dynamics.

1 Introduction

Accordingly to cell theory the fundamental unit of the living beings is the cell. In the case of the constituents of the nervous system these cell possess electrical capabilities and are called neurons. In the light of cell theory the nervous system is essentially a discrete entity and therefore discrete are the electrical properties of it. However if one regards the nervous system tissue from the appropriate spatial scale one may be temped to regard this as a continuous material. The mentioned approach is called Neural Field Theory and has spun considerable research into science from approximately the middle of the last century with the seminal articles of (Beurle, 1956) and (Wilson & Cowan, 1972), mathematical studies were carried out by (Amari, 1977), modern review articles can be found in (Ermentrout, 1998) (Bressloff, 2012).

Of particular interest to us is the pattern generation aspect of such models. A plethora of patterns have been studied like waves (Ermentrout & McLeod, 1993) (Amari, 1977), regions of localized activity called bumps Amari (1977) (Laing & Chow, 2001) and breathers (Folias & Bressloff, 2005). A particular good review of this issue can be found in (Coombes, 2005).

Since (Adrian, 1926) mean firing rate is considered one of the most important features of how neurons codify the information, especially in the periphery-sensory system. While in the early stages of processing the characteristics of a single neuron may be enough to describe the sensed features it is very unlikely that this simple idea will be able to explain higher cortical processing (Gerstner et al., 1997). The discussion in the literature around which kind of code does the brain use in the higher areas has been prolific and full of rich scientific debate (Shadlen & Newsome, 1994) (Softky, 1995) (Shadlen & Newsome, 1995) (Georgopoulos et al., 1986) Rieke (1999). Following the proposal by (Von Der Malsburg, 1994) we don not restrict our study to just the averages or first order quantities related to neuron characteristics but also consider the correlations between the activity of different networks.

Of special interest to us are bump patterns. There exists previous work in which the existence of bumps solutions in a one dimensional field of integrate and fire neurons has been proved (Laing & Chow, 2001). The initial aim of this work was to study the pattern generation possibilities of the generalization of this model to a two dimensional space.

2 The Model

We constructed an agent-based model of a neural field theory. The agents here are neurons and their interactions represent synaptic (excitatory and inhibitory) connections. Our aim is to study the emergent dynamics of this system.

2.1 The Agent - The Neuron

The nature of the agents is based on the Integrate and Fire model which is a semi-realistic biological model of neuronal dynamics. Integrate and Fire models were introduced by Lapique hundred years ago (Lapique, 1907) and are still widely used today in the scientific community to model a variety of phenomena in the nervous system (Burkitt, 2006). In this case an agents possesses an internal variable V that represents the membrane voltage. In the presence of an input I the voltage evolves according to the following equation:

$$\tau \frac{dV}{dt} = I - V$$

Furthermore every neuron possesses a time scale τ that determines how fast it grows in the presence of a stimulus. A bigger value of τ means that the system takes longer to arrive to the threshold -if indeed it arrives- whereas a small τ makes the system evolve

very fast. In our simulation the values of τ are between 1ms and 30ms. We are going to build a discrete version of our system using a simple Euler scheme. Therefore the evolution equation for V will be the following:

$$V_{i+1} = V_i + \frac{1}{\tau}(I - V_i)$$

In the Integrate and Fire mechanism the presence of the input I will make the voltage grow until it reaches a critical point V_{th} (if $V_{th} < I$). At this point we assume that an **action potential** has occurred (we also say that the neuron has fired or that a spike has occurred). Afterwards we reset the voltage to the initial value V_{th} , which is zero in this case and the mechanism begins again. In our model V_{th} is between 10mV and 30mV and we set the voltage equal to $V_{th} = 0$. The process is represented graphically in figure 1.

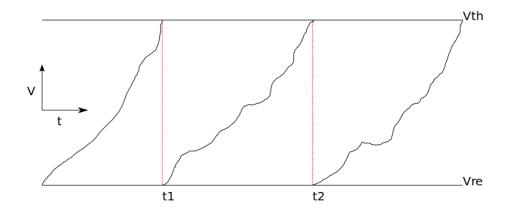


Figure 1: Schematics of Integrate and Fire Models illustrating the main features of this model. The voltage evolves according to a particular model that we chose. When the value of a particular voltage trajectory surpasses $V_{th} = 0$ we reset the value to V_{re} , register the time as an occurrence of an action potential and repeat the process again.

2.2 The Relations - Synaptic Connections

We use a model of connectivity with short range excitation and a long range inhibition (also known by the name of lateral inhibition or Mexican hat in the literature). Our setting is such that we have a 41×41 neurons in a square lattice (although the mechanism is general and can be easily scaled) interacting in the following way. If a neuron fires, all the neurons that are within a fixed range R_1 will be excited by the effect of the synapses, the neurons whose distance to the firing neuron is greater than R_1 but nevertheless smaller than R_2 will suffer from inhibition and their voltage will decrease. This mechanism is represented schematically in the figure 2 where the yellow neuron is the one firing.

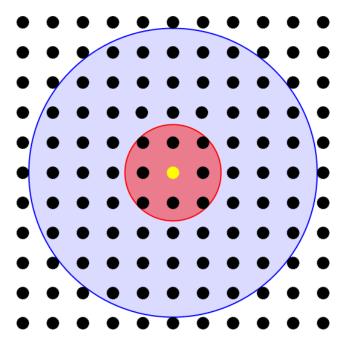


Figure 2: Schematic of the influence of the yellow neuron on the rest (here coloured black) of neurons. The neurons falling in the red radius will be excited and the ones falling in the big blue one that are not in the red will suffer from inhibition.

In our simulation distances are measured relative to the distance between adjacent neurons which we define as one. In this metric common values of R_1 and R_2 are between 0 and 30. Our range of values for α and β go from 0mV to 5mV.

Now we consider our equation in the lattice. Vectors \mathbf{x} represent our points in the lattice space. Our evolution equation in the network now looks like:

$$V_{i+1}(\mathbf{x}) = V_i(\mathbf{x}) + \frac{1}{\tau}(I - V_i(\mathbf{x})) + coupling$$

Where the coupling term is given by the following expression:

$$\sum_{k} \delta_{i,t_k} \left[\alpha H(R_1 - \|\mathbf{x_k} - \mathbf{x}\|) - \beta \left(H(\|\mathbf{x_k} - \mathbf{x}\| - R_1) - H(\|\mathbf{x_k} - \mathbf{x}\| - R_2) \right) \right]$$

Here the index k goes over all the spikes in the network history. If in the step i there is a spike then $\delta_{i,i} = 1$ and the coupling term will play its role. $\mathbf{x_k}$ here represents the particular point in the network where the spike k has occurred and $\|*\|$ is the euclidean norm. Therefore the term $\|\mathbf{x_k} - \mathbf{x}\|$ is just the distance between our point of interest and the origin of the spike. $\mathbf{H}(\mathbf{x})$ is the heavy side function which is 1 for x > 0 and 0 otherwise.

In consequence every neuron will have four parameters related to its interactions. First there is going to be an R_1 value corresponding to the spatial extent of its excitatory effect and a value α which is a measure of how strong is the effect. Secondly there will be another radius R_2 that will represent the extent to which the inhibition effects are restricted. Finally there is parameter β which is a measure of the magnitude of the inhibitory effect in the system.

3 Results

3.1 Pattern Formation

Here we present some of the patterns that our model is capable of producing. Along the lines of (Lu et al., 2011) we consider two different kind of patterns: wave-like patterns and localized excitations. Our model presents instances of both but first we present the latter.

Localized Excitations

In figures 4 and 6 we have examples of bumps or areas of localized high activity. The difference in the number of bumps from one example to the other was due to differences in the inhibition radius R_2 : the bigger it is the less is the number of bumps. R_2 works then as a parameter that controls the number of bumps in the system.

The firing rate map of both examples is presented in figures 5 and 6. We can see that outside of the high activity areas the firing rate is equal to zero because there is no fire at all there. So, as expected the activity is restricted to a specific location in space.

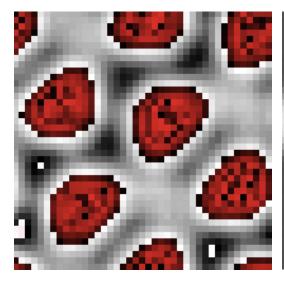


Figure 3: Snapshot of a process with localized activity in the shape of multiple bumps. The values in red indicate high voltage and the ones in white or gray low values of the voltage. Here I=30 $\tau=20$ $V_{th}=20$ $R_1=6$ $\alpha=0$ $R_2=12$ $\beta=1$

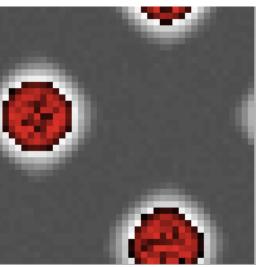
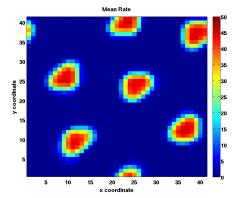


Figure 4: Snapshot of a process with localized activity in the shape of multiple bumps. The values in red indicate high voltage and the ones in white or gray low values of the voltage. Here $I=30~\tau=20~V_{th}=20~R_1=6~\alpha=0~R_2=24~\beta=1$



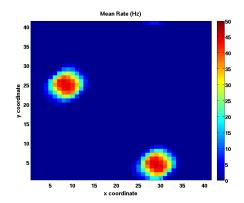
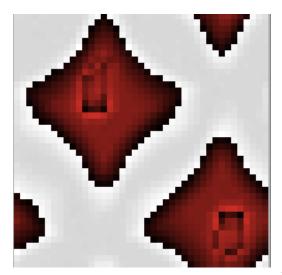


Figure 5: Firing rate pattern of the process in figure 3. Each point shows the number of spikes in a window of 500 ms. Each point is then assigned a colour from blue to red proportional to that value. Here the values of the parameters are $I=30~\tau=20~V_{th}=20~R_1=6~\alpha=0~R_2=12~\beta=1.$

Figure 6: Firing rate pattern of the process in figure 4. Each point shows the number of spikes in a window of 500 ms. Each point is then assigned a colour from blue to red proportional to that value. Here the values of the parameters are I=30 $\tau=20$ $V_{th}=20$ $R_1=6$ $\alpha=0$ $R_2=24$ $\beta=1$.

Another interesting example is provided in figure 7. In this process we also have specific areas of high activity, represented by red tones in the snapshot, but there is also a travelling pattern of inhibition inside the pattern of high activity. In the figure 8 the mean rate of the pattern is presented and we can grasp the effect of the travelling pattern: the values are quite low compared to the values for the bumps above. The reason for this is that the travelling pattern pushes the average down as it moves around.



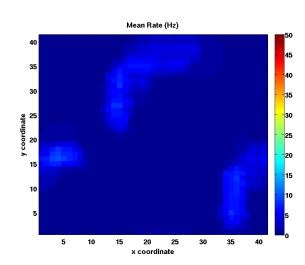


Figure 7: Snapshot of a process with localized activity and a wave like pattern inside of it (black areas are actually moving in the simulation). The values in red indicate high voltage and the ones in white or gray low values of the voltage.

Figure 8: Firing rate pattern of the process in figure 7. Each point shows the number of spikes in a window of 500 ms. Each point is then assigned a colour from blue to red proportional to that value. Here I=30 $\tau=20$ $V_{th}=20$ $R_1=2$ $\alpha=1$ $R_2=21$ $\beta=1$.

Wavelike patterns

In the figure 9 we present a wave like pattern that consists in two patterns that move across the network from left to right. In the snapshot the more red is the area the higher is the voltage for that particular point in the lattice. So we can think of these patterns a

succession of spikes along a particular line, the black areas are nothing but the neurons just a moment after the spike.

Furthermore we present in figure 9 the mean rate of firing for each spot in the lattice. We can see a dim trail of activity along the directions in which the patterns are moving.

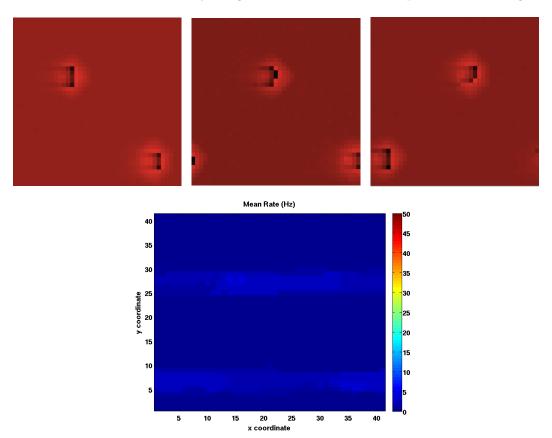


Figure 9: In the top there is a glider-like travelling pattern. Snapshots of it are taken each 50 ms to capture its movement. Here I=30 $\tau=20$ $V_{th}=20$ $R_1=1$ $\alpha=0$ $R_2=26$ $\beta=1$. Below we show the mean rate pattern that this gliders generate. Each point shows the number of spikes in a window of 500 ms. Each point is then assigned a colour from blue to red proportional to that value. Note the traces of activity in the direction that the gliders are travelling.

In the figure 10 we present a different kind of wavelike pattern. Two waves moving with direction perpendicular to each other travel across the lattice. Furthermore we present the mean firing rate pattern below in the same figure. We see that the values are quite uniform here, this is due to the fact that the waves spread almost over the entire lattice.

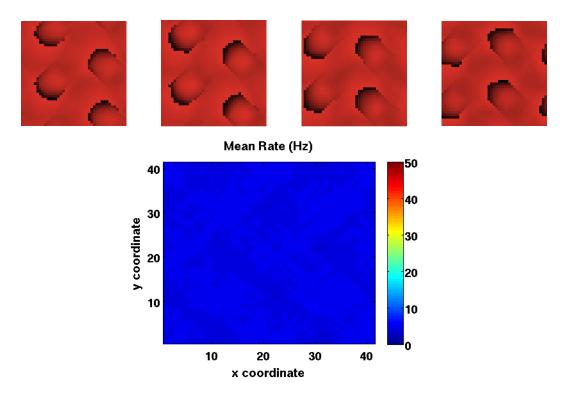


Figure 10: In the top we present a cross wave pattern. To illustrate the pattern we present successive snapshots of the process with 20 seconds between each one. Note that the patterns in the middle right of the display are moving to the upper left corner while the ones in the middle left are moving to the bottom left. Here I=21 $\tau=20$ $V_{th}=20$ $R_1=10$ $\alpha=0$ $R_2=14$ $\beta=0.10.$ Below we show the mean rate pattern that it generates. Each point shows the number of spikes in a window of 500 ms. Each point is then assigned a colour from blue to red proportional to that value. Note how the values are very low compared to other patterns presented before.

In the spirit of (Von Der Malsburg, 1994) we make a distinction between two ways of measuring and studying the neural activity. We will call first order metrics to the ones that don't involve products between different elements of the lattice (averages for example). The firing rate of a neuron falls in this category for example. On the other hand we will name second order metrics the ones that do involve second moments (correlations for example). We used this metrics to make a tentative and rough classification of our system.

3.2 First order metrics

The purpose of the metrics is to categorize and organize the possible behaviours of the model as we vary the parameters. Exploring the model we came to realize the following: waves have a high mean spatial voltage and a low firing rate. To illustrate the point an example of such behaviour is given in the figure 11.

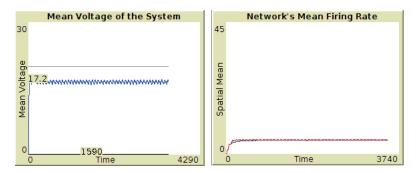


Figure 11: Mean spatial voltage and the spatial mean of the firing rate for a wave pattern. Note the characteristic high value of the voltage and the low firing rate. The gray line in the voltage plot represents the threshold. Here I=21 $\tau=20$ $V_{th}=20$ $R_1=10$ $\alpha=0$ $R_2=14$ $\beta=0.10$.

Bumps in the other hand have a profile of low mean voltage, usually below zero, and also low firing rate. The situation for bumps is illustrated in the figure 12. This rough classification makes sense because bumps being localized have only local effects. The sea of inhibition that they create in the other hand takes the average voltage down. In opposition to this, waves spread across the lattice pushing the voltage upwards everywhere.

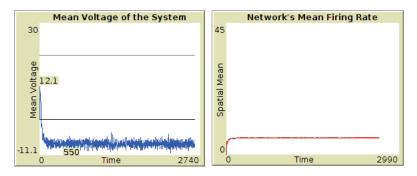


Figure 12: Mean spatial voltage and the spatial mean of the firing rate for a bump pattern. Note the characteristic low value of the voltage and also the low firing rate. The gray line in the left plot represents the threshold voltage. Here $I=30~\tau=20~V_{th}=20~R_1=6~\alpha=0~R_2=24~\beta=1$.

With this rough classification in hand we would like to know how the variation of the parameters affect the profiles of mean voltage and mean rate. General exploration with the parameters reveals that a change from a bump like regime to a wavelike regime occurs for variations in the parameters β and R_2 and therefore we will concentrate on those parameters. We detail this exploration in the figure 13 below.

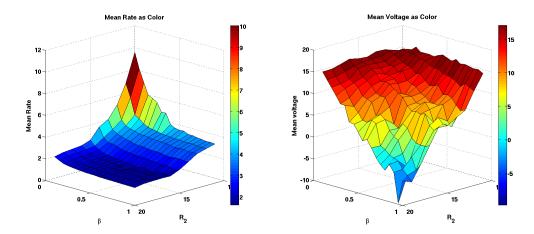


Figure 13: For each value of the parameters β and R_2 we plot the spatial mean of the firing rate in the left and the spatial mean of the voltage in the right. The means were taken 500 ms after the simulation started. For the other parameters we have I=21 $\tau=20$ $V_{th}=20$ $R_1=10$ $\alpha=0$.

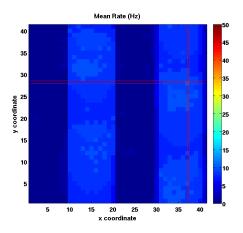
An interesting thing to note in figure 13 is that the mean voltage increases as β is reduced which is consistent with β being a measure of inhibition. However as R_2 becomes smaller the step of the increment becomes smaller. Consequently we can claim that smaller values of R_2 make up for smaller values of β .

Another interesting region provided by the heat maps is in in the corner of the rate map where this value is very high (In red in the left plot). Here we have an anomalous high value of the rate. Exploring our simulation we came to realize that this is produced by a wave that is inconsistent in its direction, that is, it seems to move randomly and wonder from place to place. The wave as it moves excites the region on its trail and therefore pushes the average rate of firing up.

We should point out that this characterisation is restricted to waves with a profile size in the order of magnitude of the lattice size. If the wave is relatively small with respect to the network the spatial average over such a big area will be small. The example provided in figure 7 lies in the boundary of such classification and is likely that the classification will fail for such type of patterns.

3.3 Second order metrics

Second order metrics provide us with the structural characteristics of the patterns under study. In order to select a neuron we picked the spot in the lattice where the maximum is attained and after that calculated the correlation coefficient of that particular neuron with all the others neurons along the x and the y axis as shown on the left of figure 14. From the plots of the correlations coefficient we can infer details about the structure of the pattern. This one in particular reveals that we are dealing with a wave with two fronts travelling in the y direction. In addition, from the same plot we come to realize that the wave consists on two crest and also that along the x axis the waves are uncorrelated (That is shown as the negative part of the correlation coefficient in the plot).



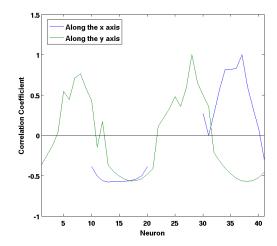
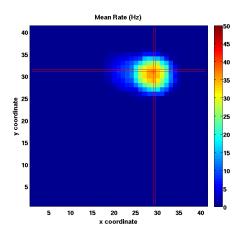


Figure 14: In the left we present the mean rate of a wavelike pattern. Furthermore the maximum is shown as the intersections between the red rectangles. It is along these lines that the correlations coefficients of the neuron in the point where the maximum is attained are calculated. The correlation coefficients are shown in the figure to the right. The points where the firing rate is zero are not defined and therefore are excluded from the plot. Note the negative correlation between one trace of the wave and the other. Here $I=21~\tau=20~V_{th}=20~R_1=10~\alpha=0~R_2=14~\beta=0.10$.

In the case of the bumps figure 15 reveals the sizes of the bumps in the plot of the correlation coefficient. Interestingly it also reveals the existence of two regimes in the bump itself negatively correlated between themselves. We can observe this as the negative part in the plot along the x axis.



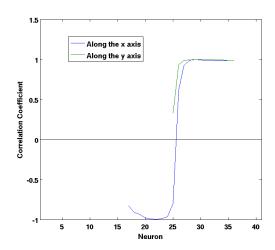
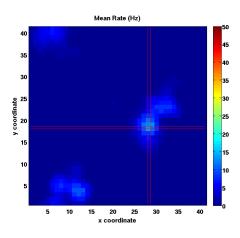


Figure 15: In the left we present the mean rate of a wavelike pattern. Furthermore the maximum is shown as the intersections between the red rectangles. Is along these lines that the correlation coefficients of the neuron in the point where the maximum is attained are calculated. The correlations coefficients are shown in the figure to the right. The points where the firing rate is zero are not defined and therefore are excluded from the plot. Note the low correlation with the zone to the left of the maximum. Here $I=30~\tau=20~V_{th}=20~R_1=6~\alpha=0~R_2=24~\beta=1$.

These two calculations show that we can obtain structural information about the pattern by considering second order metrics. However if we do the same kind of calculation for the patterns in figure 7 we obtain the results show in figure 16. The correlation coefficient plot (right) looks as an ordinary bump and the fact that there is a travelling pattern inside of

the high activity zones is not revealed by this metric. We believe that in order to obtain this information one needs to calculate lagged correlations.



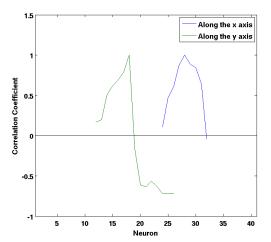


Figure 16: In the left we present the mean rate of a pattern like the one in figure 7. Furthermore the maximum is shown as the intersections between the red rectangles. Is along these lines that the correlation coefficients of the neuron in the point where the maximum is attained are calculated. The correlations coefficients are shown in the figure to the right. The points where the firing rate is zero are not defined and therefore are excluded from the plot. Note the low correlation with the zone to the left of the maximum. Here $I=30~\tau=20~V_{th}=20~R_1=6~\alpha=0~R_2=24~\beta=1$.

Finally it is important to state that during our observations we saw that the parameters I, τ and threshold are related more to the speed of the wave or the average firing rate of the bumps than to the structure of those patterns: That is, there is a degree of robustness of the structures with respect to the parameters I and τ .

On the other if the parameter α is not well tuned with respect to β the activity of the system explodes. This is due to the positive feedback effect of the excitation upon itself-more excitation means more firing more firing means more excitation-which can easily destroy any order on the network. In other words, patterns are quite sensitive to the variation of α with respect to β .

4 Discussion

We have shown how our system posses the ability to generate a plethora of patterns with Integrate and Fire neurons and simple connectivity rules. One important example is the transition from bumps to wave behaviour varying the parameters β and R_2 . We have shown how this is related to different regimes of mean spatial voltage and mean spatial rate and made a first approximation exploration through different metrics that allowed us to characterise different aspects of the emergent patterns.

Naturally our approach of characterising bumps and waves domains by mean voltage and mean rate is far from complete. As stated before by exploring our simulation we found that if the wave is very small, its trail will not cover enough area in the lattice to drive the voltage up and our classification will fail there and we will obtain a wave with low voltage. So one of the obvious ways in which this work can be taken beyond is to find better order parameters or classifiers of the patterns to tell the dynamics apart in a more conclusive way.

Another important shortcoming of the model is that it does not include the possibility of time delays. In the actual nervous system the action potential takes some time to reach from neuron to neuron after an action potential is generated. In our model the excitatory of inhibitory effects take action immediately which is an assumption far from the actual case.

Also the topology of our network is far from being realistic. We have assumed homogeneous connections but that id far from true. Modern neuroscience is aware that the neural circuitry is neither random nor homogeneous, but highly organized in a precise way that is even nowadays still under mapping (Kandel et al., 2000). Other direction that our work could take is to consider the effects of biologically based topologies on our system.

Other ways in which our model could be extended is finding a way of measuring wave velocity for any direction. This has to include a filter time because many of the wavelike behaviours in our system are inconsistent in their direction. If we could find such a parameter this could serve as an order parameter to quantify the kind of transition from waves to bumps that occur as we change β and R_2 . We believe that this involves calculating correlations of the presents signals with the past signals and this will also allow to solve the problem posed by figure 16.

Other recent works that study Integrate and Fire networks can be found in (Bressloff & Coombes, 2000) where the model is compared with a model of analogue neurons. Pattern formation systems of Integrate and Fire neurons in one dimension can be found in Bressloff (1999). More closely resembling ours is the work of (Milton et al., 1993) where the pattern formation capabilities of a randomly connected network of Integrate and Fire neurons is analysed. All the other works that we have found so far are more detailed and follow a different pattern of connectivity. Our model in the other hand is quite general and has relatively simple rules.

Finally we believe that the most important virtue of our model is its simplicity. Taking into account only a few very general details about network behaviour it nevertheless possesses an amazing potential as a pattern generating system. There is evidence that memory related phenomena is related to located persistent activity (Compte et al., 2000). In this context a simple model of pattern generation will be a stepping stone to more complex systems of this kind.

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References

- Adrian, E. D. (1926). The impulses produced by sensory nerve endings part i. *The Journal of physiology*, 61(1), 49–72.
- Amari, S.-i. (1977). Dynamics of pattern formation in lateral-inhibition type neural fields. Biological cybernetics, 27(2), 77–87.
- Beurle, R. L. (1956). Properties of a mass of cells capable of regenerating pulses. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 240 (669), 55–94.
- Bressloff, P. (1999). Synaptically generated wave propagation in excitable neural media. *Physical Review Letters*, 82(14), 2979.
- Bressloff, P. C. (2012). Spatiotemporal dynamics of continuum neural fields. *Journal of Physics A: Mathematical and Theoretical*, 45(3), 033001.
- Bressloff, P. C., & Coombes, S. (2000). Dynamics of strongly coupled spiking neurons. Neural Computation, 12(1), 91–129.

- Burkitt, A. (2006). A review of the integrate-and-fire neuron model: I. homogeneous synaptic input. *Biological cybernetics*, 95(1), 1–19.
- Compte, A., Brunel, N., Goldman-Rakic, P. S., & Wang, X.-J. (2000). Synaptic mechanisms and network dynamics underlying spatial working memory in a cortical network model. *Cerebral Cortex*, 10(9), 910–923.
- Coombes, S. (2005). Waves, bumps, and patterns in neural field theories. *Biological Cybernetics*, 93(2), 91–108.
- Ermentrout, B. (1998). Neural networks as spatio-temporal pattern-forming systems. Reports on progress in physics, 61(4), 353.
- Ermentrout, G. B., & McLeod, J. B. (1993). Existence and uniqueness of travelling waves for a neural network. *Proceedings of the Royal Society of Edinburgh: Section A Mathematics*, 123(03), 461–478.
- Folias, S. E., & Bressloff, P. C. (2005). Breathers in two-dimensional neural media. *Physical review letters*, 95 (20), 208107.
- Georgopoulos, A. P., Schwartz, A. B., & Kettner, R. E. (1986). Neuronal population coding of movement direction. *Science*, 233(4771), 1416–1419.
- Gerstner, W., Kreiter, A. K., Markram, H., & Herz, A. V. (1997). Neural codes: firing rates and beyond. *Proceedings of the National Academy of Sciences*, 94(24), 12740–12741.
- Kandel, E. R., Schwartz, J. H., Jessell, T. M., et al. (2000). Principles of neural science, vol. 4. McGraw-Hill New York.
- Laing, C. R., & Chow, C. C. (2001). Stationary bumps in networks of spiking neurons. Neural Computation, 13(7), 1473–1494.
- Lapique, L. (1907). Recherches quantitatives sur l'excitation electrique des nerfs traitee comme une polarization. *J. Physiol. Pathol. Gen*, 9, 620–635.
- Lu, Y., Sato, Y., & Amari, S.-i. (2011). Traveling bumps and their collisions in a two-dimensional neural field. *Neural computation*, 23(5), 1248–1260.
- Milton, J. G., Chu, P. H., & Cowan, J. D. (1993). Spiral waves in integrate-and-fire neural networks. Advances in neural information processing systems, (pp. 1001–1001).
- Rieke, F. (1999). Spikes: exploring the neural code. The MIT Press.
- Shadlen, M. N., & Newsome, W. T. (1994). Noise, neural codes and cortical organization. Current opinion in neurobiology, 4(4), 569–579.
- Shadlen, M. N., & Newsome, W. T. (1995). Is there a signal in the noise? Current Opinion in Neurobiology, 5(2), 248–250.
- Softky, W. R. (1995). Simple codes versus efficient codes. Current opinion in neurobiology, 5(2), 239–247.
- Von Der Malsburg, C. (1994). The correlation theory of brain function. Models of neural networks, 2, 95–119.
- Wilson, H. R., & Cowan, J. D. (1972). Excitatory and inhibitory interactions in localized populations of model neurons. *Biophysical journal*, 12(1), 1–24.