Temporal Binding by Short-Term Synaptic Plasticity

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Abstract

This thesis introduces a novel way of performing temporal binding in a network of biologically plausible spiking neurons. The neurons in the network are connected through synapses with short-term synaptic plasticity. By synchronously activating multiple patterns, the network stabilizes into a state where these multiple patterns quickly oscillate between an active and inactive state.

Using this method a simple Hopfield-like auto-associative network is created that can retrieve multiple patterns at the same time, binding neurons to a pattern by a slow variant of temporal binding.

Acknowledgment

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Contents

1 Introduction

Distributed representations in neural networks have a very strong appeal. They are easy to implement and fault tolerant. They generalize, have a large capacity and are very expressive. There has been quite a lot of research in the relations between logic and these networks.

There are however also some big problems limiting the use and expressive power of neural networks with distributed representations. One of the biggest problems is the binding problem. It is difficult to represent more then one object in such a network, since there is no information about which unit belongs to which object.

Several solutions to this problem have been proposed. One solutions that has been given a lot of attention is called "temporal binding". In this method of binding, introduced in [von der Malsburg, 1981], the exact timing of the spikes of the neuron is used to indicate which neuron belongs to which object.

Most research on temporal binding focuses on using exact synchrony of spikes to signal binding. In these models neurons firing in synchrony are said to "belong" to the same pattern. This way the network activity quickly oscillates between active patterns. Since the duration of a spike is between 2 and 10 milliseconds, the network switches patterns approximately every 5 to 20 milliseconds.

[Knoblauch and Palm, 2002] introduces a model that implements temporal binding on a much slower time-scale. Instead of neurons firing in synchrony, neurons are active in short "bursts". Neurons belonging to the same pattern are active during the same bursts. This means the network switches patterns on a much slower scale, somewhere between every 50 to 200 milliseconds.

This thesis will introduce a model that implements a variant of this binding method. The resulting binding behavior is similar to that of the model implemented by [Knoblauch and Palm, 2002]. The model in this thesis consists of a simple auto-associative network of spiking neurons, universally connected through synapses with short-term plasticity. In biological neurons the transmission of a spike changes the strength of a synapse. [Kistler and van Hemmen, 1999] introduce a model that implements this characteristic of synapses and show that short-term synaptic plasticity impacts network behavior, but does not impact the capacity of auto-associative networks with these synapses. This thesis shows that the short-term synaptic plasticity modeled in [Kistler and van Hemmen, 1999] can be used to implement a binding behavior similar to the model of [Knoblauch and Palm, 2002].

Whereas in the model of [Knoblauch and Palm, 2002] the binding behavior is implemented using a complex network consisting of multiple layers, in the proposed method the binding behavior simply emerges from a straight-forward associative network of spiking neurons which are connected through synapses with short-term plasticity. The binding method does not require any machinery added to the associative network, making it much simpler than other proposed solutions.

Section 2 gives a general introduction to neural networks. It introduces central concepts in artificial neural networks, like neurons, synapses and activity.

In biological neural networks, activation is spread through the network by short spikes. Since the exact timing of these spike did not seem to play an important role in the workings of neural networks, classical artificial neural networks do not model these spikes. Instead the average frequency of these spikes is modeled.

Since the binding method developed in this thesis uses the exact timing of spikes to perform binding, section 2 introduces a variant of artificial neural network that does model the spiking nature of neural activity. This section introduces a mathematical model of spiking neurons. Though more complex than classical neural networks, it remains fairly simple, which allows the paper to focus on the binding method.

Section 3 introduces auto-associative networks. These networks are capable of storing patterns and retrieving the stored patterns by activating parts of the stored patterns. Patterns are stored by changing the strength of the synapses connecting the neurons.

This section also shows how information can be encoded in patterns in an elegant way in neural networks. Nodes in the network represent properties of objects. Objects are represented by a pattern of these properties, i.e. the properties that that object has. These patterns can be stored in auto-associative networks and have some very attractive properties.

A problem however with these so-called distributed representations is that only one pattern can be active at the same time. When two patterns are activated we need a way to keep track of which properties belong to which object. This problem, generally called the binding problem, is introduced in section 4. Without a solution it seems impossible to model complex things like relations in distributed representations.

This section also introduces a solution to the binding problem proposed in [von der Malsburg, 1981]. The exact time of the spikes in a networks can be used to model binding in associative networks. Section 4 shows two models, that use synchrony in spikes to model binding and keep track of which active node belongs to which active pattern. Some problems with these models are discussed. The section also introduces the model of [Knoblauch and Palm, 2002], where neurons are bound to patterns on a slower time-scale.

Section 5 introduces a novel way to perform temporal binding in an auto-associative network on a slow time scale similar to that of [Knoblauch and Palm, 2002]. The binding emerges in a standard auto-associative network of spiking neurons with short-term synaptic plasticity from [Kistler and van Hemmen, 1999]. Short-term plasticity, the fact that synapses fatigue when transmitting spike and thus become less and less effective, controls the activity in the network, resulting in a temporal binding behavior but with much less added complexity.

A computer model of the binding method developed in section 5 is used to perform simulations in section 6. A simple network of spiking neurons is used to retrieve one, two and three patterns simultaneously. The simulations show that the method can indeed be used to perform binding in a simple network of spiking neurons and short-term plasticity.

Section 7 introduces some aspect of the binding method that might be interesting to the develop in future work, and gives a conclusion to the thesis.

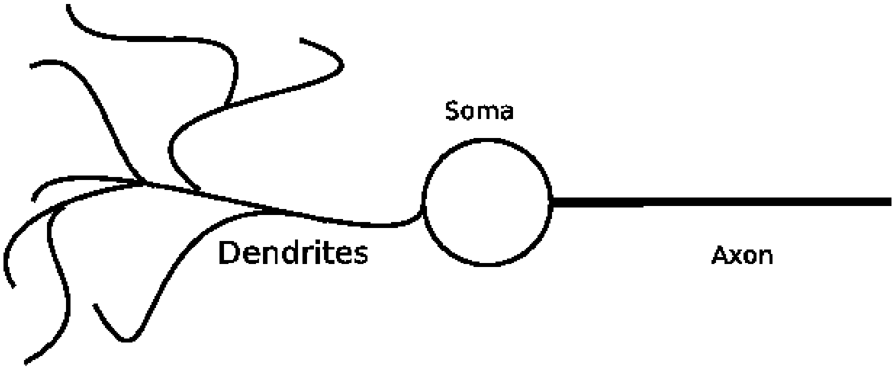


Figure 1: A schematic representation of a biological neuron

2 Neural Networks

Over a hundred years of biological research have given us a lot of insight in the structure of our brain. This research showed that neurons are the primary processing units in our brain. The brain consists of a huge number of these neurons connected to each other in a complex network. The estimated number of neurons is about 10^{12}. A typical neuron is connected to approximately 10^4 other neurons [Maass and Bishop, 1999].

A typical neuron consists of three main parts, see figure 1. The *dendrites* of a neuron consist of a tree that collects pulses from pre-synaptic neurons, i.e. the neurons which connect to the current neuron. The body of a neuron is called the *soma*. The incoming pulses collected by the dendrites cause a potential change in the soma. If this potential crosses a threshold, the soma emits a pulse. This pulse is propagated to the post-synaptic neurons, i.e. the neurons to which the current neuron is connected, by the *axon*.

The duration of a pulse is typically 1-2 ms. It is generally assumed that the exact shape and duration of a spike carries no information. Only the time of a pulse and the number of pulses emitted matter.

The place where the axon of one neuron meets the dendrite of another neuron is called the synapse (hence the term pre- and post-synaptic). When a pulse of the pre-synaptic neuron reaches this point, a highly complex chain of chemical reactions causes a changes in the potential of the post-synaptic neuron. The size of the change is determined by the strength of the synapse. The changes can either be positive (the synapse is excitatory) of negative (the synapse is inhibitory).

2.1 Classical Neural Networks

Classical artificial neural networks give a simple mathematical model of neural networks as described in the previous section. Essentially a network consists of a set of nodes representing the neurons, and a matrix of weights representing the synapses connecting the neurons.

Each node has an activation value associated with it. This activation value represents the firing rate of the neuron. The higher the firing rate, the higher the activation of the node.

The reaction depends on the type and strength of the synapse connecting neuron i and j. This is modeled by the activation level a of neuron k depends on the activation level of the pre-synaptic neurons and the strength of the synapses connecting the pre-synaptic neurons.

The strength of the synapse is models by w_{ij} (the weight of the connection from neuron j to neuron i). If w_{ij} is positive, the synapse is excitatory. If a neuron i receives input from an excitatory neuron, the activation level of neuron i will increase. If w_{ij} is negative, the synapse is inhibitory. If neuron i receives a spike from an inhibitory neuron the activation level of the neuron will decrease. The value of w_{ij} determines the strength of the synapse. The stronger the synapse the more the activation level of the neuron will increase or decrease.

The sum of the activation level a_j of the pre-synaptic neurons $j \neq k$ multiplied by the synaptic strength w_{jk} of the synapses connecting neuron k and j is usually called the input of the neuron. So the input, s_k of neuron k at time $t + 1$ is:

$$s_k(t+1) = \sum_{j \neq k} a_j(t) w_{jk} \tag{1}$$

The way the activation level of a neuron depends on it's input is called the activation function. Several activation functions are used in artificial neural networks. The simplest activation function is the binary activation function. Units that have a binary activation function have an activation level of 1 if the input exceeds a certain threshold T and 0 if the input is below the threshold T.

$$a_k(t+1) = 1 \text{ if } s_k(t+1) > T, 0 \text{ otherwise} \tag{2}$$

Another popular activation function is the sigmodial activation function:

$$a_k(t+1) = \frac{1}{1 + \exp[-\beta s_k(t+1)]} \tag{3}$$

Where β determines the slope of the sigmoid. See section 2.3.3.

2.2 Spiking Neural Networks

Classical neural networks as described in section 2.1 give a simple mathematical model of networks of neurons. These models allow for empirical and theoretical research. Because mathematically these models are relatively simple, it is possible to make rigorous proofs, such as the one mentioned in 3.1.

One of the simplifications that often proves too strong is the fact that the exact firing times of the neurons are not modeled. In biological neural networks, the activity is spread through the network by neurons that fire small spikes. In classical neural networks it is assumed that the exact timing of the spikes carries no meaning.

So to simplify the model, activity in the network is modeled by the activation level of a neuron, which can roughly be interpreted as the number of times a neuron fires a spike within a certain time period. Instead of carrying spikes through the network, the synapses are modeled to transport these activation levels.

This greatly simplifies the model, however it often proves too much of a simplification. The binding method developed in this thesis uses the exact timing of spikes to bind neurons to a pattern. So classical models of artificial neural networks can not be used to implement the binding method.

2.3 The Spike Response Model

In this section I will introduce a precise mathematical model of a network of neurons called the Spike Response Model [Maass and Bishop, 1999]. This model abstracts from the exact biological details of the neurons. In this way the model can be fairly simple. However it is powerful enough to explain various phenomena of biological neural networks.

The method of binding developed in this thesis uses the exact timing of spikes to perform binding. To implement the binding method we thus needs to implement a model of spiking neural networks. The spike response model is relatively simple to implement while staying relatively close to biological neurons. The spike response model is also the model chosen in [Kistler and van Hemmen, 1999] to implement short-term synaptic plasticity, hence it was the obvious choice for this thesis.

2.3.1 The Model

The state of a neuron i at time t is modeled by the action potential $\mu_i(t)$ of that neuron. Whether or not a neuron fires a pulse to its post-synaptic neurons is controlled by this action potential. If the action potential of neuron i crosses the neuron's firing threshold θ_i the neuron will emit a pulse along it's axon. So the set F_i of firing times t_i (the times a neurons emits a pulse) is defined by the exact times the action potential of the neuron crosses the firing threshold of a neuron:

$$F_i = \{t \| \mu_i(t) = \theta_i\} \tag{4}$$

There are two processes that contribute to the value of the action potential μ_i of neuron i. First, there is the reaction of a neuron to it's own pulse, it's so-called refractoriness, this is modeled by a function $\eta_i(t)$.

And second, the reaction of a neuron i to pulses of a pre-synaptic neuron j, is modeled by $\epsilon_{ij}(t)$. The potential at time t is determined by all reactions to it's own spikes and by all reactions to the spikes of the neuron's pre-synaptic neurons. I.e.:

$$u_i(t) = \sum_{t_f \in F_i} \eta_i(t - t_f) + \sum_{j \in \Gamma_i} \sum_{t_g \in F_j} \epsilon_{ij}(t - t_g) \tag{5}$$

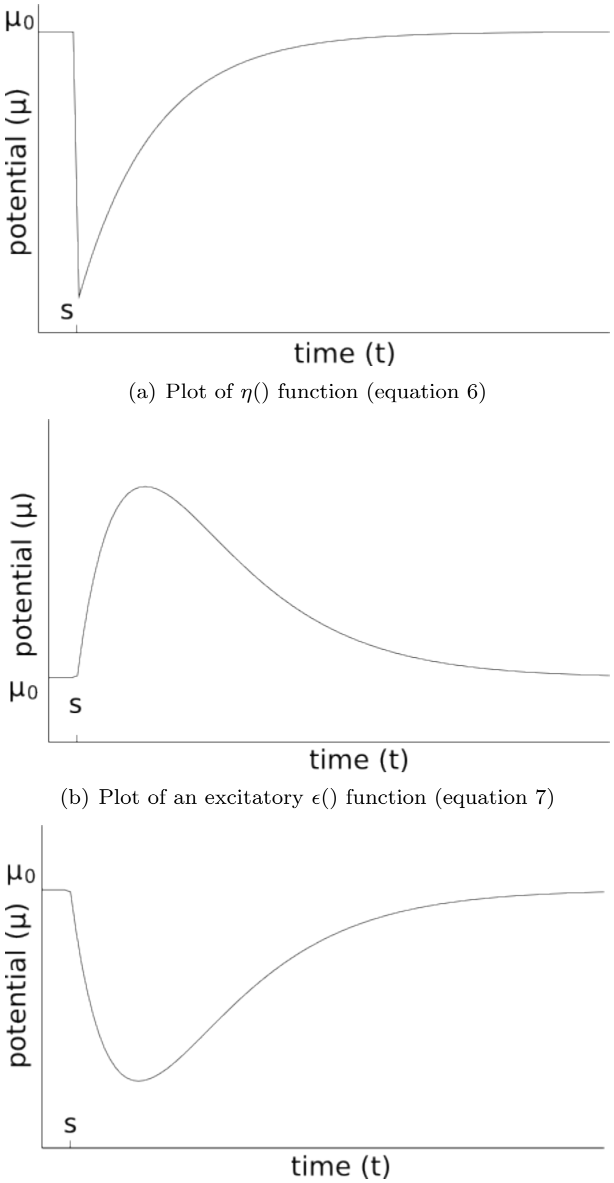
where Γ_i is the set of pre-synaptic neurons of i. The first term of the right side of equation 5 represents the response of i to it's own firing, the second term corresponds to i's response to firing of it's pre-synaptic neurons.

After a neuron emits a pulse it cannot emit any pulses for a short while. This phenomena is called absolute refractoriness. After that the potential μ_i is lowered to a value below the resting potential μ_i^{rest}, i.e. the value to which the potential of the neuron converges if it receives no pulses. The lowering of the potential has the effect that it is more difficult for the neuron to fire after emitting a pulse. This phenomena is called relative refractoriness.

So the reaction of a neuron i to it's own pulse at time s can be modeled by:

$$\eta_i(\Delta t) = \begin{cases} -\mu_{\text{refrac}} \exp[-(\Delta t)/\tau] & \text{if } \Delta t \geq \Delta_{\text{abs}} \\ -\infty & \text{if } 0 \leq (\Delta t) < \Delta_{\text{abs}} \\ 0 & \text{if } (\Delta t) < 0 \end{cases} \tag{6}$$

Where Δ_{abs} is the absolute refractory period, τ is a time constant



(a) Plot of $\eta()$ function (equation 6)

(b) Plot of an excitatory $\epsilon()$ function (equation 7)

(c) Plot of an inhibitory $\epsilon()$ function (equation 7)

Figure 2: Plots of the functions $\eta()$ and $\epsilon()$ as defined in equations 6 and 7. Figure (a) shows the reaction of a neuron to its own pulse at time s. The potential is first lowered to μ_{refrac} and then goes back to it's resting potential $\mu = 0$. (Note that the absolute refractoriness is not shown here). Figures (b) and (c) show the reaction of a neuron to a pre-synaptic pulse at time s. In figure (b) the reaction is excitatory, whereas the reaction in figure (c) is inhibitory.

determining the length of the relative refractory period, and μ_{refrac} a constant determining the amount the potential is lowered due to a spike. Figure 2 shows a graph explaining equation 6.

For simplicity I will assume the same η for every neuron. [Maass and Bishop, 1999] uses equation 6 in most parts of the book. It is however possible to choose a different equation and for example model different types of biological neurons.

If neuron i receives a pulse from a pre-synaptic neuron $j \in \Gamma_i$, this pulse will cause a reaction of the potential μ_i of neuron i. The weight of the synapses determines the direction and magnitude of the reaction. As in the models of classical artificial neural networks in the previous section, this is modeled by w_{ij}.

When a pulse arrives at the neuron, the potential changes rapidly. After reaching the full potential change the potential will gradually recover to the resting potential. [Maass and Bishop, 1999] models this as:

$$\epsilon_{ij}(\Delta t) = \begin{cases} w_{ij}[\exp[-(\frac{(\Delta t)-\Delta^{ax}}{\tau_m})] - \exp[-(\frac{\Delta t-\Delta^{ax}}{\tau_s})]] & \text{if } (\Delta t) \geq \Delta^{ax} \\ 0 & \text{otherwise} \end{cases} \tag{7}$$

Where τ_s and τ_m are time constants that determine how fast the potential recovers, and where Δ^{ax} models the axonal delay (i.e. the time it takes for a pulse to reach the post-synaptic neuron).

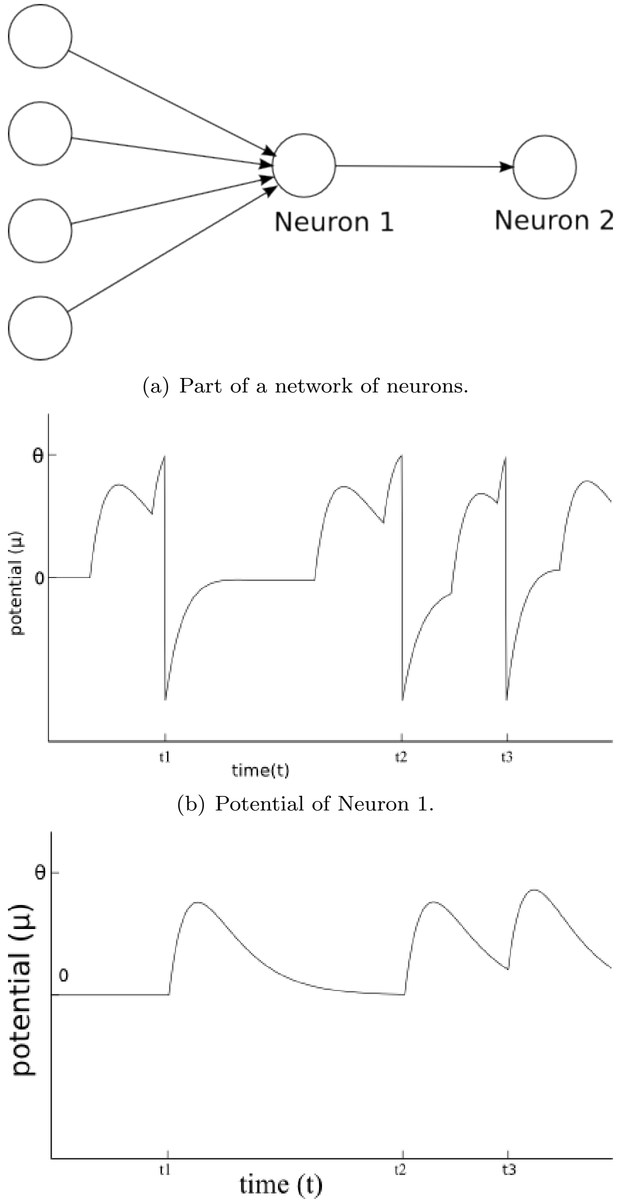
Again for simplicity I assume the same ϵ for every pair of neurons. Throughout the simulations equation 7 is used to model a neurons reaction to it's own pulses.

The equations in this section make up the basic structure of spike response model. They completely abstract away from the biological processes involved. The model just gives a basic structure of how neurons react to pulses. However it is possible to choose more involved equations for η and ϵ and create a models that more precisely models the chemical processes. For our purpose, a simple model suffices, since the model does not crucially depend on any of the low-level chemical processes.

2.3.2 Example

Consider the figures 3(b) and 3(c). The figure shows a part of a network of neurons (figure 3(a). Neuron 1 is connected to neurons in the network that fire randomly. Neuron 2 is connected to Neuron 1 by an excitatory synapse.

Figure 3(b) shows the potential of Neuron 1 plotted against the time.



(a) Part of a network of neurons.

(b) Potential of Neuron 1.

(c) Potential of Neuron 2.

Figure 3: Plots of the potential of two neurons. The neuron in figure (b) (Neuron 1) receives input from several excitatorily connected neurons. When the potential of the neuron crosses it's threshold θ it fires a pulse and it's potential is lowered below it resting potential, making it more difficult for the neuron to fire again. The neuron in figure (c) (Neuron 2) receives excitatory input from Neuron 1. Every time Neuron 1 fires the potential of Neuron 2 is raised and returns slowly to it's resting potential

At time $t = 0$ the potential is equal to the resting potential μ_{rest}. Neuron 1 receives excitatory input from other neurons in the network. Every pulse that is emitted by the pre-synaptic neurons of Neuron 1 causes a change in the potential of the neuron, as modeled by equation 7. At time $t = t_1$ the potential of of neuron 1 crosses the threshold. This means that at t_1 Neuron 1 fires a pulse as modeled by equation 4. The firing causes a negative contribution to be added to the potential of the neuron as modeled by equation 6.

Neuron 2 is connected to Neuron 1 through an excitatory synapse. When the spike reaches the synapse connecting the neurons at $t_1 + \Delta_{axon}$ a positive contribution of $\epsilon()$ is added to the potential of Neuron 2 as modeled by equation 7 (figure 3(c)). At times t_2 and t_3 the potential crosses the threshold again, resulting again in a raising of the potential of Neuron 2.

2.3.3 Activity in the Spike Response Model

The spike response model introduced above gives a simplified model of biological neurons. This subsection shows how the spikes emitted by spike response neurons can be interpreted to resemble the activity of classical neurons (see section 2.1).

The activity of neuron neuron i at time t, $a_i(t)$, can be interpreted as the firing rate of the neuron a time t. This is defined as the total number of pulses a neuron emits over the time interval s [Maass and Bishop, 1999]:

$$a_i(t) = |\{t_f \in F | (t - s) < t_f < t\}| \tag{8}$$

Using this definition we can describe the state of a network at time t by a vector $\overline{a}(t) = \{a_1(t), \ldots, a_n(t)\}$, just like we can represent the activity of a classical network by it's activity vector.

[Gerstner, 1999] shows that the activation function of a spike response neuron with absolute refractoriness can be modeled by a sigmoidial function. Figure 4 shows a plot of a simulation performed using the model described above. The input of a neuron is plotted against the average firing rate of the neuron. The plot clearly shows that the activation function of a spike response neuron can be modeled by a sigmoid, as introduced in equation 3.

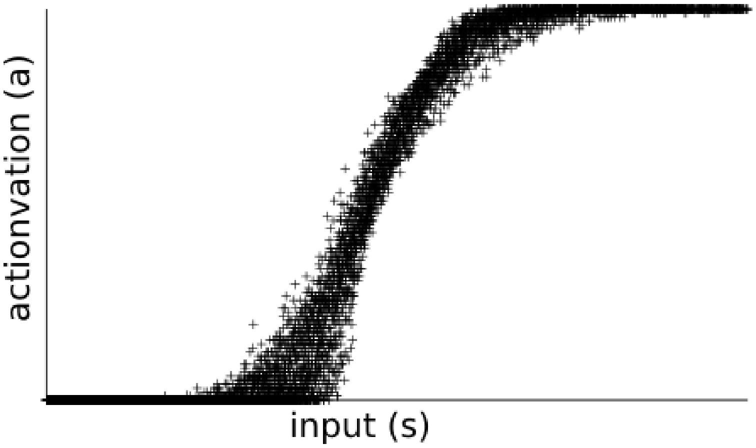


Figure 4: Result of a simulation of a spike response neurons. The figure plots the received input of a neuron against the firing rate of the neuron.

3 Auto-associative Networks

Networks of neurons generally perform a computation by activating neurons and letting the activation spread through the network. The activity of some neurons is raised, and through the excitatory synapses, post-synaptic neurons are activated. They perform a mapping of one set of activation vectors $\overline{x}_1, \overline{x}_2, \ldots, \overline{x}_n$ to another set of activation vectors $\overline{y}_1, \overline{y}_2, \ldots, \overline{y}_n$.

Two types of mappings can by distinguished. In the first type, the activation values of one set of neurons are mapped to the activation values of another set of neurons. Such network are called hetero-associative. The network can also perform a mapping of the activation values of a set of neurons to the activation values of the same set of neurons. These second type of networks are called auto-associative.

Attractor neural networks are a special type of auto-associative networks. They consist of universally connected neurons, i.e. every neuron is synaptically linked to all other neurons in the network. By changing the weights of the synapses, patterns can be stored in the network. If a partial pattern is activated, the activation spreads through the network activating the rest of the pattern, essentially implementing a type of memory.

3.1 Associative Neural Networks

[Hopfield, 1982] showed that a certain class of neural networks will always converge to a stable state. These networks, called Hopfield networks, consist of elements described by equations 1 and 2, which are updated asynchronously. This means that at every time t the activation value of only one (randomly selected) neuron is updated. The elements are connected by symmetrical weights, i.e. the weight connecting neuron i to neuron j must be the same as the weight connecting neuron j to i, or more formally: $\forall i, j : w_{ij} = w_{ji}$. Hopfield showed that if a group of neurons in such a network is activated the network will always converge to a stable state.

3.2 Storing Patterns

If the neurons in a network are connected through symmetrical synapses, the network will converge to a stable state after activating certain neurons. What states are stable depends on the weights of the synapses in the network. By changing these weights it is possible to change the attractor states in the network.

[Hebb, 1949] introduced a method of changing the strength of a synapse based on the activity of the pre- and post-synaptic neurons of the synapse. The process of changing the weight of a synapse according to the activity of the neurons it connects is called synaptic plasticity.

Hebb's idea was that simultaneous activity of two neurons can be interpreted as a way of "belonging together" of the two neurons. "Neurons that fire together wire together". By increasing the strength of the connection between two neurons if they are active together, this information can be stored in the network. If the connection between the neurons is strong enough and one of the two neurons is active, the other neuron will be activated because of the strong positive connection between them. The network has "learned" that the neurons belong together.

This general idea of long-term synaptic plasticity can be used to store patterns in a network. Patterns are stored by presenting an activation pattern to the network, and then adjusting the weights according to Hebb's idea about long-term synaptic plasticity. If two neurons belong to the same pattern their connection is strengthened.

The stronger positive connections between two neurons belonging to the same pattern will mean that activation of one of the neurons will heighten the potential of the other neuron. Looking at the complete pattern, if part of the pattern is activated, the positive connections will activate the rest of the pattern.

More formally Hebb's idea can be expressed as

$$\Delta w_{ij} = \gamma * (x_i x_j) \tag{9}$$

where x_i is the activation of neuron i and γ is usually called the learning rate.

Note that when the activation of the neurons in the presented patterns is positive the weights in the network continue to grow. Often when storing binary patterns, $\{-1, 1\}$ are used as activation values. This has the effect that besides positive connections, also negative connections are created.

When one of the neurons is active and the other is not, the connection between the two neurons is weakened instead of strengthened.

3.3 Distributed Representation

In classical computers information is retrieved from memory by finding the exact address of the stored item. If an item has to be retrieved the exact location of the item in memory has to be computed, which is not necessarily trivial.

The previous subsections showed how a simple network of neurons can be used to implement a content addressable memory. Using a simple rule, patterns can be stored, and later retrieved by activating a part of that pattern. There are various ways to store information in such patterns, for this thesis however I will focus on the two most obvious and different techniques: local representation and distributed representation.

Classical cognitive theory tends to adhere to local representations. Objects are represented in one place in the system, i.e. a memory address, a node in the network or, from a classical analogy for human memory, a drawer in a big closet. If information about an object is to be retrieved, first the location of the object is retrieved, from which the information about the object can then be retrieved.

The auto-associative networks from the previous subsection suggests a different but elegant way to store objects. Instead of letting the nodes in a network represent objects, they represent features of that object. An object is represented by an activation vector. Active nodes in the vector represent features that belong to the object, inactive nodes represent features that do not belong to the object.

Consider figure 5, it shows a network of 6 nodes. The 2 nodes on the top represent color, the central nodes represent size, and the bottom nodes represent shape. A small yellow triangle can be represented by activating the nodes $(small, yellow, triangle)$.

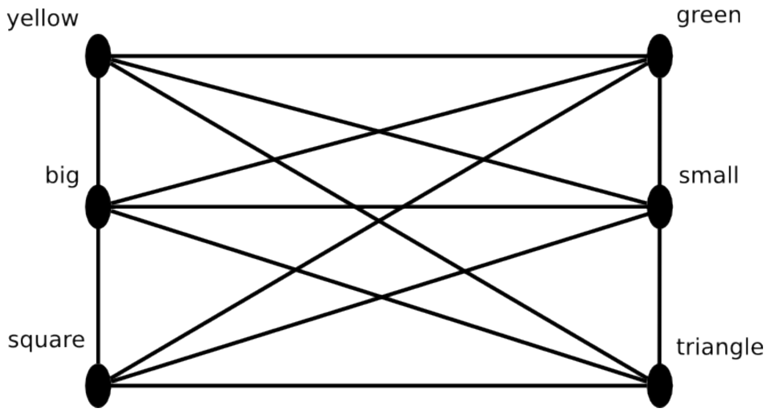


Figure 5: Example of a network using a distributed representation

The example above uses binary units (see 2.1). Using analog units would give us an even more expressive network, "where smallish" and "yellowish" objects can be represented.

Representations similar to the representation in figure 5 are called distributed representations (see [Rumelhart and McClelland, 1987] for a good overview). The classical types of representation where objects are represented in one place are called local representations.

Distributed representations have some advantages over local representations. For one, using local representations n objects can be represented using n nodes. Using a binary distributed representation 2^n objects can be represented using n nodes, since every different pattern represents a different object. So a network that uses a distributed representation can represent exponentially more objects than a local representation can.

Using a local representation, representing new objects requires special mechanisms, since new nodes need to be assigned for the new objects. There are methods for this, however if implemented in a neural network, there has to be some machinery and bookkeeping to do this. In a distributed representation, new object do not need to be assigned to a node, the object can just be activated by activating the corresponding pattern.

Distributed representations are fault tolerant. If a feature of an object is misrepresented, the network will usually repair that, because of the feedback from the network. In a local representation this is much more difficult.

Distributed representations are much more robust then local representation. Losing one node in the network only gives a small loss in functionality. Losing a node in a local representation results in the loss of an object.

4 Binding Problem

The previous section shows how a simple network of neuron-like elements can implement a content-addressable memory, and how these networks suggest a simple but extremely powerful way to represent objects in a network. Although distributed representations have many nice features, they also have some severe shortcomings.

One of the biggest problems with distributed representations (see section 3.3) in classical neural networks, was pointed out by Frank Rosenblatt [Rosenblatt, 1962] using the example from figure 5. The figure shows how configurations of a square and a triangle can by represented using a distributed representation. A small green triangle is represented by the features $(small, green, triangle)$, a big yellow square is represented by the features $(big, yellow, square)$.

The problem arises when we want to represent a small green triangle *and* a big yellow square. This will be represented by (*small*, *green*, *triangle*, *big*, *yellow*, *square*). A small yellow square and a big green triangle is represented by (*small*, *green*, *triangle*, *big*, *yellow*, *square*). It is impossible to tell both representations apart, because there is no way to tell which feature belongs to which object.

In general this problem always arises when more than one object is to be represented using a distributed representation. There has to be a way to bind features to objects if more than one object has to be represented. This problem is known as the binding problem [von der Malsburg, 1981].

The problem does not only occur if visual information has to be represented in a distributed way, it also occurs if information from different modalities (i.e. visual and auditive) has to integrated into one object.

The next sections introduces a solution to the binding problem as proposed in [von der Malsburg, 1981]. This method uses the exact timing of spikes in a network of neurons to perform binding. Three implementations of this method are discussed in the following couple of sections. Section 5 develops a novel way to perform temporal binding, where temporal binding emerges from the use of short-term synaptic plasticity. The proposed method is both more biologically plausible and less complex, in the sense that it can be implemented in a simple network of fully connected spike response neuron, without the need for complex neuronal units or a complex network structure.

Various other solutions have been proposed to solve the binding problem. [Smolensky, 1990] proposes a mathematical solution called tensor product representation. This solution use a distributed representation of of both objects and variables, and represents the binding using the tensor product of the two.

Another proposed solution is that the problem is solved hierarchically. The world is represented in successively more complex representations. Nodes in the layers of higher complexity represent more and more specific things, making it possible to distinguish objects from each other.

Recently temporal solutions of binding have received a lot of attention (see for example the special issue of *Neuron* on binding: [Shadlen and Movshon, 1999], [Roskies, 1999]) for example), and various solutions have been proposed. The general idea of using spike times for binding seems very elegant and simple. However most of the proposed models that perform binding this way tend to be complex, or have various other problems that limit the elegance and representational power of these models (see section 4.2.3). This thesis develops a model of temporal binding which uses short-term synaptic plasticity to implement slow temporal binding.

4.1 Temporal Binding

This thesis focuses on temporal binding, as introduced in [von der Malsburg, 1981]. There it is noted that the exact timing of spikes which is usually considered without meaning in classical neural network could be used to implement binding.

[von der Malsburg, 1981] proposes to use the exact timing of the spikes for binding, hence the name temporal binding. A visual illustration of this idea, makes it clear how this works. Consider figure 6, which shows firing times for the neurons from figure 5. Note that the firing rate, and thus the activation level of all the neurons is equal. When looking only at the firing rate we have a similar pattern as before, all neurons are active, making it impossible to tell if this represents “a large green triangle and a small yellow square” or “a large yellow triangle and a small green square”.

When looking at the exact firing times however it is possible to see what is represented. The spikes for “large”, “green” and “square” are always synchronous, as are the spikes for “small”, “yellow” and “triangle”. The exact timing of the spikes make it possible to bind patterns of neurons to objects, making it possible to represent more than one object at the same time.

[von der Malsburg, 1981] notes that this synchronicity is almost certainly unconscious. People are not capable of consciously perceiving change within a certain small period. This period is referred to by psychologist as the “psychological moment”. The psychological moment lasts

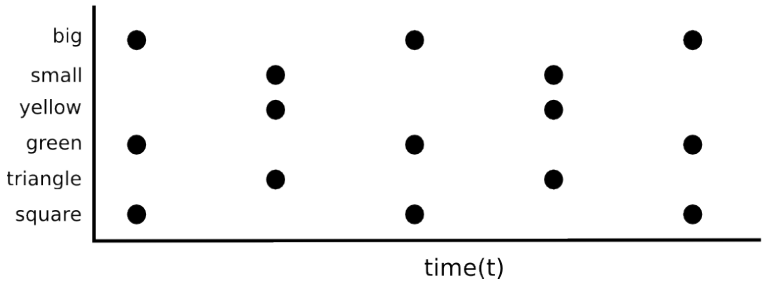


Figure 6: Binding through synchronous firing. Network activity of a network representing a small yellow triangle and a big green square. Each dot represents a particular neuron firing a pulse. The fact that the neurons representing the features "small", "yellow" "and triangle" fire in synchrony indicates that they are features of the same object. This synchrony "binds" the neurons together. Note that the same holds for the neurons representing "big", "green" and "square".

somewhere between 200ms and 500 ms, so the synchrony of the neurons would not be something that is consciously perceived.

The duration of the psychological moment is much longer than the duration of a single spike, making it possible to implement temporal binding using other methods than exact synchrony. Short burst of activity as depicted in figure 7 are also possible, for example.

Section 4.3 shows a model that implements this type of binding. This thesis develops a novel way of implementing this slow temporal binding using short-term synaptic plasticity (See section 5).

One of the things to notice is that although more than one pattern can be distinguished using this method, the number of different patterns remains small. The more different patterns are active the closer the timings of the spike come together. Since the timings of the spikes of the neurons are inherently noisy, the upper limit is probably rather low.

Various researchers ([von der Malsburg, 1981], [Shastri and Ajjanagadd, 1993] for example) have argued that this is possibly in accordance with studies from cognitive psychology. People are not capable of focusing on more than a handful of objects at the same time, and most people can not keep more than about 6 words in active memory. This would mean that this low and hard barrier on simultaneous representation does not have to be a problem.

Also note that although it is possible to *retrieve* more than one object at the same time, it is not necessarily possible to *store* configurations

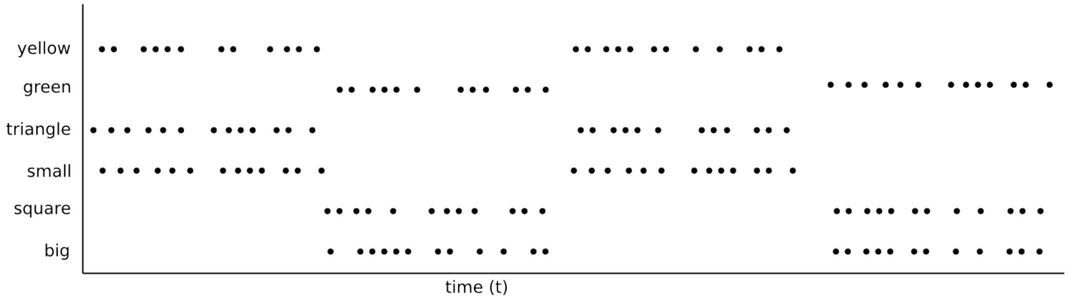


Figure 7: Binding through bursts of activation. Network activity of a network representing a small yellow triangle and a big green square. Neurons are not bound by synchrony of the spikes. Instead, the neurons belonging to one pattern are simultaneously active in short burst. Since the length of the bursts is still much lower than the psychological moment, the changes in activation will still be unconscious.

(or scenes) consisting of more than one object. In fact most methods of temporal binding do not offer a way to store scenes of objects (except for the method in section 4.2.1).

4.2 Synchronous temporal binding

There has been a lot of research into the possible implementation of temporal binding in spiking neural networks using synchronous pulses. This section will introduce two of the more prominent models. After this, some disadvantages of these models are discussed.

4.2.1 Shruti

Lokendra Shastri [Shastri and Ajjanagadd, 1993], implements “a connectionist model of knowledge representation and reflexive reasoning” inspired by the ideas on temporal binding from [von der Malsburg, 1981]. In this work a network of simple processing units is constructed, that can, in a distributed manner, perform reasoning tasks. Binding is achieved by explicitly synchronizing firing times of nodes in the network.

[Blutner and Doherty, 1997] shows that associative networks implement a form of non-monotonic logic. Without binding however, the expressive power of these models is severely limited. To represent a statement like “John loves Mary” in a distributed fashion there has to be a way to simultaneously represent “John” and “Mary”.

[Shastri and Ajjanagadd, 1993] represents relations such as "John loves Mary", by synchronous firing of the nodes *john* and *lover*, and synchronous firing of the nodes *mary* and *beloved*, and thus binding the nodes for *john* and *lover* to the same object, and simultaneously binding the nodes for *mary* and *beloved* to another object.

To achieve this Shastri et al. introduce p-btu nodes and τ-and nodes. Both these types of nodes are simple neuron-like processing units that fire pulses to connected nodes. They however have some special properties that makes it possible to control the synchronization of the firing times of nodes.

p-btu nodes behave as follows:

- If a node A is connected to node B, the activity of node B synchronizes with the activity of node A.
- The periodic activity of node A leads to synchronous periodic activity in node B within one period.
- A threshold, n, associated with a node indicates that the node will fire only if it receives n or more synchronous inputs.

In this way p-btu nodes can form chains of synchronous firing. In [Shastri and Ajjanagadd, 1993] this is used to encode rules. The nodes are used to implement the synchronization between roles (arguments of a predicate) and fillers (objects that fill these predicate arguments) and of arguments of the antecedent predicates to the arguments of the consequent predicates. In this way it is possible to implement simple first-order like rules, in a distributed way.

τ-nodes behave as follows:

- A τ-and node becomes active if it receives an uninterrupted pulse train, i.e. it receives pulses such that the gap between pulses is less that a pulse width.
- So a τ-and node receiving periodic pulses with period π produce a periodic pulse with period π.
- A threshold, n, associated with a τ-and node indicates that the node will only fire if it receives more than n pulses within the length of a pulse.

τ-and nodes make it possible to encode facts. This is done by creating *fact-nodes* that fire if the activation pattern for that first order encoded fact is active. These fact nodes can then be used for other steps in the reasoning process.

[Shastri and Ajjanagadd, 1993] shows how a network of these two types of nodes can perform various reasoning and query-answering task by encoding facts and rules in a network of these nodes and activating the network in a way that represents a question.

4.2.2 Neural Oscillators

[Ursino et al., 2006] constructs a network of biologically plausible spiking neurons that perform binding using synchronous firing.

A network of neural oscillators is constructed. An oscillator is formed by coupling an inhibitory neuron with an excitatory neuron. Activating the excitatory neuron will result in periodic firing of the excitatory neuron due to the feedback of the inhibitory neuron. These neural oscillators are called Wilson-Cowan oscillators.

An associative network is constructed by connecting the excitatory neurons in the oscillator. Patterns can be stored in this network by basic Hebbian learning. When two oscillators are connected, a positive connection (i.e. excitatory synapses) favors synchronization, whereas a negative connection (i.e. inhibitory synapses) favors de-synchronization.

An inhibitory layer is used to make sure that only approximately one pattern can be active. This, together with the synchronization/de-synchronization behavior of the oscillators, achieves a segregation of the input.

Shortly after the activation of more than one pattern, the pulses of the neurons belonging to the same pattern synchronize, whereas pulses of neurons belonging to different patterns desynchronize, effectively binding neurons to the pattern.

4.2.3 Disadvantages of synchronous binding methods

The nodes in the model of [Shastri and Ajjanagadd, 1993] are “Neuron like”, in the sense that they are simple processing nodes connected to each other in a network. It is however hard to see how these nodes will be constructed from more biologically realistic neural units. Biological units are noisy and imprecise and do not seem to have mechanisms for explicit synchronization.

This makes it difficult to see how the model of [Shastri and Ajjanagadd, 1993] could be implemented in a biological system.

The units in the model of [Ursino et al., 2006] are much closer to biological neurons. It does however not seem to be the case that as in the model of [Ursino et al., 2006] every neuron is coupled to another neuron to form an oscillator. These constructions might be found but do not seem to be ubiquitous enough to facilitate binding on a large scale.

Besides these problems with biological realization of these models, models that use exact synchrony, are argued to be biologically implausible in general. [Shadlen and Movshon, 1999] argues that analysis of biological brain activity shows that there is not enough correlation between firing times of neurons for temporal synchrony of neurons to play a role in binding.

A very compelling feature of distributed representations is that the activation level (i.e. the firing rate) of a neuron signals the strength of the feature in the represented object. I.e. the more active the neuron encoding the feature “red” is, the redder the represented object is. This rate coding makes distributed representations highly expressive.

In most model of synchronous temporal binding it is not possible for active neurons to have a different firing rate. Either neurons are active and continuously fire in synchrony or they are not active at all. This makes rate coding effectively impossible.

Another problem with synchronous temporal binding related to this is that the refractoring period of neurons make it impossible for a neuron to fire immediately after firing. This plays an essential role in the synchronization in the model of [Ursino et al., 2006] and other models.

However this also makes it impossible for a neuron to reliably be active in more than one pattern. A neuron can only be active in one pattern, making it much more complex to represent two different but similar objects. It is not clear how to activate more than one overlapping pattern at the same time.

4.3 Slow Temporal Binding

[Knoblauch and Palm, 2002] implements temporal binding, but on a different time-scale. The network in the model consist of two areas. A peripheral area P, which models the visual cortex and a more central area C which acts as an associative memory, receiving input from area P.

Area P models the visual cortex receiving an image as input. Neighboring neurons in this section are inhibitorily connected, whereas neurons further apart are excitatorily connected. This has the effect that area separates distinct visual object from the input. Neurons representing the same pattern will fire synchronously, effectively binding neurons in this area to visual pattern.

In other words, this area performs a segmentation of the visual input.

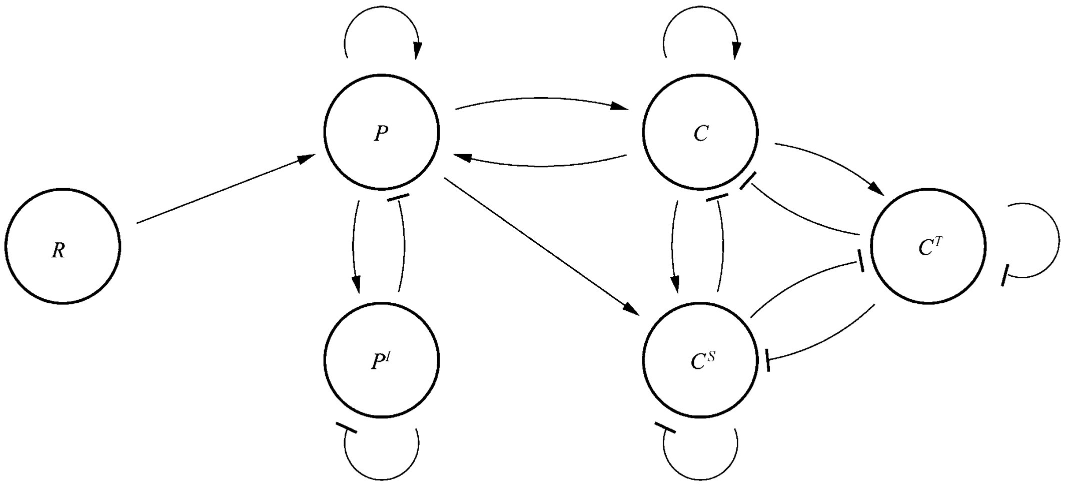


Figure 8: Topology of the network that implements the segmentation and retrieval. Adapted from [Knoblauch and Palm, 2002]

Different visual shapes are separated into different patterns. Fire time synchrony is used to indicate which neuron belong to which pattern in the segmentation.

Area P serves as input for area C. This area is connected through Hebbian learning, i.e. it is an associative memory. The patterns that are stored represent visual patterns presented to area P. When a partial pattern is activated in area C, the retrieval process of the associative network will retrieve the full pattern.

If two overlapping patterns are activated in area P, these visual patterns are separated through the synaptic connections in this area. The activation in area P is spread to area C starting a retrieval process for the full pattern that are stored in this area.

The neurons in area C are not bound through synchronous firing however. The associative area C is connected to two other areas that together govern the binding process (see figure 8).

Area C^s, the separation area, is activated through area C, and gives inhibitory input to area C. It inhibits all neurons not belonging to the current pattern. This has the effect that only one pattern can be active at the same time. When more than one pattern is active, a process of competition makes sure only one pattern remains active.

Area C^t, the terminating layer, also receives input from area C and inhibits area C. But whereas the inhibition of area C^s specifically inhibits the other patterns in the network, area C^t inhibits area C unspecifically. It also works on a much slower scale. After a period of activity in area C, area C^t terminates the activity.

The interaction of the three areas C, C^s, and C^t has the effect that only one pattern is active at the same time in area C, and that a pattern remains only active for a short period.

The resulting network behavior in area C (the associative area) is similar to that of figure 7. One of the retrieved patterns is active for a short period until C^t terminates that pattern's activity, another pattern takes over and is again active until area C^t terminates it's activity again. This way the network continually switches between patterns, with each pattern active for a short amount of time. So the network binds neurons to patterns using time, but on a much slower scale.

The periods of activity are much smaller than the psychological moment, making the switches between pattern unconscious. [von der Malsburg, 1981] already indicates that this type of temporal binding would also be a valid form of temporal binding.

Note that crossover of neurons between patterns is much more unlikely in this model than in models of synchronous binding. It is also no problem for neurons to be active in more than one pattern at the same time.

The next section introduces a novel method of implementing this slow temporal binding. Instead of having a series of layers that implement the pattern switching, the model in the next section the binding emerges in a simple auto-associative network with short-term synaptic plasticity as modeled in [Kistler and van Hemmen, 1999].

5 Temporal Binding by Short-Term Synaptic Plasticity

Section 3 showed how networks of neurons can be used to implement an associative memory.

This section aims to implement an auto-associative network that can retrieve more than one pattern at the same time. Section 4 showed how having more than one pattern active in the network poses a problem, because it becomes unclear which neurons belong to which pattern. The same problem arises when patterns are activated. If patterns of fifty neurons are stored in a network of hundred neurons, and two non-overlapping patterns are to be activated, this has the effect that all the neurons in the network are activated. There has to be a way to bind activated neurons to their pattern

Section 4.1 showed a method of binding neurons to a pattern by using time as an extra dimension. Neurons that fire in phase belong to the same pattern, whereas neurons that fire in a different phase belong to a different pattern, see also figure 6. Section 4.3 showed a method that uses a slow version of temporal binding, where neurons belonging to the same pattern fire in simultaneous bursts.

This section introduces a novel method of binding that uses short-term plasticity to achieve temporal binding on a time-scale similar to [Knoblauch and Palm, 2002]. An associative network of spike response neurons is constructed from which multiple patterns can be retrieved simultaneously. The resulting network behavior is similar to the behavior of the network developed by [Knoblauch and Palm, 2002], however the network consists of one simple layer of neurons that are trained using standard Hebbian learning. This model implements slow temporal binding in a simple Hopfield-like network of spike response neurons. The model does not suffer from the general problems models of synchronous binding suffer from (as explained in section 4.2.3). The network topology of the model is much simpler than the model proposed by [Knoblauch and Palm, 2002].

5.1 Pattern Retrieval

Section 3 showed how a network of neurons can be used to store and retrieve patterns. Patterns are retrieved from the network by activating part of the pattern. In a network of classical neurons these neurons are activated by setting their activation level to a certain value.

[Sommer, 2001] implements such an auto-associative network using a network of spike response neurons. Retrieving a pattern in such a network is a little bit more complicated, since neurons can be activated in various ways.

One way is to simulate pulses from neurons outside the network, i.e. activating neurons is done by sending pulses to the neuron, similar to pulses it receives from neurons inside the network. The exact timing of these pulses can be used to group the activated neurons together in a similar way to the binding solution of [von der Malsburg, 1981].

[Maass and Bishop, 1999] notes that pulses arriving close together have a bigger effect on a neuron's potential then spikes arriving far apart. Figure 9 shows the effect on the potential of two pulses arriving close together (a) and two pulse arriving further apart (b). The maximum of the potential of the neuron is much higher in figure 9 (a) than in figure 9 (b)).

The fact that pulses close together have a bigger effect on the potential of a neuron can be used to bind activated neurons to a pattern. If the neurons of one pattern are activated by pulses that arrive simultaneously to all activated neuron belonging to that specific pattern, the potential of these neurons will cross the threshold at an almost equal time. Because the activated neurons belonging to one pattern fire close together they have a much bigger effect on the potential of their post-synaptic neurons. Neurons belonging to different patterns will not cross their threshold simultaneously and thus have a much smaller effect on the potential of their post-synaptic neurons.

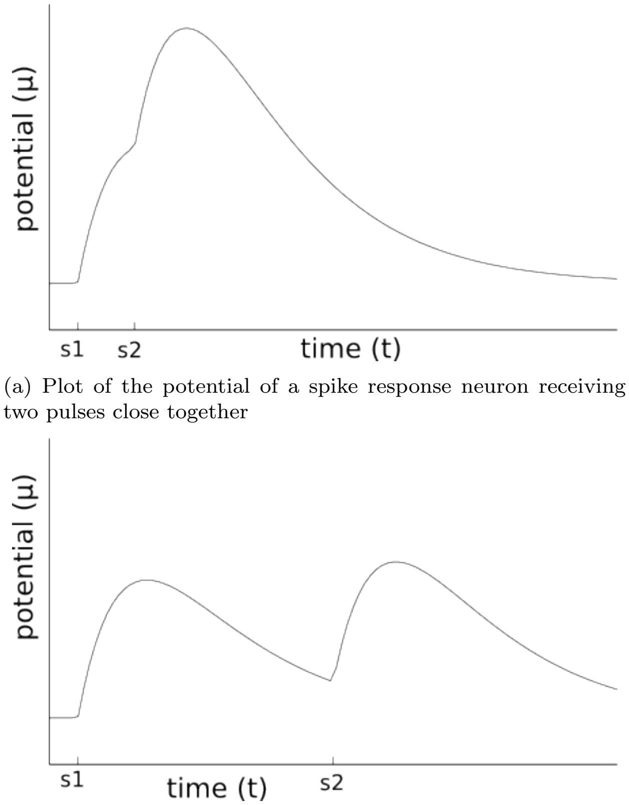
5.2 Pattern separation

As mentioned in section 3.2 the Hebb rule (equation 9), can be used to store patterns in a network of universally connected neurons. Using this rule, patterns can be stored by (locally) changing the synaptic strength between neurons.

For simplicity we only look at binary patterns in this thesis. When presenting the pattern to the network as values in $\{0, 1\}$, the result will be that with each stored pattern, the strength of the synapses will increase.

When part of a pattern is activated, the excitatory connections will activate the remainder of the pattern, thus retrieving the full pattern. When two partial patterns are activated, the excitatory connections usually activate the superposition of both patterns.

When we present patterns to the network of values from $\{-1, 1\}$, be-



(a) Plot of the potential of a spike response neuron receiving two pulses close together

(b) Plot of the potential of the same spike response neuron receiving two pulses further apart

Figure 9: Plots of the potential of two neurons. Neuron 1 receives two pulse ($s1$, $s2$) close together, whereas Neuron 2 receives two pulses far apart. Note that the potential of of Neuron 1 reaches a much higher level then that of Neuron 2

sides positive connections, negative connections will be created between neurons from different patterns. When a partial pattern is activated in the network the excitatory connections still retrieve the full pattern.

When two partial patterns are simultaneously presented to the network, the negative connections between the two patterns will make sure the network stabilizes to a state where only one pattern is active. This form of competition is used in the proposed binding method to make sure there is only one pattern active at any moment in time.

Note that this active pattern need not be a completion of one of the two partial patterns. There might be more than two partial patterns in the superposition of both activated partial patterns.

However, as described in the previous section, by synchronously activating neurons belonging to the same partial pattern, one of the two activated partial patterns has a much better chance at becoming the retrieved pattern than any of the possible spurious patterns in the superposition of the two partial patterns, since, as the previous section explained, the effect of simultaneous pulses is much bigger than non-simultaneous pulses.

The combination of the inhibitory connections created when storing patterns and the synchronous activation of patterns makes sure that only one of the activated patterns can be retrieved at any moment in time.

5.2.1 Short-Term Synaptic Plasticity

Section 3 described how the strengths of synapses can be changed to store patterns in a network of neurons. This type of synaptic plasticity was described in [Hebb, 1949]. It takes places on a long timescale, from seconds to even hours. For modeling retrieval from the network, the synaptic strengths are actually assumed to be constant.

[Kistler and van Hemmen, 1999] describes an extension of the spike response model where a different type of plasticity can be modeled. This type of plasticity takes places on a much shorter time-scale, approximately on the time-scale of normal network activity. This type of synaptic plasticity is called short-term synaptic plasticity.

Besides the differences in time-scales, there is also a difference in what influences the synaptic strength. In long-term plasticity, the synaptic strength is influenced by both the pre-synaptic, and post-synaptic neuron's activity. If both neuron are simultaneously active the synapse is strengthened. If only one of the neurons is active, the synapse is weakened (see equation 9).

With short-term plasticity the strength of the synapses is only influenced by the activity of the pre-synaptic neuron. The general idea is that transmitting a spike from the pre-synaptic neuron to the post-synaptic neuron takes up some kind of “resource” ([Kistler and van Hemmen, 1999], section 2), i.e. by transferring the spike across the synapses, chemicals and energy is used. The use of these resources results in a temporary change of synaptic strength. Either the synapse is weakened, which is called short-term depression, or the synapse is strengthened which is called short-term facilitation. After a spike is transmitted, the resources are recollected, and the synaptic strength goes back to it’s original value.

[Kistler and van Hemmen, 1999] models both short-term depression and short-term facilitation. Here I will focus on short-term depression, as only this is relevant for this thesis.

In the spike response model the potential of a neuron is modeled by equation 7. In this equation w_{ij} models the synaptic strength. [Kistler and van Hemmen, 1999] proposes to replace the constants w_{ij} with functions $w_{ij}(t)$:

$$w_{ij}(t) = w_{ij}^0 Z_{ij}(t) \tag{10}$$

Where $Z(t)$ can be interpreted as the amount of resource available at the synapse at time t. Each transmitted spike lowers this amount of resources with a certain amount r. After the spike is transmitted the resource is recollected. So the amount of resource R_{ij} taken by a transmitted spike since the moment of the spike can be modelled as:

$$R_{ij}(\Delta t) = \begin{cases} r \exp[-(\Delta t)/\tau] & \text{if } (\Delta t) \geq 0 \\ 0 & \text{otherwise} \end{cases} \tag{11}$$

A subsequent spike lowers the amount of resources again with r until the resource is fully depleted. This yields the following equation for the amount of resources Z_{ij} at time t.

$$Z_{ij}(t) = max(\{0, 1 - \sum_{t^f \in F_i} R_{ij}(t - t^f)\}) \tag{12}$$

where F_i

Figure 10 shows the effect of short-term synaptic plasticity on the strength of a synapse. After the synapse has carried a spike, it’s strength is decreased. Another spike decreases the strength of the synapse even more. After the spikes are transmitted, the strength of the synapse recovers to it’s original value.

[Bibitchkov et al., 2002] studies the effect of short-term synaptic plas-

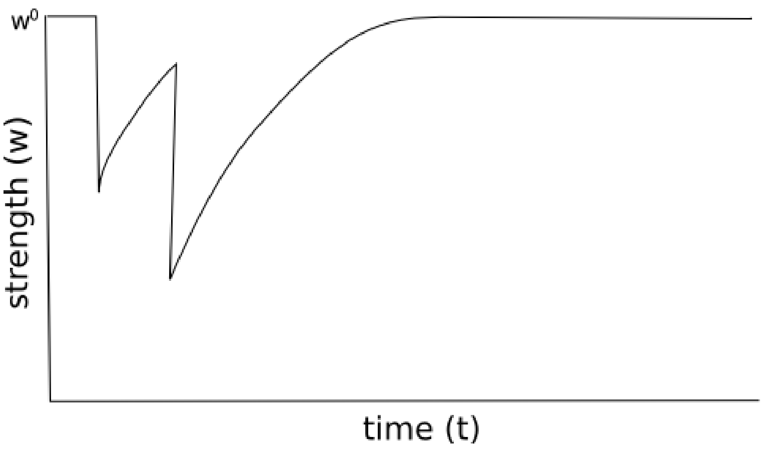


Figure 10: Plot of the synaptic strength of a synapse carrying a pulse

ticity on associative memory. They conclude that

> . . . associative memory networks with synaptic depression are capable of carrying out their functions, although with a lower capacity ([Bibitchkov et al., 2002], 334)

and

> The problem of lower storage capacity for networks with depression can be relieved if one requires just a certain time window for a stable activity in a pattern instead of sustained activity ([Bibitchkov et al., 2002], 334).

If an associative memory is created with short-term depressing synapses, the network retrieves the same patterns as a network with static synapses. When a pattern is retrieved however, the patterns become more and more susceptible to noise, and the patterns become unstable, retrieving spurious patterns.

When the network performs slow temporal binding, the long term stability is not very interesting. Patterns are meant to stay stable for a short while.

[Bibitchkov et al., 2002] shows that associative networks with short-term depressing synapses exhibit a novel behavior where the network quickly switches from one pattern to another, due to noise. The synapses connected to the active neurons in the pattern become weaker and weaker due to their reducing resources. The decreasing strength of the active synapses makes the pattern less stable, since the relative strength of the reaction of neurons to the noise increases.

This behavior of pattern switching will be used in the next section to implement binding in an associative network that can retrieve more than one pattern at the same time.

5.3 Switching Patterns

Using the techniques described in the previous two subsections, it is possible to implement an auto-associative network of spike response neurons, that can retrieve more than one pattern simultaneously.

Patterns are stored using Hebbian learning (see equation 9). The inhibitory synapse makes sure only one pattern can be active at any moment in time as explained in section 5.2. Patterns are activated using the method described in section 5.1.

The neurons are connected by short-term depressing synapses. When one pattern is active in the network the strength of the post-synaptic synapses of the neurons belonging to the pattern is decreased. [Bibitchkov et al., 2002] shows that the network will tend to switch to another pattern if the strength of the synapses gets low enough. In [Bibitchkov et al., 2002] this switch was induced through noise, and the network would switch to an random pattern. If more than one pattern is activated, the network will however switch to one of the suppressed patterns.

If a pattern has been active for a while, the post-synaptic synapses of the neurons belonging to the active pattern will be very weak due to continuous short-term depression. The strength of the post-synaptic synapses of the neurons belonging to one of the suppressed patterns will be high, as they will be fully recovered because they have been suppressed for a while. So the active pattern hardly suppresses the other patterns any more due to the weakened inhibitory synapses. The suppressed neurons will strongly excite neurons in their pattern and strongly suppress neurons in the other patterns. A new competition is started between the suppressed patterns. One pattern will win and suppress the other patterns, until the synapses are weakened again and a following competition is started.

Figure 11 shows a network where two patterns are activated in an auto-associative network. At first, the red pattern is active, and suppresses the green pattern. The strength of the active synapses decreases, lowering the suppression of the green pattern. The synapses of the green pattern are fully recovered, so once the suppression of the green pattern is sufficiently diminished and some of the neurons start firing, the red pattern becomes suppressed and the green pattern becomes active.

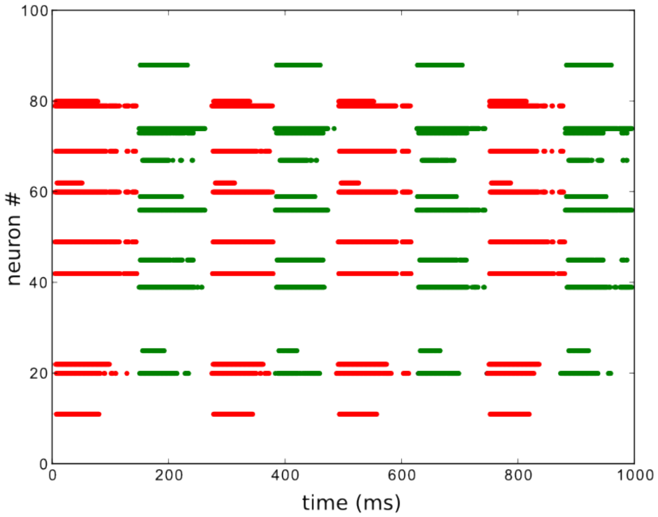


Figure 11: Plot of the firing rates of neurons in a network of 100 neurons (y-axis). The x axis show the time in milliseconds. Two patterns are activated in the network simultaneously. During approximately the first 120 milliseconds, 10 neurons are active, all belonging to the same activated pattern. At around 120 milliseconds, 10 different neurons, belonging to the other activated pattern become active. When the activation of this pattern dies down, the first pattern takes over again.

Using the techniques from the previous section it is possible to implement a network that retrieves more than one pattern and binding the neurons to a pattern using temporal binding as suggested by [von der Malsburg, 1981], however not on the scale of single spike, but on the scale of a couple of spikes.

Note that it is actually possible to changes the time-scale on which the binding is performed by manipulating the strength of the short-term plasticity.

5.4 Measuring Binding

Section 5.3 shows how to implement an auto-associative network that can retrieve more than one pattern at the same time. Neurons are bound to patterns by short periods of activity using short-term-plasticity.

This section shows a method to measure to which patterns a neuron belongs. Intuitively, neurons that are active in a period belong to the same pattern. A neuron that is continuously active belongs to all patterns, and a neuron that is not active at all belongs to no pattern. Figure 11 clearly shows two groups of neurons that are bound using temporal binding. Some neurons are active in the first 120 milliseconds, some neurons are active in the second 120 milliseconds and so forth.

However if we want to do experiments or simulations we need a formal definition of when a neuron is bound to a pattern. In other words, we need a definition of when neurons are active together, and when neurons are not active together.

Activity of a neuron is measured by it's firing rate (see equation 8). An active neuron has a high firing rate, whereas a inactive neuron has a low firing rate.

One way to measure the relation of the firing rate of two neurons is by measuring the the covariance of the firing rate of the neurons. The covariance of the firing rate of two neurons is expressed by equation 13

$$cov_{r_1(t)r_2(t)} = E(r_1(t)r_2(t)) - E(r_1(t))E(r_2(t)) \tag{13}$$

Covariance measures the relatedness of the two firing rates. If both firing rates are high and low at the same times, the covariance is high. If the firing rate of one neuron is high when the firing rate of the other is low the covariance is low.

If neurons are bound using the technique described in the previous sections, the firing rate of a neuron will go up and down as the pattern switches from suppressed states to active states. If neurons belong to the same pattern, they will go up and down around the same times. The covariance of their firing rates will thus be high. If neurons do not belong to the same pattern the opposite will be true, and the covariance will be low.

One problem with measuring binding this way is that it fails if a neuron belongs to two active patterns. The neuron will then be active in more than one period. It's firing rate will not match with the firing rate of any of the other neurons, however intuitively it should belong to two patterns

A high covariance indicates that neurons belong to the *same* pattern, however a low covariance does not indicate that the neurons belong to a *different* pattern. So covariance cannot be a decisive measure for slow temporal binding.

Intuitively, neuron n belongs to the same patterns as neuron m if the firing rate of n is high when the firing rate of neuron m high. Conversely neuron m belongs to the same patterns as neuron n if the firing rate of m is high when the firing rate of n is high. If during a period the firing rate of n is high, but the firing rate of m is low, this does not indicate anything with regard to binding, since neuron n might be active in multiple patterns.

So $r_n(t) \gg 0$ and $r_m(t) \gg 0$ can be taken as an indication that the neurons belong together. We can thus define the *relatedness* B of n and m as

$$B(n, m) = \sum_t r_n(t) r_m(t) \tag{14}$$

where $r_n(t)$ is the firing rate of neuron n at time t. Neuron n and m belong to the same pattern if $B(n, m) \gg 0$.

6 Simulations and Results

6.1 Simulations

I implemented the model of temporal binding developed in the previous section in C++ (see http://github.com/eodolphi/Spiking to download the code). This section shows some experimental results from running this implementation. The implementation creates a network of 100 spike response neurons (See section 2.3), with $\tau_m = 4, \tau_s = 2; \tau_r = 2, \Delta_{abs} = 2$ and a threshold of 0.2.

These neurons are universally connected through synapses with short-term plasticity (See section 5.2.1).

Patterns are stored using the Hebbian learning rule from equation 9. 20 patterns of 10 neurons are stored in the network of 100 neurons. Patterns are retrieved by simultaneously activating 5 neurons from a pattern using the method described in section 5.1.

This network setup is used in the next three sections to retrieve one, two and three simultaneous patterns.

6.1.1 Retrieving one pattern

Figure 12 shows the activation of the neurons in the network, when 5 neurons of one of the patterns are activated by simultaneous pulses. The other neurons belonging to the pattern are immediately retrieved. When the synapses become fatigued, the strength of the synapses becomes lower and the retrieved neurons become inactive again.

This confirms the result of [Bibitchkov et al., 2002]. Note that in this case the activity just dies out. In other case spurious patterns might be retrieved.

6.1.2 Retrieving two patterns

Figure 13 shows what happens if two patterns are retrieved simultaneously. The inhibiting connections between the two patterns ensure that only one pattern can be active at the same time. The depressed synapses however make the active pattern unstable after a certain period of activity.

At this time the other pattern will take over and become active. The instability encountered in the previous section with one pattern, causes the other pattern to become active.

When the synapses of the neurons in the second pattern become fatigued, the second pattern becomes unstable, at this time the first pattern will take over again.

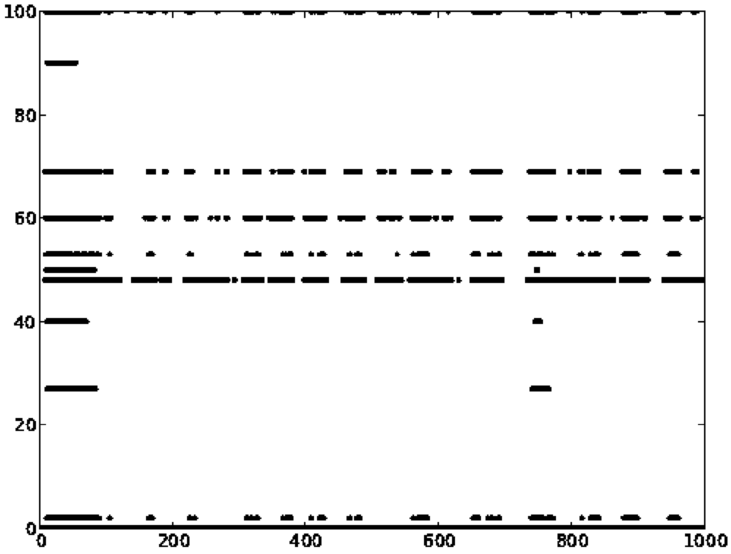


Figure 12: Results of a simulation with one active pattern, $r = .01$, $\tau_r = 100$. Repeated from figure 11.

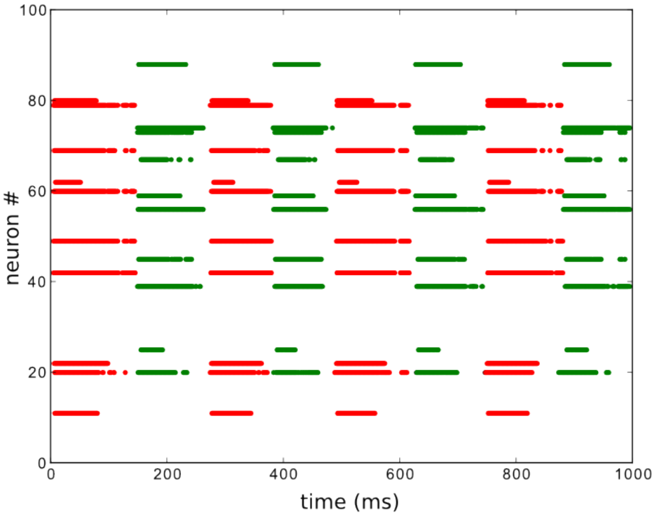


Figure 13: Results of a simulation with two active patterns, $r = .02$, $\tau_r = 50$. Repeated from figure 11.

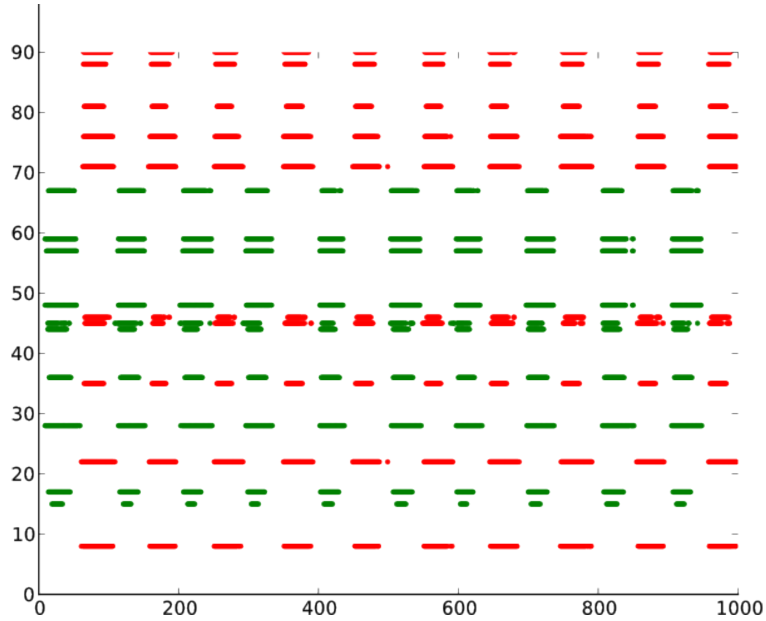


Figure 14: Results of a simulation with two active patterns, $r = .04$, $\tau_r = 50$.

Figure 14 shows the behavior of a network with a higher r (see equation 11), i.e. the carrying of a spike causes a bigger reaction in the synaptic strength. So it takes less time for the synaptic strength of the active pattern to be lowered enough for the suppressed pattern to take over. This has the effect that the periods of activity become shorter.

When the period of activation becomes too low, the patterns do not stabilize any more.

6.1.3 More patterns

When the number of active patterns is increased further, the retrieval becomes gradually worse. Figure 15 show how the network behaves when three patterns are simultaneously activated. Note that the three patterns are again active in distinct periods. However around 550 ms two neurons from the red pattern are active during the activity of the green pattern.

The moment an active pattern fatigues, the two other patterns compete for activation. The more patterns compete the higher the chance a spurious patterns is retrieved.

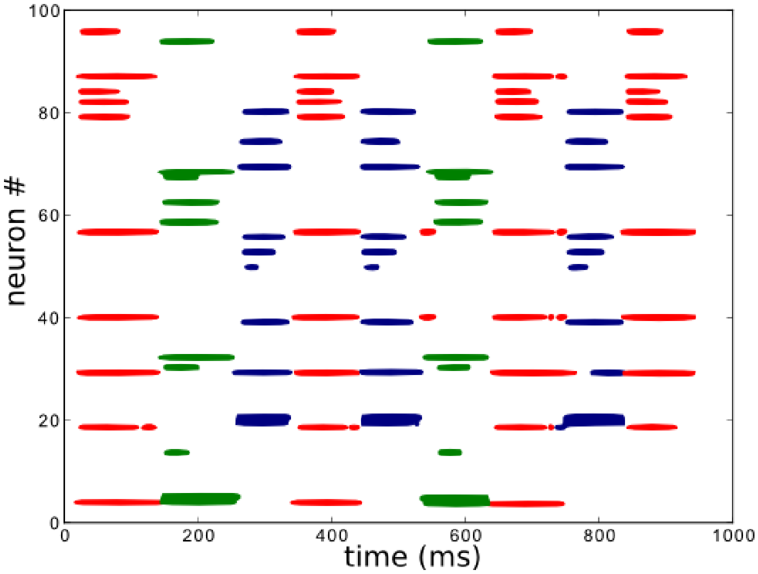


Figure 15: Results of a simulation with three active patterns

6.2 Results

The previous section showed some simulations of a spike response network that retreives one, two and three pattern simultaneously. The plots of the network activity show that the network binds neurons to their pattern by slow temporal binding.

This section analyzes the retrieval performance of the network when retrieving one, two, and three patterns.

6.2.1 One pattern

[Bibitchkov et al., 2002] shows that the capacity of an auto-associative network is not affected by short-term synaptic plasticity. However, the stability of the retrieved pattern *is* affected. When a partial pattern is activated, the activation will spread and activate the full pattern just as in normal auto-associative networks.

The synapses connecting the neurons in the pattern quickly weaken because of the short-term plasticity, which makes the retrieved pattern unstable. With the synapses connecting the stored pattern weakened, noise and the now relatively strong other synapses will have the effect that a different pattern is retrieved or that the retrieved pattern dies out.

Figure 16 shows the performance of an auto-associative network of spike response neurons. Each figure plots the error percentage of the retrievals against the number of stored patterns.

To test the storage capacity and retrieval performance of the network described in section 5, a simulation is run with a network consisting of a 100 nodes, similar to the simulations performed in the previous section.

Classical Hopfield networks have what is called a storage capacity. When a small number of patterns is stored, the patterns are retrieved without error. However when a certain limit is reached, the performance of the network quickly degrades until it levels of at a point where the network does not perform any better than it would by pure chance.

For classical Hopfield networks of N nodes, storing binary pattern where half of the neurons are active in each pattern, this limit is about $0.13N$, i.e. in a network of 100 nodes, 13 patterns can be stored reliably.

Figure 16(a) shows the network's performance without short-term synaptic plasticity. The plot shows a similar behavior of that of classical Hopfield networks. If less then 20 patterns are stored, the retrieval error of the network is very low. At around 20 patterns the retrieval error quickly rises and levels of.

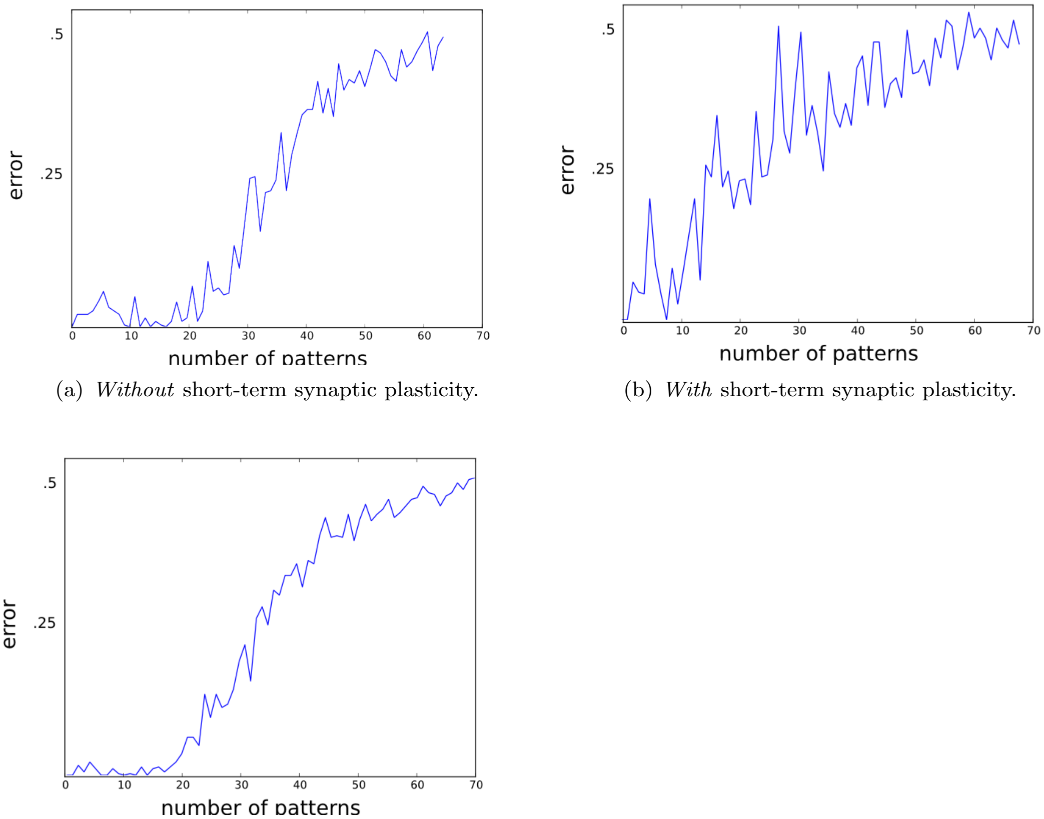
The storage capacity of the network in figure 16(a), however is much lower than the storage capacity of classical Hopfield networks. In a classical Hopfield network of 100 nodes it is possible to store $13 * 50 \approx 650$ bytes of information. The network in figure 16(a) has a storage capacity of about 20 patterns, but only pattern of 10 neurons are stored. This gives the network a storage capacity of $20 * 10 \approx 200$ bytes of information.

It is however to be expected that the storage capacity of auto-associative spike-response networks is lower than that of classical Hopfield networks. Choosing the optimal threshold for example is not at all obvious. Since the focus of this thesis was the binding behavior of the network and not the absolute storage capacity, the network was not optimized for a high storage capacity.

Figure 16(b) shows a plot of the retrieval error of the same network but with synaptic plasticity. It is easy to see that the network's performance is much worse than that of the network without plasticity. The error rate seems to rise approximately linearly before leveling of around the level of pure chance.

Figure 16(c) shows the performance of a network with short-term synaptic plasticity, but here only the first 20 milliseconds of the retrieval are taken into account. Note that the slope of figure 16(c) is very similar to that of figure 16(a).

This confirms the result of [Bibitchkov et al., 2002], who found that



(a) *Without* short-term synaptic plasticity.

(b) *With* short-term synaptic plasticity.

(c) *With* short-term synaptic plasticity. Only the first 20 ms of retrieval.

Figure 16: Plots of the error percentage against the number of stored patterns. The network consists of 100 spike response neurons. Patterns consist of 10 randomly selected neurons. Patterns are stored by simple Hebbian learning. Figure (a) shows the network's performance *without* short-term synaptic plasticity. Figure (b) shows the network's performance *with* synaptic plasticity. Figure (c) shows the network's performance *with* synaptic plasticity when only the first 20 milliseconds of retrieval are taken into account. Note that the figures for 16(a) and 16(c) have a highly similar shape, confirming the results of [Bibitchkov et al., 2002]

short-term synaptic plasticity does not significantly impact the storage capacity of an auto-associative network. The stability of the retrieved patterns however *is* affected.

[Bibitchkov et al., 2002] showed that a network with short-term synaptic plasticity retrieves the same patterns as a network without short-term synaptic plasticity. However when a pattern is retrieved, the strength of the synapses connecting the neuron in the active pattern quickly diminishes. This means the retrieved pattern will die out, making it possible for other wrong patterns to take over. It is exactly this property of short-term synaptic plasticity that is used in this thesis to implement slow temporal binding.

When only looking at the first part of the retrieval process of a network with short-term synaptic plasticity, the retrieval performance should not be affected. The highly similar slope of figures 16(a) and 16(c) confirms this.

6.2.2 Multiple patterns

Figure 17 plots the retrieval errors of the network against the number of stored patterns, but in this case multiple patterns are retrieved simultaneously. As with the simulations in the previous section, the network consists again of 100 nodes. In these simulations the nodes are all connected through synapses with short-term plasticity.

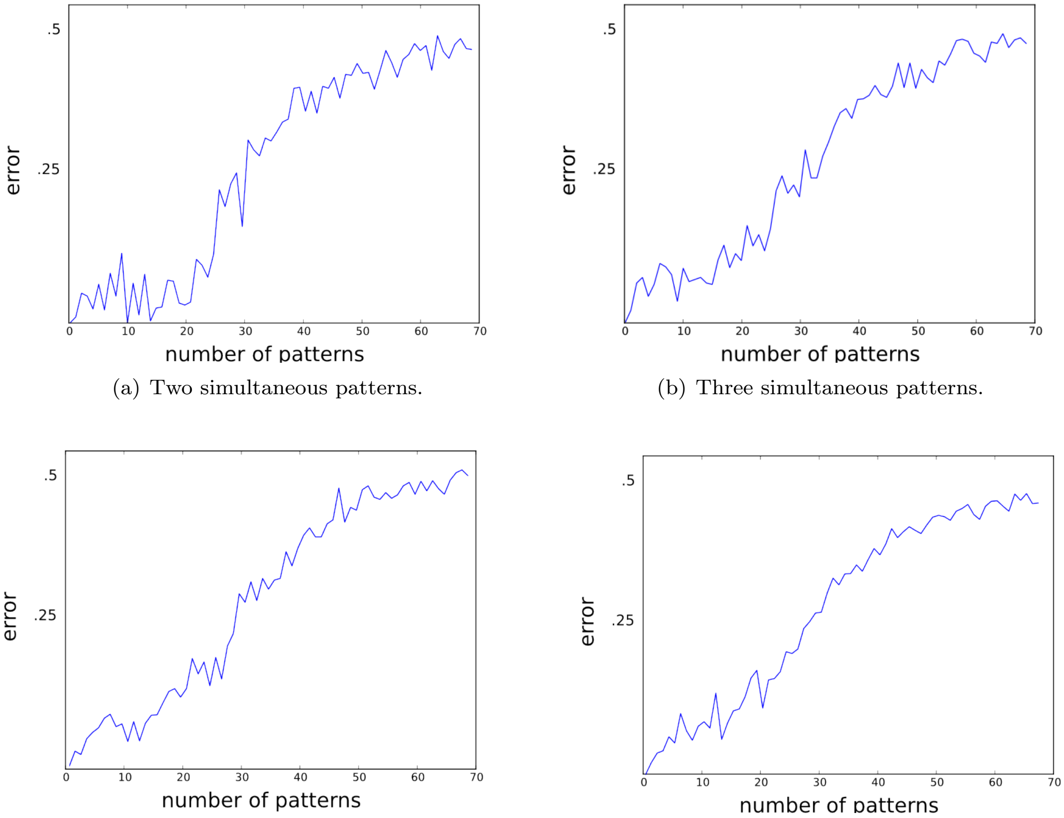
In these simulations however more than one pattern is retrieved simultaneously. Binding is achieved through short-term synaptic plasticity.

Figure 17(a) shows the performance of the network when two patterns are retrieved simultaneously.

Short-term synaptic plasticity reduces the stability of the retrieved pattern. When only one pattern is retrieved, the strength of the synapses connecting neurons in the retrieved pattern diminishes quickly, making the pattern unstable and making it possible for erroneous patterns to be activated.

When more than one pattern is retrieved, the diminished strength of the neurons connecting the first retrieved pattern make the pattern unstable as well. However, at that moment the synapses connecting the neurons in the other activated patterns are fully recovered, which results in a retrieval of one of those patterns, instead of an erroneous pattern.

Note that whereas in the previous section synaptic plasticity greatly degraded the network's performance, and only meaningful results where achieved by looking at the first 20 milliseconds of the retrieval, here the



(a) Two simultaneous patterns.

(b) Three simultaneous patterns.

(c) Four simultaneous patterns.

(d) Five simultaneous patterns.

Figure 17: Plots of the retrieval error against the number of stored patterns. As in figure 16 the network consist of 100 spike response neurons connected through short-term plasticity. Patterns consist of 20 randomly chosen neurons. Patterns are retrieved simultaneously and neurons are bound to a pattern by the method described in section 5. Figure (a) show the performance of the network when retrieving 2 patterns simultaneously, figure (b) shows the performance when three patterns are retrieved simultaneously, figure (c) shows the performance when four patterns are retrieved simultaneously and figure (d) shows the performance when five patterns are retrieved simultaneously.

slope of the retrieval error is very similar to that of figure 16(a) and 16(c).

The retrieval error of the network is low and approximately stable when less then 20 patterns are stored.Above 20 patterns the retrieval error quickly rises and levels of at a level around chance, indicating that the network performs a meaningful retrieval task.

Note however that below the storage capacity of the network, the performance is worse than when only one pattern is stored.

Figure 17(b), 17(c) and 17(d) show the performance of the network when 3, 4 and respectively 5 patterns are retrieved. Note that the performance degrades more with every extra pattern that is retrieved, resulting is an almost linear slope when retrieving 5 patterns simultaneously.

When measuring the relatedness of the neurons in the retrieved patterns (See section 5.4), neurons belonging to the same pattern shows a very high level of relatedness, whereas neurons belonging to different patterns show almost no relatedness. In over 99.9% of the time the retrieved nodes were bound to the correct patterns.

When retrieving a small number (2 or 3) patterns simultaneously, the network performs worse than when retrieving only one pattern, however the network does retrieve the correct patterns with a low probability of error, binding the retrieved neurons to the correct pattern. For higher numbers of simultaneous patterns the performance quickly degrades however.

[von der Malsburg, 1981] mentions that from a psychological perspective a low upper bound on the number of simultaneously retrieved objects does not have to be a problem. Humans generally cannot keep more than 7 ± 2 objects in active memory. This number, called the Miller number, is noticeable for example when remembering phone-numbers. People generally have trouble repeating phone number longer than 7 digits.

Note that in our model the upper bound on the number of simultaneous patterns is around 3.

7 Future Work and Conclusion

7.1 Future Work

7.1.1 More Realistic Domain

In the model in this thesis, only random patterns are stored in the network. These patterns can be retrieved simultaneously, achieving slow temporal binding. The assumption of random pattern is no very realistic. Besides that it is also not very interesting.

It would be interesting to see how the model performs when not storing purely random patterns.

It would for example be interesting to see what would happen if to related patterns where activated. When switching between patterns the current pattern can potentially affect the other pattern. When storing random patterns, this could potentially result in a spurious pattern. When retrieving related patterns, the influence of the previous pattern could actually be an aid for retrieving a more specific pattern.

7.1.2 Whole/Parts Modeling

Inhibiting synapses in the model induce a form of competition in the model introduced above, separating two or more simultaneously activated patterns. The pattern that comes out on top stays active for a short while, dying out when the synapses connecting neurons in the active pattern fatigue.

When there is only one pattern active in the network it might be possible to start a period of competition by strengthening the inhibiting synapses. This would result in a form of segmentation of the active pattern. Essentially breaking up the pattern into sub-patterns, neurons will be bound to the sub-pattern by the same temporal mechanism.

The sub-pattern that will arise by breaking up the active pattern will be stable patterns, stored by Hebbian plasticity, that are strongly related to the original. The retrieval process started by the induced competition will retrieve neurons not in the original pattern.

What exact pattern will become stable depends on relations between the stored patterns, but is might be possible that this process could be used to model the whole and parts of objects, with the original pattern representing the whole of the object, and the patterns that arise representing the relevant parts of the whole.

7.2 Conclusion

This thesis introduces a model that performs slow temporal binding in a network of simple spike response neurons. Patterns are stored in the network using simple Hebbian learning. These patterns can be retrieved by activating partial patterns in the network.

More than one pattern can be retrieved simultaneously from the network by activating the neurons belonging to the same pattern synchronously. Inhibiting connections formed in the training phase make sure that only one pattern can be active at one moment in time.

The fact that synchronous pulses have a stronger effect on the potential of a neuron than non-synchronous pulses makes sure that the pattern retrieved is one of the activated patterns.

Short-term plasticity (the fact that the strength of a neuron temporarily decreases when a synapse carries a pulse to another neuron), makes sure that the retrieved pattern stays stable for only a short period of time. When the synaptic strength of the retrieved pattern decreases enough another of the activated patterns takes over.

The network behavior that emerges is that the network retrieves more than one pattern, binding neurons to a pattern using time as proposed in [von der Malsburg, 1981]. However the binding is performed on a much slower time scale. Patterns are active in short alternating burst of activity. Because the time it takes to switch between various patterns is far below the psychological moment, these switches, and thus the binding will be unconscious. The strength of the short-term synaptic plasticity decides how quick the patterns switch.

The result is a network that binds patterns by slow temporal binding similar to the model of [Knoblauch and Palm, 2002]. As section 4.2.3 explained slow temporal binding does not suffer from some of the problems that synchronous binding does.

The network has an extremely simple topology: The nodes in the network are universally and symmetrically connected, just as in standard auto-associative network. The nodes and synapses in the network are modeled to be close to biological units. Other models of temporal binding tend to be much more complex or biologically not feasible.

Looking at the model of [Knoblauch and Palm, 2002] for example, the network topology used in this thesis only consist of one layer, consisting of universally connected neurons. The network of [Knoblauch and Palm, 2002] consist of various layers, with various connection types.

Some of the problems inherent in model of synchronous temporal binding are not present in the model developed in this thesis. Neurons can, for example, be active in two patterns simultaneously, which is prevented in synchronous models by the refractoriness of the neurons. The slow nature of the temporal binding also prevents crossover from one pattern to the other.

The model is biologically plausible in the sense that it only uses local features of the network. The model developed in this thesis uses a very simple modification to the synapses to perform the binding. This modification, short-term synaptic plasticity, is seen in biological neural networks, and independently studied in for example [Bibitchkov et al., 2002] and [Kistler and van Hemmen, 1999].

Simulations show that the model is capable of retrieving two or three patterns simultaneously, binding the nodes to the right pattern using slow temporal binding. The more patterns are retrieved simultaneously, the more the retrieval error rises. The storage capacity of the network turns out to be low however.

Note however that the performance of the network with only one active pattern and without short-term synaptic plasticity was low as well, indicating that the binding is not responsible for this low capacity. Some of the techniques from [Gerstner, 1999] could be implemented to achieve a higher storage capacity.

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