



Christoph Rieger, Bsc.

# **Hierarchical architectures for spiking Winner-Take-All networks**

## **Master's Thesis**

to achieve the university degree of

Master of Science

Master's degree programme: Biomedical Engineering

submitted to

**Graz University of Technology**

Supervisor

Univ.-Prof. Dipl.-Ing. Dr.techn. Robert Legenstein

Institute of Theoretical Computer Science

Head: Univ.-Prof. Dipl.-Ing. Dr.techn. Robert Legenstein

Graz, April 2023



# Contents

|          |  |           |
|----------|--|-----------|
| <b>1</b> | <b>Introduction</b>  | <b>1</b>  |
| <b>2</b> | <b>Biological background</b>   | <b>3</b>  |
| 2.1      | Winner-Take-All networks . . . . .   | 3         |
| 2.2      | The hierarchical structure of the brain . . . . .  | 4         |
| 2.3      | Visual cortex . . . . .  | 4         |
| 2.4      | Probabilistic brain . . . . .  | 6         |
| 2.5      | Feedback in the visual cortex . . . . .  | 6         |
| 2.6      | Plasticity . . . . .   | 7         |
| 2.7      | Spiking neural networks . . . . .  | 9         |
| <b>3</b> | <b>Theoretical background</b>  | <b>11</b> |
| 3.1      | Bayes' theorem . . . . .   | 11        |
| 3.2      | Bayesian inference . . . . .   | 11        |
| 3.3      | Network model . . . . .  | 12        |
| 3.4      | Mathematical link between the spiking Winner-Take-All network model and Bayesian inference . . . . . | 17        |
| <b>4</b> | <b>Experiments</b>   | <b>21</b> |
| 4.1      | Experiment 1: Horizontal and vertical bars . . . . .   | 21        |
| 4.1.1    | Introduction . . . . .   | 21        |
| 4.1.2    | Methods . . . . .  | 21        |
| 4.1.3    | Results . . . . .  | 24        |
| 4.2      | Experiment 5: Mathematical analysis and simulation of a 1D network . . . . .                         | 32        |
| 4.2.1    | Introduction . . . . .   | 32        |
| 4.2.2    | Methods . . . . .  | 32        |
| 4.2.3    | Results . . . . .  | 35        |
| 4.2.4    | Discussion . . . . .   | 47        |

## Contents

---

|          |  |           |
|----------|--|-----------|
| 4.3      | Experiment 6: Simulation of the 1D network with double size                      | 50        |
| 4.3.1    | Introduction . . . . .   | 50        |
| 4.3.2    | Methods . . . . .  | 51        |
| 4.3.3    | Results . . . . .  | 51        |
| 4.3.4    | Discussion . . . . .   | 54        |
| 4.4      | Experiment 7: Training of the 1D network with predetermined parameters . . . . . | 54        |
| 4.4.1    | Introduction . . . . .   | 54        |
| 4.4.2    | Methods . . . . .  | 55        |
| 4.4.3    | Results . . . . .  | 55        |
| 4.4.4    | Discussion . . . . .   | 55        |
| <b>5</b> | <b>Discussion</b>  | <b>63</b> |
|          | <b>Bibliography</b>  | <b>65</b> |

# 1 Introduction

Functional networks of the human brain have a hierarchical modular organization. This means the execution of one specific task, for example vision, involves several modules which are interconnected (Meunier et al., 2009). Traditional views of the visual pathway of the brain hypothesized that the sensory input is passed on from lower to higher visual areas in a feed-forward system. However, Lee TS (2003) shows neurophysiological experimental evidence that there is feedback from high-level to low-level areas of the visual cortex. That feedback information is thought to be "explaining away" information, or putting emphasis on specific information of the low-level area. Through this mechanism can attention be realized and different cortex areas are able to adopt the same interpretation of some input.

The brain needs to handle a high degree of uncertainty in sensory input. When it first receives input it does not know what the information could represent, thus not knowing which parts of the input are most relevant. Several experiments on animals show that the computation of sensory input that the cerebral cortex performs can be explained and modelled by Bayesian inference (Funamizu Akihiro, 2016; Lee TS, 2003; Parr and Friston, 2018). They hypothesize that the brain functions as a generative and probabilistic model to reach its conclusions. This means the brain expresses information via probability distributions, rather than utilizing static neural codes. Bayes theorem yields a posterior probability, by multiplying a likelihood with a prior probability. In the context of cortical computation one can postulate that the posterior is represented by the output of a neural network. The likelihood can be computed based on the sensory input to the network and the feedback it receives from other cortical areas. The feedback from high-level to low-level cortical areas can be modelled as the prior probability (Nessler et al., 2013).

## 1 Introduction

---

There are various models for the computational dynamics of biological neurons (Gerstner and Kistler, 2002).

TODO 1. discuss spiking neurons 2. discuss briefly synaptic plasticity 3. explain synaptic plasticity in biological background

The plasticity of neural networks is often modelled as Spike-timing-dependent plasticity (STDP), as it agrees with biological experiments (Feldman, 2012; Dan Yang, 2004).

TODO!!!!!! 1. Talk about the canonical cortical microcircuit (softWTA paper douglas) 2. Say that WTA was postulated as a key computational motif To select the output of a neural network the soft Winner-Take-All mechanism is well established. Neurons with this mechanism choose what information is forwarded vertically into another layer and inhibit their horizontal neighbours of the same layer. This mechanism resembles the way biological pyramidal neurons function (Rodney J Douglas, 2004). Furthermore Winner-Take-All modules have a higher computational power than threshold-gates (Maass, 2000).

Nessler et al. (2013) and Guo et al. (2019) created Winner-Take-All spiking neural networks which perform Bayesian inference. Both of those works did not include feedback that comes from a network higher up in the hierarchy. As such feedback is proven to exist by experiments this thesis aims to expand the model. The hierarchical network model of Nessler et al. (2013) is taken and expanded to simulate a functional neural network that receives visual input and also feedback from another network higher up in the hierarchy. TODO: 1. summarize what we do and the main results

In Chapter 2 the biological background for this thesis and the underlying hierarchical spiking Winner-Take-All network will be given. The theoretical background, explaining the mathematical model used for the neural networks in this thesis, will be explained in Chapter 3. (Chapter 4 is a work in progress). Finally, in Chapter 5, the results of the experiments will be summarized and their implications will be discussed.

## 2 Biological background

### 2.1 Winner-Take-All networks

It has been discovered that pyramidal neurons on layers 2/3 and 5/6 of the neocortex form selection networks. This means that one pyramidal neuron is allowed to fire, while others within the same layer are inhibited. This horizontal selection mechanism determines what is vertically sent on to the neurons of cortical layers higher up in the hierarchy. For example pyramidal neurons in layer 5 have a selection behaviour that determines the output to motor structures. Their inhibition is performed by basket and chandelier cells (Rodney J Douglas, 2004). Basket cells connect to the soma of other neurons and control the action potential discharge rate of those neurons. Their dendritic branches wrap around the target soma, forming a "basket" giving them their name (Jones, 1984). Chandelier cells perform inhibition directly at the axonal initial segment of pyramidal neurons where action potentials are initiated. (Contreras, 2004). The selection of one pyramidal neuron performed this way is called soft winner-take-all mechanism and is used in various neuronal network models (Rodney J Douglas, 2004). The mechanism is called "soft" because it uses a softmax function, which controls how many winners there can be, and how likely each neuron is to win (Arbib, 2003). It has been shown that winner-take-all mechanisms are computationally more powerful when compared to threshold gates (McCulloch-Pitts neurons) and sigmoidal gates. Furthermore, arbitrary continuous functions can be approximated by circuits that only include one soft winner-take-all gate as their only nonlinear operator (Maass, 2000).

### 2.2 The hierarchical structure of the brain

The brain is made up of modular structures that connect with each other in a hierarchical organization. These modules have a high level of connectivity within themselves and a low level to other modules. This means that there are different categories of neurons within a module, depending on their function in the network. For one there are provincial hub neurons that primarily connect to other neurons of the same module and are responsible for the function the module expresses. Then there are connector hub neurons that transfer information from the module to other modules. Such modules form networks which are connected in a hierarchical manner, where each module is adding to the output of the previous module (Meunier et al., 2009). Most of the information flows upwards along the hierarchy, representing bottom-up observations. But there is physiological experimental data that shows that information is also passed downwards and influences the activity of modules lower in the hierarchy, representing top-down context. This will be explained for the visual cortex.

### 2.3 Visual cortex

The visual cortex is the region of the brain that processes visual information coming from the retina. From the retina the information is sent to the lateral geniculate nucleus in the thalamus and then further to the primary visual cortex, also called visual area 1 (V1). The visual cortex consists of five visual areas (V1 to V5), which are divided by their function and structure. These areas are located in the occipital lobe of the cerebral cortex. The purpose of the visual areas is to process visual information to recognize objects, perform spatial tasks or to perform visual-motor skills. Neurons of the visual cortex often respond to stimuli within a specific receptive field. It is assumed that each subsequent visual area is more specialized than the previous and due to that neurons in different visual areas respond to the same receptive fields, but to different types of stimuli. There are various specialized cells in the visual cortex. For example simple cells and complex cells are well studied. Simple cells which mainly occur in V1 respond primarily to oriented edges



and lines within a receptive field. For example a simple cell would always generate action potentials when there is a horizontal line in its receptive field. Complex cells can be found in V<sub>1</sub>, V<sub>2</sub> and V<sub>3</sub> and also respond primarily to oriented edges and lines. However their receptive fields are larger and an horizontal edge for example does not have to be at a specific location in the receptive field to activate the cell. Some complex cells even respond primarily to movement of edges (Huff T, 2024). This activation of neurons depending on the stimulus is called neuronal tuning. The stimuli the complex cells respond to get more complex, the higher up in the visual cortex hierarchy they are located. For example in the inferior temporal cortex, which receives visual information from V<sub>4</sub>, there are complex cells that respond to faces (Riesenhuber and Poggio, 2002). According to Palmer (1999) the larger receptive fields of complex cells are due to the hierarchical convergent nature of visual processing. This property follows from the complex cell receiving input from many simple cells which is summed and integrated.

Visual information first enters V<sub>1</sub>, which is the best-understood part of the visual cortex. It consists of six layers that function differently. Layer 4 receives the input from the lateral geniculate nucleus. It has the most simple cells of the six layers and thus processes visual information of small receptive fields. On layers 2, 3 and 6 there are complex cells, which combine the result of layer 4 into larger receptive fields. Through that V<sub>1</sub> outputs simple visual components with their orientation or direction. The processed information is then sent on to V<sub>2</sub> which further processes it and thus responds to more visual complex patterns. V<sub>2</sub> was also found to respond to differences in color and spatial frequency, additional to the more complex patterns and object orientation. After processing V<sub>2</sub> sends its information on to V<sub>3</sub>, V<sub>4</sub> and V<sub>5</sub>. Furthermore it also has feedback connections to V<sub>1</sub>, which will be discussed later. After V<sub>2</sub> the visual information is split up into the dorsal and ventral streams, which each specialize in processing different features of the visual information. The dorsal stream is involved in guidance of motor actions and in recognizing where objects are in space. The ventral stream on the other hand is responsible for object recognition and form representation. (Huff T, 2024)

### 2.4 Probabilistic brain

When observing the activity of neurons during a task it varies from trial to trial. This suggests that no static neural code exists. It rather seems that the averaged activity of a neural network matters. Because of that neuronal responses are typically treated statistically or probabilistically (Gerstner and Kistler, 2002). Pouget et al. (2013) state that there is strong behavioural and physiological evidence that the brain both represents probability distributions and performs probabilistic inference. Because of that there are several experiments that support a mathematical framework based on Bayesian inference (see Chapter 3.2) to model brain computations. (Funamizu Akihiro, 2016; Lee TS, 2003; Parr and Friston, 2018; Darlington, Beck, and Lisberger, 2018). An advantage of these probabilistic models is their generality, meaning that they can be applied to various tasks that the brain performs (Pouget et al., 2013). Because of this evidence the neural network model of this thesis can be thought to perform Bayesian computation. The mathematical link between the spiking Winner-Take-All network model and Bayesian inference will be shown in Section 3.4.

### 2.5 Feedback in the visual cortex

Lee TS (2003) showed that feedback in the visual cortex is not only used for attentional selection or biased competition, but also to modulate the processing of the early visual cortex. Furthermore they showed how this modulated processing can be explained via hierarchical Bayesian inference. One hypothetical example for the modulation of lower hierarchical areas that they give is a human looking at a picture of a face which is partially in shadow. First  $V_1$  receives the information of the image and performs edge and line detection. In this initial processing the detected edges are in the well lit portion of the image, while in the shadowy part almost no edges are found. As this information is passed on upwards along the visual cortex hierarchy it is processed further, until it reaches the inferior temporal cortex where the conclusion is made that there is a face in the picture. After that, feedback is sent from the inferior temporal cortex back

to V1. This feedback tells V1 that there should be edges hidden in the shadow. With this additional prior information V1 then is able to detect the faint edge in the shadow and complete the contour of the face. In one of their experiments they made a monkey look at a fixation spot on a screen while Kanizsa squares were presented one at a time in different locations. Kanizsa squares are optical illusions where an illusory square can be seen between four partial disks. One such image can be seen in Figure 2.1. The illusory square is seen because the brain chooses the simplest interpretation that a white square is lying on top of the black circles, occluding them. During the presentation neuronal activity in V1 and V2 was measured. When looking at a single neuron in V1, which has a receptive field size of less than 0.8 degrees, they reported that it responds with increased spiking activity within 45 ms after a real line appears in its receptive field. When that neuron has an illusory line of the Kanizsa square in its receptive field it is not active within 45 ms. However after 100 ms it begins to respond, indicating that it starts seeing the illusory line. In contrast, the measured population of 39 V2 neurons responded to the illusory contour after 65 ms, 35 ms before V1. They explained this behaviour as V2 detecting the illusory contour with information from a spatially more global context and then feeding back that information (prior) to V1. V1 then, convinced by V2, starts hallucinating the illusory line, agreeing with the most likely interpretation of the image. This experiment provides strong evidence that feedback is happening in the hierarchical structure of the visual cortex.

## 2.6 Plasticity

Electrophysiological experiments showed that the response amplitude of neurons changes over time. Depending on the stimulation a neuron receives the postsynaptic response change systematically. These changes can persist short term for hours or days. However, the stimulation paradigm can also induce persistent changes in the synapses of a neuron. These changes are supposed to reflect 'learning' and 'memory'. If the change increases the postsynaptic response it is called long-term potentiation (LTP). If it decreases the response it is called long-term depression (LTD). In neural network models a weight parameter between two neurons is used to indicate



Figure 2.1: Kanizsa square shown to the monkey by Lee TS (2003)

the strength of the postsynaptic response. When training a neural network model these weights can be adjusted to improve the performance of the network for a given task. By iteratively optimizing the weights the network learns to solve its task. Via a defined learning rule the network is able to determine the way in which to adapt the weights. There are different ways to define such a learning rule. One simple learning rule is to increase the weights of neurons that are more active than others. This is called Rate-Based Hebbian Learning. An improved version of this learning rule is Spike Timing Dependent Plasticity (STDP). It also factors in the exact timing of presynaptic neuronal activity, compared to the timing of postsynaptic neuronal activity (Gerstner and Kistler, 2002). This is the learning rule used for the neural network model of this thesis and will be explained further in the next section.

## 2.7 Spiking neural networks

Spiking neural networks (SNNs) are artificial neural networks that resemble biological neural networks more closely. Neurons in typical neural networks used in machine learning transmit information at every propagation cycle. This, however, is not how biological neurons operate. They generate action potentials (neuron spikes) to convey information between each other. These action potentials are only generated when their membrane potential exceeds a threshold. SNN models take this behaviour into account by keeping track of each neurons membrane potential and then determining when they should produce an action potential (Gerstner and Kistler, 2002).

Previously it was believed that biological neural networks encode information within the spike rates of neurons. However neurobiological research shows evidence that at high speed processing this alone can not be sufficient. For example image recognition tasks can be performed at a speed at which each neuron in the involved layers has only less than 10 ms to process the information. Such a time frame is too short for rate coding to occur. Instead it has been shown that high speed processing tasks can be performed using the precise timing of spikes. Furthermore it requires more energy for a neuron to spike many times to express a spike rate, rather

than spiking just once and having the timing of the spike considered. As the brain evolutionarily aims to minimize its energy consumption this is a strong argument for spike timing encoded information. Also the information encoding capacity is higher in a small set of spiking neurons, compared to rate encoding. (Taherkhani et al., 2020) Because of that STDP is often used as learning rule in SNNs. STDP models the synaptic weight changes of neurons depending on the relative timing of pre- and postsynaptic spikes. If a presynaptic spike arrives shortly before the postsynaptic spike the synaptic weight is increased. The size of that increase depends exponentially on the time between both spikes, according to a time constant. However, when the presynaptic spike occurs after the postsynaptic spike the synaptic weight is decreased. These two mechanisms are called long-term potentiation and long-term depression respectively. Although STDP is often modelled like this, biological experiments show that the standard pair-based approach does not fully explain it in biological neurons. However, there is experimental evidence that multiple-spike protocols like triplets STDP are biologically more plausible. (Taherkhani et al., 2020)

## 3 Theoretical background

### 3.1 Bayes' theorem

Bayes' theorem describes the probability of an event to occur, depending on the prior knowledge of conditions related to the event (Joyce, 2019).

$$P(A|B) = \frac{P(B|A)P(A)}{P(B)}. \quad (3.1)$$

$P(A|B)$  is the posterior probability of A given that B is true.  $P(B|A)$  is called conditional probability of B given A being true.  $P(A)$  is the prior probability, the probability of A occurring without any additional information. Finally  $P(B)$  is the marginal probability of B without any given condition. This theorem is often used for Bayesian inference where it expresses how a belief, which is represented as probability changes due to related evidence.

### 3.2 Bayesian inference

Bayesian inference is a process of data analysis to calculate the probability of a hypothesis depending on the available related evidence. As over time more and more evidence becomes available the probabilities can be updated yielding a more sophisticated view on the hypothesis. It is given, according to Bayes' theorem, by

$$P(H|E) = \frac{P(E|H)P(H)}{P(E)}, \quad (3.2)$$

where H represents a hypothesis and E some related evidence.  $P(H|E)$  is the posterior probability which signifies the probability of the hypothesis

after the evidence was observed.  $P(E|H)$  is called likelihood and it is the probability of observing the evidence given the hypothesis. It is a measure of the compatibility of the observed evidence with the given hypothesis.  $P(H)$  is the prior probability which is the probability of the hypothesis before any evidence is considered or obtained.  $P(E)$  is called marginal likelihood that represents the probability of the evidence being observed. However it is the same independent of the chosen hypothesis. Thus, it is not factored in when comparing different hypotheses. Bayesian inference can be applied to the "face in shadow" example of Section 2.5. There a neuron in V1 sees a small part of the visual field and signals if it sees an edge or not. At first it has the evidence of the observed pixels available and from it can calculate the likelihood that an edge is present. At first it has no prior knowledge of how probable an edge being present is, meaning that the prior probabilities for there being an edge or no edge are equal. With that likelihood and the prior probabilities it can conclude the posterior probability for the hypothesis "there is an edge" and decides that there is no edge. Later the inferior temporal cortex determines that there is a face in the picture and feeds this information back to V1. This influences the prior probabilities and changes the posterior probability in a way that the V1 neuron starts to see the hypothesis that there is an edge as more likely, in order to complete the contour of the face. We now define  $X$  as a binary random vector of the visual input,  $Y$  as a multinomial variable of the output of V1 and  $Z$  as a multinomial variable of the feedback of the inferior temporal cortex. When plugging these variables into Equation 3.2 with the posterior given by  $P(Y|X, Z)$ , the likelihood given by  $P(X|Y)$  and the prior given by  $P(Y|Z)$  we get

$$P(Y = i|X = x, Z = j) = \frac{P(X = x|Y = i)P(Y = i|Z = j)}{\sum_k P(X = x|Y = k)P(Y = k|Z = j)}. \quad (3.3)$$

### 3.3 Network model

The network model used for the experiments in this thesis was taken from Nessler et al. (2013) and expanded by an additional layer to include some hierarchical feedback information.



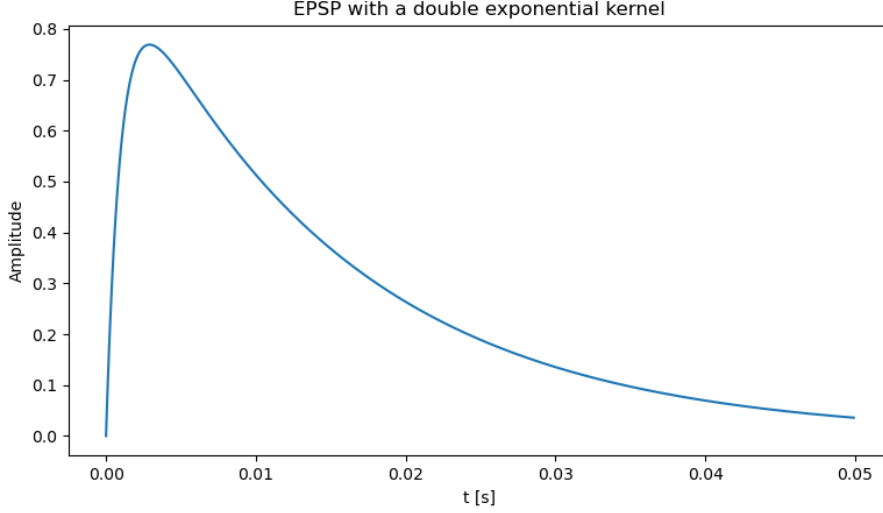


Figure 3.1: Form of an excitatory post synaptic potential generated by an input neuron over time. A double exponential kernel was used to generate this signal. These signals are fed to the next layer of the network.

**Neuron model** As in Nessler et al. (2013) the input neurons  $x_1, \dots, x_n$  are firing according to a poisson process with an average firing rate  $f_{input}$  when active and with 0 Hz when in an inactive state. The input neurons receive a binary input, for example a black or white pixel of an image. The excitatory post synaptic potentials (EPSPs)  $x_i(t)$  that these neurons produce can be seen in Figure 3.1. A double exponential kernel was used to generate the EPSP. The kernel has a time constant for the rise of the signal  $\tau_{rise}$  and a time constant for the decay of the signal  $\tau_{decay}$ . The addition of the time step size  $\delta t$  was necessary to get the time  $t$  at the end of the current simulation step.  $t_f$  is the time at which the spike of  $x_i$  occurred

$$x_i(t) = e^{-(t+\delta t-t_f)/\tau_{decay}} - e^{-(t+\delta t-t_f)/\tau_{rise}}. \quad (3.4)$$

Analogously the EPSP of the prior neurons  $z_j(t)$  are given by

$$z_j(t) = e^{-(t+\delta t-t_f)/\tau_{decay}} - e^{-(t+\delta t-t_f)/\tau_{rise}}. \quad (3.5)$$

The membrane potential  $u_k$  of each output neuron is calculated by multiplying the EPSP of each input neuron times the input weight  $w_{ki}^i$  of the

### 3 Theoretical background

---

connection between them, plus the EPSP of each prior neuron times the prior weight  $w_{kj}^p$

$$u_k(t) = \sum_{i=1}^N w_{ki}^i \cdot x_i(t) + \sum_{j=1}^J w_{kj}^p \cdot z_j(t). \quad (3.6)$$

In Nessler et al. (2013) each output neuron  $y_k$  also had an intrinsic excitability  $w_{k0}$  which was learned for each neuron. For the experiments of this thesis however it was omitted, as the different classes of input images were equally likely, thus the intrinsic excitabilities of the output neurons would all end up being equal to each other.

The output neurons are modelled in a winner-takes-all (WTA) circuit. The WTA behaviour was implemented via an adaptive inhibition signal. The adaptive inhibition is used to regulate the membrane potentials of the output neurons so that all of them together fire with a total firing rate  $R(t) = 200\text{Hz}$  on average. Due to that there never is a time window in which no output neuron may fire. However, it is unlikely for an output neuron to fire right after another output neuron has fired.

The inhibition signal was chosen to depend on the current membrane potential of the output neurons. Solving Equation 3.13 for  $I(t)$  yields

$$R(t) = \frac{\sum_{k=1}^K e^{u_k(t)}}{e^{I(t)}} \quad (3.7)$$

$$e^{I(t)} = \frac{\sum_{k=1}^K e^{u_k(t)}}{R(t)} \quad (3.8)$$

$$I(t) = \ln \frac{\sum_{k=1}^K e^{u_k(t)}}{R(t)} \quad (3.9)$$

$$I(t) = -\ln R(t) + \ln \sum_{k=1}^K e^{u_k(t)}. \quad (3.10)$$

Nessler et al. (2013) defined that the firing probability of an output neuron  $y_k$  is exponentially proportional to its membrane potential  $u_k$  minus the received inhibition  $I(t)$

$$p(y_k \text{ fires at time } t) \propto e^{u_k(t) - I(t)}. \quad (3.11)$$

This stochastic firing model is supported by experimental biological evidence (Jolivet et al., 2006). Through this definition the firing rate  $r_k(t)$  of an output neuron is then modelled by an inhomogeneous Poisson process as

$$r_k(t) = e^{u_k(t) - I(t)}. \quad (3.12)$$

At every timestep of the simulation the inhibition signal  $I(t)$  is subtracted from the membrane potential  $u_k(t)$  of every output neuron. By that the membrane potentials are altered to always yield a spiking frequency of 200 Hz, regardless if it would be lower or higher without it. This means that the adaptive inhibition signal can also function as an excitatory signal.

The total firing rate of the output neurons is obtained when summing up the firing rates of all output neurons, yielding

$$R(t) = \sum_{k=1}^K e^{u_k(t) - I(t)}. \quad (3.13)$$

The probability of an individual output neuron to fire within a time step  $\delta t$  is given by

$$r_k(t) \delta t. \quad (3.14)$$

The conditional probability  $q_k(t)$  that a spike originated from the output neuron  $y_k$  is given by

$$q_k(t) = \frac{r_k(t) \delta t}{R(t) \delta t} = \frac{e^{u_k(t) - I(t)}}{\sum_{k'=1}^K e^{u_{k'}(t) - I(t)}} = \frac{e^{u_k(t)}}{\sum_{k'=1}^K e^{u_{k'}(t)}}. \quad (3.15)$$

The inhibition term cancels out because all output neurons receive the same inhibition, meaning that it is independent of  $k$ .

**Spike timing dependent plasticity** The input weights  $w_{ki}^i$  between neurons  $x_i$  and  $y_k$  are updated whenever an output neuron fires.  $\sigma$  indicates the time window, after which spikes are no longer considered. If  $y_k$  produces a spike all its weights to the input neurons are updated as

$$\Delta w_{ki}^i = \begin{cases} \lambda \cdot (ce^{-w_{ki}^i} - 1) & \text{if } x_i \text{ fired in } [t^f - \sigma, t^f] \\ \lambda \cdot (-1) & \text{if } x_i \text{ did not fire in } [t^f - \sigma, t^f], \end{cases} \quad (3.16)$$

### 3 Theoretical background

---

where  $\lambda$  is the learning rate, the parameter  $c$  shifts the weight values,  $t^f$  is the time when  $y_k$  spiked and  $\sigma$  is the time window in which input spikes are considered as "before" an output spike. As the membrane potentials  $u_k$  of the output neurons result from the addition of the EPSPs of the input neurons times the corresponding weight, a way to control the average size of  $u$  is needed. If  $u$  is too small the output neurons will fire too sparsely and if  $u$  is too big it will impair the learning process. So to limit  $u$ , the size of the weights is controlled via the parameter  $c$ . The learning rate  $\lambda$  is needed to control the size of each weight update. If it is too big few output neurons will respond to multiple input classes and others will only respond too little or not at all. On the other hand if  $\lambda$  is too small the network will learn very slowly and may never converge. The prior weights  $w_{kj}^p$  are also updated whenever an output neuron fires, in the same way as  $w_{ki}^i$

$$\Delta w_{kj}^p = \begin{cases} \lambda \cdot (ce^{-w_{kj}^p} - 1) & \text{if } z_j \text{ fired in } [t^f - \sigma, t^f] \\ \lambda \cdot (-1) & \text{if } z_j \text{ did not fire in } [t^f - \sigma, t^f], \end{cases} \quad (3.17)$$

**Network architecture** Each pixel of an input image was connected to two neurons. The first of these neurons is in an active state when the pixel is black and in an inactive state otherwise. The second neuron expresses the opposite behaviour. As a consequence the network needs  $(width \cdot height \cdot 2)$  excitatory input neurons  $x_1, \dots, x_N$ . These input neurons are fully connected to the excitatory output neurons  $y_1, \dots, y_K$ . This means that every input neuron  $x_i$  is connected to each output neuron  $y_k$ . To simulate the feedback from the inferior temporal cortex prior neurons  $z_1, \dots, z_J$  were added to the network. The prior neurons were also fully connected to the output neurons. A visualization of the network architecture can be seen in Figure 3.2.

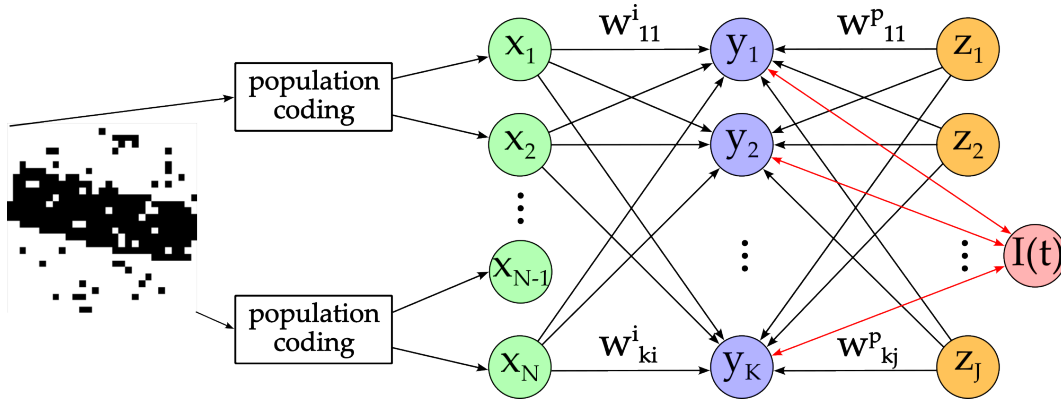


Figure 3.2: Architecture of the network.

### 3.4 Mathematical link between the spiking Winner-Take-All network model and Bayesian inference

Nessler et al. (2013) hypothesized that the ensemble of weights of a neuron can be understood as a generative model. They further claimed that every synaptic weight, due to STDP-induced changes, converges stochastically to the log of the conditional probability that the presynaptic neuron has fired just before the postsynaptic neuron, given that the postsynaptic neuron fires. This connection is given by

$$w_{ki}^i = \log(p(x_i = 1 | y_k = 1)) \quad (3.18)$$

an will be analysed in Section 4.2. Furthermore they claimed that in a Bayesian inference context every input spike provides evidence for an observed variable and every output spike represents one stochastic sample from the posterior distribution over hidden causes, which are encoded in the circuit.

To show the connection between the spiking Winner-Take-All network model and Bayesian inference it will be shown that the posterior probability of Bayesian inference given in Equation 4.1 is equal to the relative firing probability  $q_k(t)$ , given in Equation 3.15.

### 3 Theoretical background

---

As explained in Section 3.2 the visual input, modelled by the input neurons can be thought of as the Bayesian likelihood and the feedback, modelled by the prior neurons, as the Bayesian prior. As defined in Equation 3.11 the firing probability of an output neuron is proportional to the exponent of its membrane potential minus the inhibition. To obtain the Bayesian likelihood and prior we first split the membrane potential into the contributions of the input and prior neurons. The first part that signifies the contribution of the input neurons is given by

$$e^{u_x} = e^{\sum_{i=1}^N w_{ki}^i \cdot x_i(t)}. \quad (3.19)$$

The second part gives the contribution of the prior neurons as

$$e^{u_z} = e^{\sum_{j=1}^I w_{kj}^p \cdot z_j(t)}. \quad (3.20)$$

These two parts can be seen as two partial membrane potentials. By inserting each of them into Equation 3.11 we get the likelihood

$$P(X|Y) = e^{u_x - I(t)}. \quad (3.21)$$

and the prior

$$P(Y|Z) = e^{u_z - I(t)}. \quad (3.22)$$

When inserting the likelihood and the prior into Equation 4.1 we get

### 3.4 Mathematical link between the spiking Winner-Take-All network model and Bayesian inference

---

$$\begin{aligned}
P(Y = k | X = x, Z = j) &= \frac{e^{\sum_{i=1}^N w_{ki} \cdot x_i(t) - I(t)} \cdot e^{\sum_{j=1}^J w_{kj}^p \cdot z_j(t) - I(t)}}{\sum_{k'=1}^K e^{\sum_{i=1}^N w_{k'i} \cdot x_i(t) - I(t)} \cdot e^{\sum_{j=1}^J w_{k'j}^p \cdot z_j(t) - I(t)}} \\
&= \frac{e^{-I(t) \cdot N + \sum_{i=1}^N w_{ki}^i \cdot x_i(t)} \cdot e^{-I(t) \cdot J + \sum_{j=1}^J w_{kj}^p \cdot z_j(t)}}{\sum_{k'=1}^K e^{-I(t) \cdot N + \sum_{i=1}^N w_{k'i}^i \cdot x_i(t)} \cdot e^{-I(t) \cdot J + \sum_{j=1}^J w_{k'j}^p \cdot z_j(t)}} \\
&= \frac{e^{-I(t) \cdot N} \cdot e^{\sum_{i=1}^N w_{ki}^i \cdot x_i(t)} \cdot e^{-I(t) \cdot J} \cdot e^{\sum_{j=1}^J w_{kj}^p \cdot z_j(t)}}{e^{-I(t) \cdot N} \cdot e^{-I(t) \cdot J} \cdot \sum_{k'=1}^K e^{\sum_{i=1}^N w_{k'i}^i \cdot x_i(t)} \cdot e^{\sum_{j=1}^J w_{k'j}^p \cdot z_j(t)}} \\
&= \frac{e^{\sum_{i=1}^N w_{ki}^i \cdot x_i(t) + \sum_{j=1}^J w_{kj}^p \cdot z_j(t)}}{\sum_{k'=1}^K e^{\sum_{i=1}^N w_{k'i}^i \cdot x_i(t) + \sum_{j=1}^J w_{k'j}^p \cdot z_j(t)}} \\
&= \frac{e^{U_k(t)}}{\sum_{k'=1}^K e^{U_{k'}(t)}} \\
&= q_k(t)
\end{aligned} \tag{3.23}$$





## 4 Experiments

### 4.1 Experiment 1: Horizontal and vertical bars

#### 4.1.1 Introduction

For this experiment the WTA network will be shown images of either horizontal or vertical bars. Through unsupervised learning the output neurons will learn to cluster the images together, depending on the orientation and position of the bars. The unsupervised clustering process will be visualized and analysed. Further, the effect of the prior neurons will be demonstrated by generating ambiguous images which show a horizontal and a vertical bar at the same time. The output of the network will be analysed, depending on the activity of the prior neurons.

#### 4.1.2 Methods

**Input data** Black bars with a width of seven pixels were drawn onto a white background with a size of  $35 \times 35$  pixels. The bars could be oriented either horizontally or vertically. The network is supposed to cluster ten different groups within these images, five horizontally and five vertically. With a given bar width of seven pixels, and five groups in each direction the image height and width were determined as 35 pixels, to yield equally sized groups. The orientation of the training images was chosen randomly via a uniform distribution. The position of the bars in the images were uniformly distributed along the 35 pixels of either axis. To simulate noise each pixel of an image had a chance of ten percent to have its color flipped after the generation. During the training of the network random images were

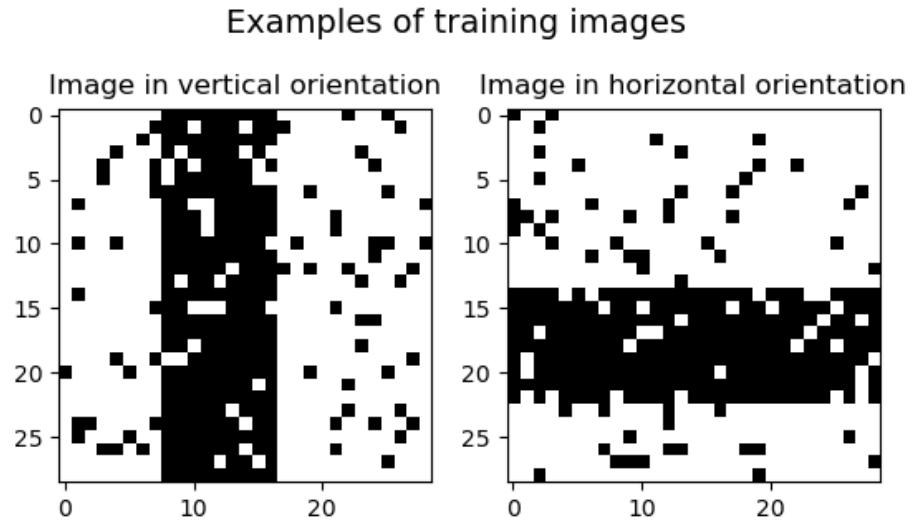


Figure 4.1: Training images generated for experiment 1. One image of each possible orientation at a random position.

generated and presented for 200 ms. As the simulation had a duration of 800 seconds this resulted in 4000 images shown to the network. Examples of the input data can be seen in Figure 4.1. To show the value of the added a-priori information, validation images with two bars forming a cross were also generated, seen in Figure 4.2. When shown to the network in the validation process the prior neurons were given the information that a cross is either of horizontal or vertical orientation.

**Network architecture** As every pixel of the shown images was connected to two input neurons the network had 2450 input neurons. Each of these neurons had a firing frequency of 20 Hz, when in the active state. Then there were ten output neurons, one for each possible group. Lastly, there were

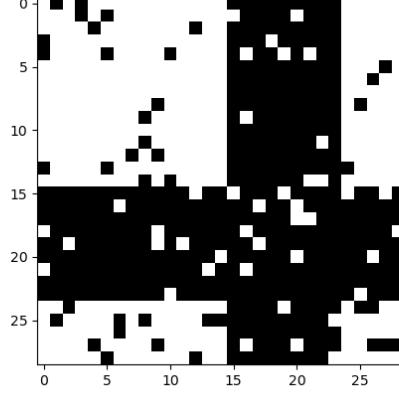


Figure 4.2: Generated cross image which can represent either horizontal or vertical orientation.

two equal sized groups of prior neurons. During training the first group  $z^h$  was active when the image was of horizontal orientation and the other group  $z^v$  was active for vertical orientation. The number of prior neurons and their firing frequency had to be determined via grid search, as they needed to be set at values where the impact of the a-priori information is neither too strong nor too weak.

**Network and simulation parameters** The simulation of the experiment was performed in time steps of 1 ms. This step size was used for all experiments. As given by Nessler et al. (2013) the time window  $\sigma$  was 10 ms, the time constant for the rise of the EPSPs  $\tau_{rise}$  was 1 ms and the time constant for the decay of the EPSPs  $\tau_{decay}$  was 15 ms. Before performing this experiment, Experiment 2 of Nessler et al. (2013) was reproduced to validate that the implementation of the simulation was correct. This proof of concept was omitted in this work, however within it the weight shift parameter  $c = 20$  and the learning rate  $\lambda = 10^{-3}$  were determined via grid search. These parameter values were reused for this experiment as the input data, as well as the network architecture, were similar.

### 4.1.3 Results

First different numbers of prior neurons were tried. Simulations with 10, 20, 50, 100 and 200 prior neurons were performed. For 50, 100 and 200 prior neurons the training process was impaired by the activity of the prior neurons. Some output neurons were responding to too large areas, while other prior neurons were not responding to any specific areas at all. This happened for example because the first output neuron that generates a spike for a horizontal bar gets reinforced by the prior neurons to respond to all horizontal bars, no matter the position. Thus other output neurons are less likely to respond to horizontal bars, resulting in output neurons that are not responding to any specific orientation or area at all. With a number of 10 and 20 prior neurons each of the output neurons learned to respond to equally sized areas of the images and the prior neurons learned to respond to either horizontal or vertical images. To maximize the impact of the a-priori information the validation of the network was performed with 20 prior neurons, as it was the largest number that resulted in a properly trained network. The results of the training process can be seen in Figure 4.3. In Figure 4.3A examples of input images are shown. They were positioned without overlapping each others bars, thus showing the optimal areas output neurons should learn to respond to. The areas that output neurons did learn to respond to can be seen in the visualization of the input weights in Figure 4.3B. It can be seen that the training was successful as five output neurons respond to horizontal bars and the other five to vertical bars. Furthermore each output neuron responded to different areas of the input image and there was minimal overlap between each other. The training progress of the network is given in Figure 4.3E. When the network has completed the training it should mostly have only one or two output neurons being active for any input image. Although there may be more active output neurons sporadically, due to the stochastic nature of the model. According to this plot the training process could have been stopped earlier after 2000 shown images. However, as there was no danger of overfitting the data more images were shown to ensure that the network is always finished with the training when the simulation stops. In Figure 4.3F the relative activity of the most active output neuron can be seen. Firstly it can also be used to judge the progress of the training process, as it increased

over time. Furthermore it can also be seen as a measure of how clearly an image belonged to the area the most active output neuron responds to. If the position of an image is exactly in the middle of the learned area of the most active output neuron the relative activity should be one. However, when the position is on the border between two learned areas of output neurons the relative activity should only be 0.5, as the image belongs to both areas. The learned prior weights can be seen in Figure 4.4. There it can be seen that the first 10 prior neurons learned the same pattern, as all of them were in an active state whenever vertical bars were shown to the network. When comparing these prior weights to the input weights in Figure 4.3B it can be seen that the five highest prior weights of each prior neuron are between themselves and output neurons that learned to respond to vertical bars. The last 10 prior weights showed exactly the opposite pattern, having their five highest weight values between themselves and output neurons that responded to horizontal bars.

To validate the learned patterns the network was shown horizontal bars with a height of seven pixels with their centers at every possible position, beginning at position zero and incrementing in steps of one. Each image was shown for 200 ms each, while recording the output neuron activity. To visualize which output neuron is the most active for each position a horizontal bar with a height of one was drawn into a  $35 \times 35$  pixel image, color-coded to represent the most active output neuron for that position. This can be seen in Figure 4.5A.  $y_7$  and  $y_{10}$  claimed areas with heights of eight pixels, while the areas of  $y_9$  and  $y_4$  had only a height of six pixels. Only  $y_2$  had an area height of the expected seven pixels. These varying heights were expected to happen, due to the unsupervised learning method applied in this thesis. Depending on the randomly generated images the network received during the training process there may be more images on one side of the border between two output neurons than on the other side. This would result in stronger weights around the border area of the favoured neuron and thus in a larger area that the neuron is most active for. The output spikes of the network can be seen in 4.5B. It can be seen that outside of the border areas between the output neurons there was mostly only one neuron active. However, shortly after two seconds  $y_8$  was active. The time frame between 2 seconds and 2.2 seconds this happened in corresponds to position 10.  $y_8$  should mostly be active for vertical bars,

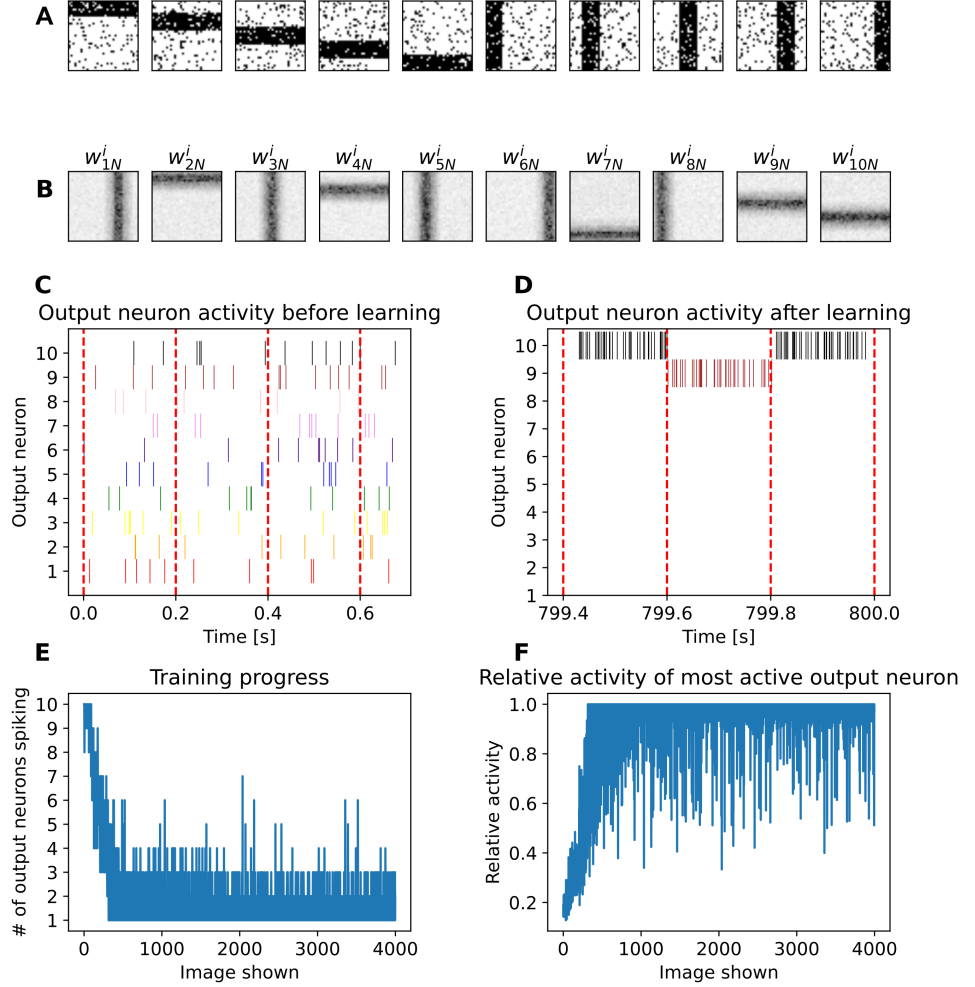


Figure 4.3: **Training with 20 prior neurons.** **A** Examples of  $35 \times 35$ -pixel input images of horizontal and vertical bars with background noise. They were positioned without overlapping each others bars, thus showing the optimal areas output neurons should learn to respond to. **B** Learned weights of the connections between input the neurons that were active for black pixels of the input image and output neurons. As each there was one such input neuron per pixel of the image the weights could be plotted in the same format as the image to easily interpret them. **C, D** Spike activity expressed by the output neurons before and after the training of the network. **E** Number of active output neurons during the presentation duration of each training image. **F** This shows the number of spikes the most active output neuron generated, relative to the number of spikes all other output neurons generated combined.

## 4.1 Experiment 1: Horizontal and vertical bars

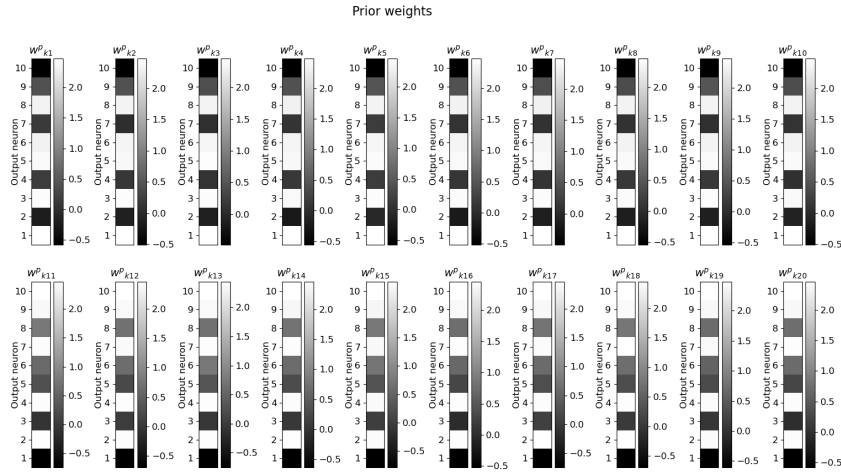


Figure 4.4: Learned weights of the connections between prior and output neurons.

however its learned area has some overlap with with a horizontal bar at position ten and thus there always is a small chance for it to generate a spike. 4.5C the number of active output neurons for each position is given. The validation process was repeated ten times and the mean and standard deviation of the number were calculated. In this plot four peaks appeared. These peaks are around the borders between the adjacent areas of output neurons seen in Figure 4.5A. Around the border areas a number of active output neurons bigger than one was expected, as the horizontal bars reach into the areas of two output neurons at once. When looking at the number of active output neurons at position 10, which is approximately 1.1 with a high standard deviation, it shows that  $y_8$  did not falsely learn to be active for horizontal bars, but rather that it is a stochastic outlier. Figure 4.5D shows the relative activity of the most active output neuron. Compared to Figure 4.5C it provides the additional information of how split the activity of neighbouring output neurons is in the border areas. For example it can be seen that at position 22  $y_4$  with a relative activity of 0.62 was only barely able to be the most active neuron and might almost have had only an active area with a height of five pixels.

The validation process for the vertical bars was done analogously to the

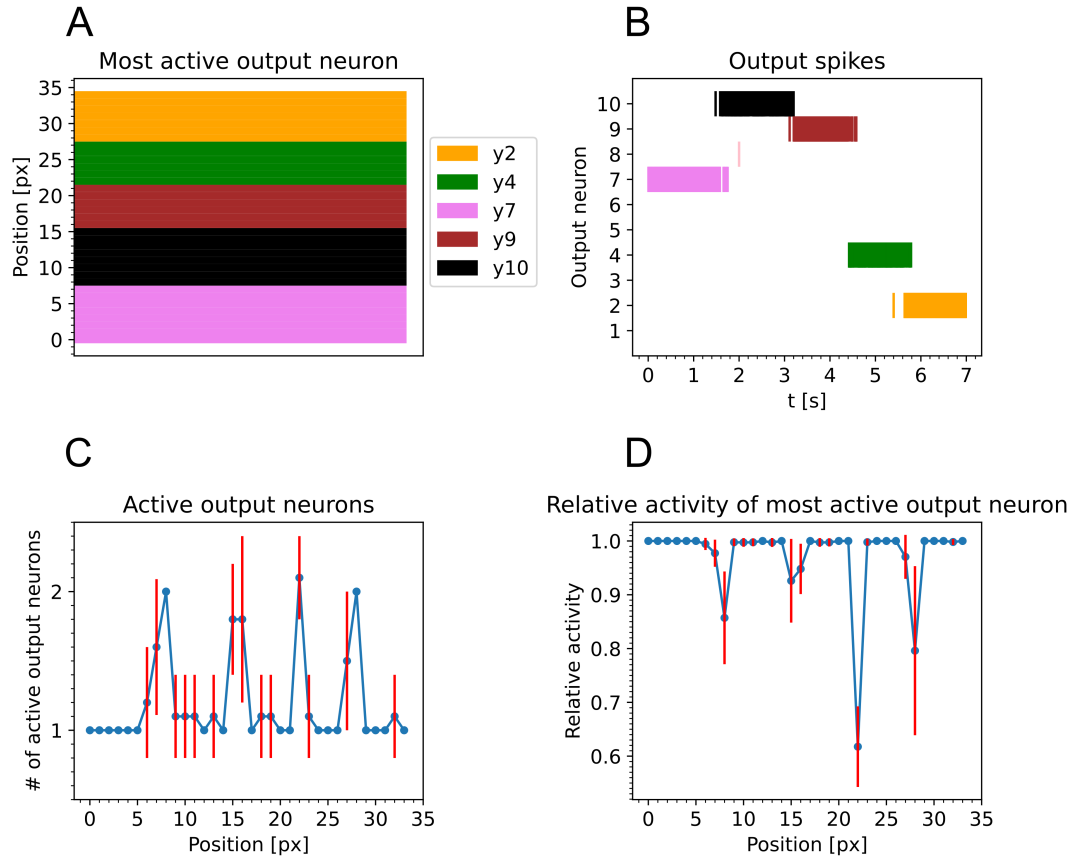


Figure 4.5: **Horizontal validation.** Horizontal bars with a height of seven pixels were shown to the network at different positions. **A** Most active output neuron, depending on the vertical position of the center of a horizontal bar. **B** Output spikes during the validation process. The ticks of the x-axis are in steps of 0.2 seconds, thus each tick signifies the start of a new image being shown. **C** The mean number of active output neurons, depending on the vertical position of a horizontal bar. The standard deviation is given by the red bars. **D** This shows the number of spikes the most active output neuron generated, relative to the number of spikes all other output neurons generated combined. The blue dots indicate the mean and the red bars the standard deviation.



horizontal bars. Its results are given in Figure 4.6.

Next the impact of the prior was analysed. An image with a horizontal bar at position 12 and a vertical bar at position 5 on it was generated. First the prior neurons  $z^v$  were activated and  $z^h$  were deactivated. Then the image was shown to the network for 200 ms. After that the activity of the prior neurons was reversed and the image was shown again. The results can be seen in Figure 4.7. In that figure it can be seen that the output of the network completely changes depending of the prior activity. The prior neurons determine if the network focuses on the vertical or horizontal bar of the image.

To further illustrate the dependence of the output on the prior the firing frequencies of the prior neurons were gradually changed. The starting firing frequency of  $z^h$  was set to 200 Hz and to 0 Hz for  $z^v$ . For those firing frequencies a cross image was shown to the network for 200 ms. It had a horizontal bar at position 31 and a vertical bar at position 3. These position are as far at the edge of the image as possible, while still displaying the whole width of the bars. After each image presentation duration the firing frequency of  $z^h$  was decreased by 1 Hz and increased by 1 Hz for  $z^v$ . The used cross image can be seen in Figure 4.8 A. The firing frequency of the 2 most active output neurons depending on the firing frequency of  $z^v$  can be seen in Figure 4.8 B. At the beginning  $y_2$ , which represents the horizontal part of the cross image, was the most active neuron, which is correct as the prior neurons fully supported the horizontal interpretation of the input image. With rising firing frequency of  $z^v$  the activity of the  $y_2$  decreased and the activity of  $y_8$  increased. This happened because the prior neurons gradually supported the interpretation of the image as vertical more and more. It was expected that the crossing point of the two graphs in Figure 4.8 B would be at a firing frequency of  $z^v$  of 100 Hz, however the graphs crossed at 58.6 Hz. In Figure 4.5 D the relative activity of  $y_2$  at the edge of the bar at position 28 was 0.79. In Figure 4.6 D the relative activity of  $y_8$  at the edge of the bar at position 6 was 1.0.  $y_8$  has a higher relative activity at that position than  $y_2$  at position 28, because  $y_8$  has an active area of width 8, making position 6 not the border of the active area.

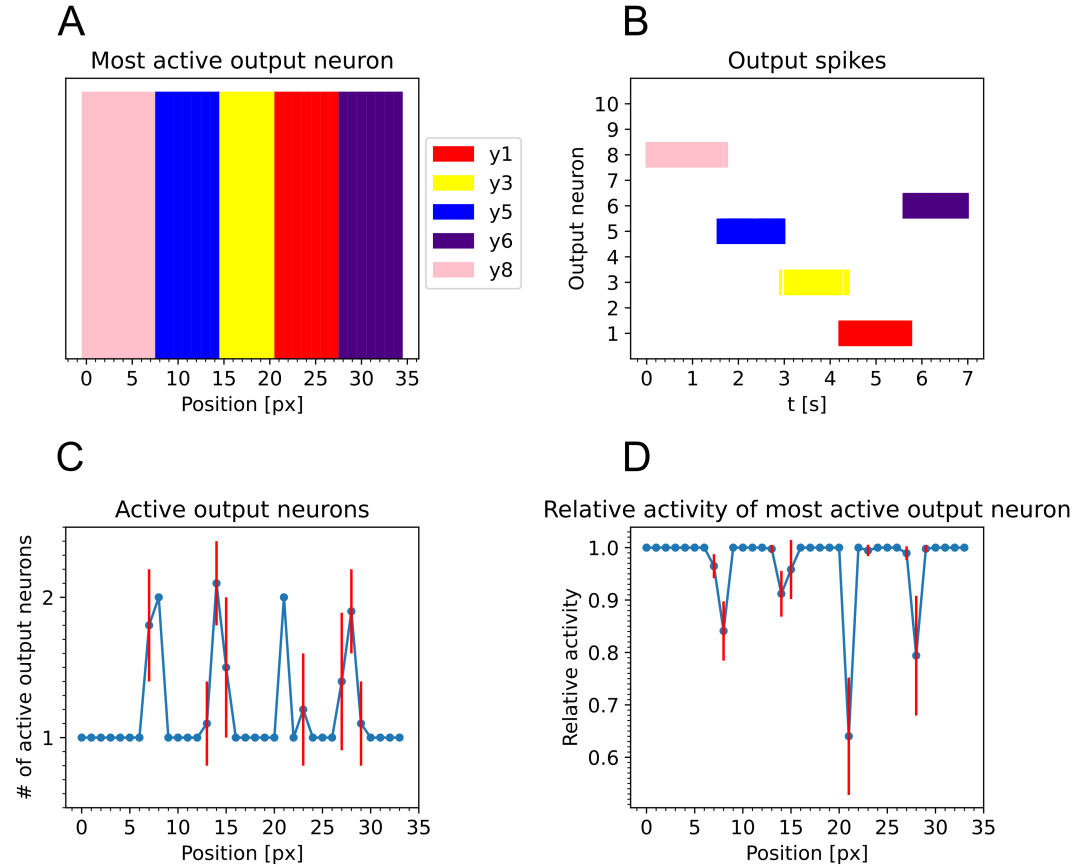


Figure 4.6: **Vertical validation.** Vertical bars with a height of seven pixels were shown to the network at different positions. **A** Most active output neuron, depending on the horizontal position of the center of a vertical bar. **B** Output spikes during the validation process. The ticks of the x-axis are in steps of 0.2 seconds, thus each tick signifies the start of a new image being shown. **C** The mean number of active output neurons, depending on the horizontal position of a vertical bar. The standard deviation is given by the red bars. **D** This shows the of number of spikes the most active output neuron generated, relative to the number of spikes all other output neurons generated combined. The blue dots indicate the mean and the red bars the standard deviation.

## 4.1 Experiment 1: Horizontal and vertical bars

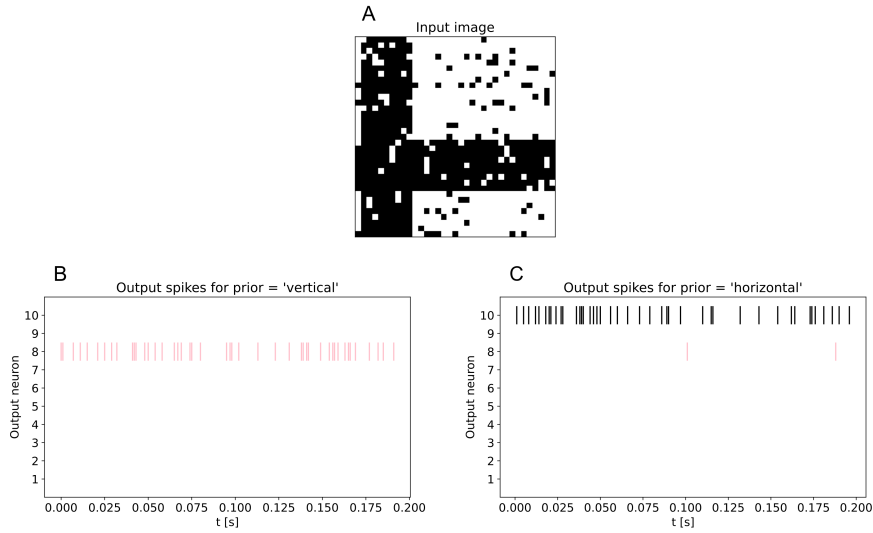


Figure 4.7: **Impact of the prior Neurons.** **A** Image with a horizontal and a vertical bar on it that was given to the network. **B** Spiking activity of the output neurons with  $z^v$  being active. **C** Spiking activity of the output neurons with  $z^h$  being active.

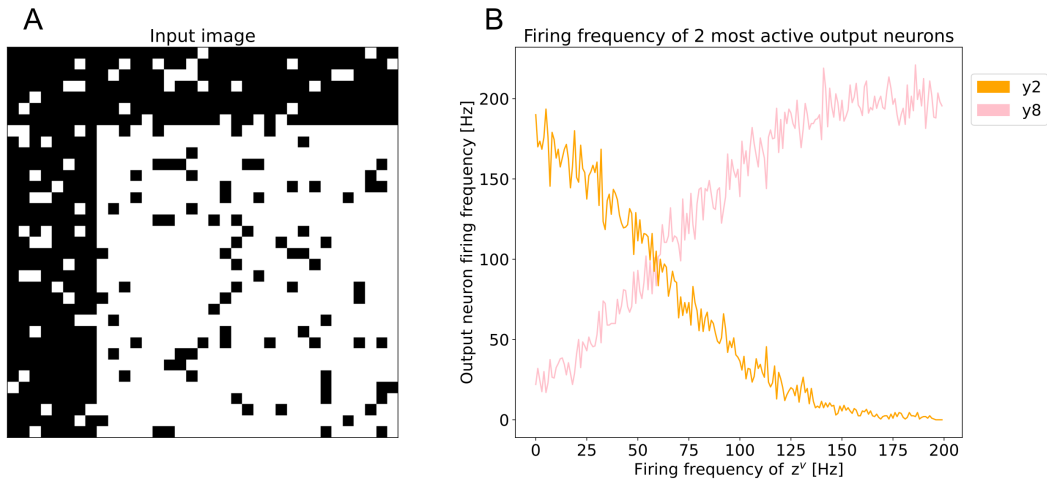


Figure 4.8: **Cross image with varying prior neuron activity.** **A** Cross image shown to the network. **B** Firing frequency of the 2 most active output neurons depending on the firing frequency of  $z^v$ . The output neuron firing frequencies were averaged over 10 runs to smooth the graph.

# 4.2 Experiment 5: Mathematical analysis and simulation of a 1D network

## 4.2.1 Introduction

The purpose of this experiment was to mathematically analyse a simpler network, thus providing a definitive way to verify the performance of the simulation. The network was scaled down to be one-dimensional with 18 input neurons, four prior neurons and four output neurons, making it easier to analyse. The conditional probabilities of the input and output neurons of the network were calculated by hand and then used to determine the theoretical posterior probability of the network. These probabilities were then used to calculate the weights for the simulation of the network. The distribution of the output spikes was then used to calculate the posterior probability of the simulation. The posterior probabilities of both the mathematical analysis and the simulation are compared, and by varying three parameters of the simulation it is tuned to approximate the analytical solution as closely as possible.

## 4.2.2 Methods

**Network structure** The architecture of this network remained the same as in previous experiments (with adaptive inhibition and a noise level of 10%), only the amount of neurons was changed. The input image consists of nine pixels in a horizontal line. Within those nine pixels four output classes can be represented. Each output class consists of three pixels next to each other. This results in each output class overlapping its neighbour classes by one pixel. Thus the centres of the output classes are at position 1, 3, 5 and 7. As there have to be 2 input neurons for each pixel, one neuron being active if the pixel is white and one if the pixel is black, the network has 18 input neurons. Furthermore four prior neurons were implemented, of which only one is being active for one of the output classes at a time. Lastly the network has four output neurons.

**Mathematical Analysis** The posterior probability of the network was calculated by using

$$P(Y = i|X = x, Z = j) = \frac{P(X = x|Y = i)P(Y = i|Z = j)}{\sum_k P(X = x, Y = k)P(Y = k|Z = j)}. \quad (4.1)$$

$P(X = x|Y = i)$  and  $P(Y = i|Z = j)$  were derived by hand corresponding to the paradigm of the experiment. The calculation of  $P(X = x|Y = i)$  was split into two parts. First the contribution of the active input neurons was calculated by determining the matrix  $P^{X|Y}$ . This matrix is of size  $4 \times 9$  and contains the conditional probabilities of each input neuron  $y_i$  being active, given that an output neuron  $x_l$  is active. These probabilities were calculated by determining which input neurons are active depending on the output class and which input neurons are inactive, as dictated by the network structure. Furthermore the noise that was applied to the input neurons had to be taken into account. For input neurons belonging to the output class the conditional probability was determined as 1 and lowered by the noise level, while for the input neurons outside of the 3-wide pixel block belonging to the output class it was determined as 0 and raised by the noise level. According to this algorithm  $P^{X|Y}$  is given by

$$P_{i,l}^{X|Y} = \begin{cases} 1 - \text{noise level} & \text{if } x_l \text{ is in the active area of } y_i, \\ 0 + \text{noise level} & \text{if } x_l \text{ is not in the active area of } y_i \end{cases}. \quad (4.2)$$

After calculating all entries of  $P^{X|Y}$  its rows were multiplied with the input image vector

$$P_1(X = x|Y = i) = P_{i,*}^{X|Y} \cdot x \quad (4.3)$$

resulting in a conditional probability for each output class depending on the input vector. The input vector was given with entries of 1 for active pixels and with entries of 0 for inactive pixels. Next to include the contribution of the input neurons that are spiking when a pixel is inactive the conditional probability of the input neurons that are active for the entries where  $x_i = 0$  had to be calculated. To achieve this complementary conditional probability at first  $P^{X|Y}$  was subtracted from one. To include the correct conditional probabilities for the complementary case the input image vector  $x$  was then also subtracted from one.  $1 - P^{X|Y}$  and  $1 - x$  were multiplied to yield

$$P_2(X = x|Y = i) = (1 - P_{i,*}^{X|Y}) \cdot (1 - x). \quad (4.4)$$

The results of both calculations were then multiplied element-wise to yield

$$P(X = x|Y = i) = P_1(X = x|Y = i) \odot P_2(X = x|Y = i). \quad (4.5)$$

$P(Y = i|Z = j)$  was determined by first calculating the matrix  $P^{Y|Z}$ . It has a dimension of  $4 \times 4$  and contains the conditional probabilities for the output neuron  $y_i$ , given the prior neuron  $z_j$  being active. For each output class there exists one corresponding prior neuron. As there can never be more than one active prior neuron at a time  $P^{Y|Z}$  is given by

$$P_{ji}^{Y|Z} = \begin{cases} 1 - \text{noise level} & \text{if } i = j, \\ 0 + \frac{1}{3} \text{noise level} & \text{if } i \neq j. \end{cases} \quad (4.6)$$

$P(Y = i|Z = j)$  was then obtained by

$$P(Y = i|Z = j) = P^{Y|Z} \cdot z \quad (4.7)$$

where  $z$  is given by a  $4 \times 1$  one-hot encoded vector of the prior.

**Simulation** The input weights for the simulation were calculated as two separate sets. First weights  $w^{i1}$  for the input neurons that are active for active input pixels were determined by

$$w^{i1} = \ln(P^{X|Y}). \quad (4.8)$$

Second complementary input weights  $w^{i2}$  were calculated for input neurons representing non active input pixels with

$$w^{i2} = \ln(1 - P^{X|Y}). \quad (4.9)$$

The prior weights  $w^p$  were derived by

$$w^p = \ln(P^{Y|Z}). \quad (4.10)$$

The network was simulated for six different input images for each parameter set. After the image presentation period of each input image the amount of the output spikes of different classes were counted and their proportions

## 4.2 Experiment 5: Mathematical analysis and simulation of a 1D network

were calculated to yield the "simulation output probabilities" in later plots. The Kullback-Leibler divergence was chosen to compare the divergence of the analytic and the simulated results of the network. This metric indicates how much two probability distributions diverge from each other. The goal of the parameter search of the simulation was to minimize the Kullback-Leibler divergence. Upon completion of the simulation of an output image the Kullback-Leibler divergence was calculated for that image

$$D_{KL}(P_{analysis}(Y = i|X, Z)||P_{simulation}(Y = i|X, Z)) = \sum_{i=1}^K P_{analysis}(Y = i|X, Z) \cdot \ln\left(\frac{P_{analysis}(Y = i|X, Z)}{P_{simulation}(Y = i|X, Z)}\right) \quad (4.11)$$

where  $K$  is the number of output neurons and  $P_{analysis}(Y = i|X, Z)$  and  $P_{simulation}(Y = i|X, Z)$  are the "analysis output probabilities" and "simulation output probabilities". The six resulting Kullback-Leibler divergences for each parameter set were then averaged to create a single metric by which the performance of the different parameter sets was compared. The three parameters input firing rate  $f_{input}$ , prior firing rate  $f_{prior}$  and the membrane constant  $\tau_{decay}$  were varied to inspect their influence on the result, as well as to approximate the analytical solution as closely as possible. Each input image is presented to the network for 20 seconds to reduce the variance between runs. Furthermore each simulation was repeated 20 times with the same parameter set to obtain the mean and standard deviation of the simulation output probabilities and of the Kullback-Leibler divergence.

### 4.2.3 Results

**Analytic Results** First the matrix  $P^{X|Y}$  was analytically calculated by using Equation 4.2

$$P^{X|Y} = \begin{bmatrix} 0.9 & 0.9 & 0.9 & 0.1 & 0.1 & 0.1 & 0.1 & 0.1 & 0.1 \\ 0.1 & 0.1 & 0.9 & 0.9 & 0.9 & 0.1 & 0.1 & 0.1 & 0.1 \\ 0.1 & 0.1 & 0.1 & 0.1 & 0.9 & 0.9 & 0.9 & 0.1 & 0.1 \\ 0.1 & 0.1 & 0.1 & 0.1 & 0.1 & 0.1 & 0.9 & 0.9 & 0.9 \end{bmatrix}. \quad (4.12)$$

Next the matrix  $P^{Y|Z}$  was analytically calculated by using Equation 4.6

$$P^{Y|Z} = \begin{bmatrix} 0.9 & 0.0333 & 0.0333 & 0.0333 \\ 0.0333 & 0.9 & 0.0333 & 0.0333 \\ 0.0333 & 0.0333 & 0.9 & 0.0333 \\ 0.0333 & 0.0333 & 0.0333 & 0.9 \end{bmatrix}. \quad (4.13)$$

For each input image these two matrices were then multiplied with the input vector and prior vector as described Equations 4.3, 4.4, 4.5 and 4.7 to yield  $P(X = x|Y = i)$  and  $P(Y = i|Z = j)$ . Using 4.1 then yielded  $P(Y = i|X = x, Z = j)$  also called "Analysis output probabilities" in later plots.

**Simulation results without prior** To simplify the parameter fitting process the network was at first simulated with inactive prior neurons. Only after determining the best values for  $f_{input}$  and  $\tau_{decay}$  were the prior neurons reactivated and  $f_{prior}$  was fitted. The values 0.015 seconds and 0.004 seconds for  $\tau_{decay}$  were used for the simulation and compared. For each of these values an optimal value for  $f_{input}$  was found by simulating different values and looking for the value that yields the smallest Kullback-Leibler divergence.

$\tau_{decay} = 0.015\text{seconds}$ ,  $f_{prior} = 0\text{Hz}$  Values for  $f_{input}$  between 10 and 110 Hz in steps of 10 Hz were simulated. After identifying the input firing rate with the smallest Kullback-Leibler divergence the network was simulated again for  $f_{input}$  values  $\pm 10$  Hz in steps of 2 Hz of the best value. The result of this search can be seen in Figure 4.9. This process yielded the best input firing rate of 42 Hz. The results of this parameter combination can be seen in Figure 4.10. In this figure six different input images can be seen marked with the letter "A". The active pixels are shown in black. The posterior probability of the mathematical analysis can be seen next to the letter "B". And finally the proportion of output spikes of the different output neurons can be seen next to the letter "C". Each probability of "C" has a standard deviation next to it, which was calculated over 20 runs of the network. At the bottom the value of the Kullback-Leibler divergence is given, with its standard deviation next to it.



## 4.2 Experiment 5: Mathematical analysis and simulation of a 1D network

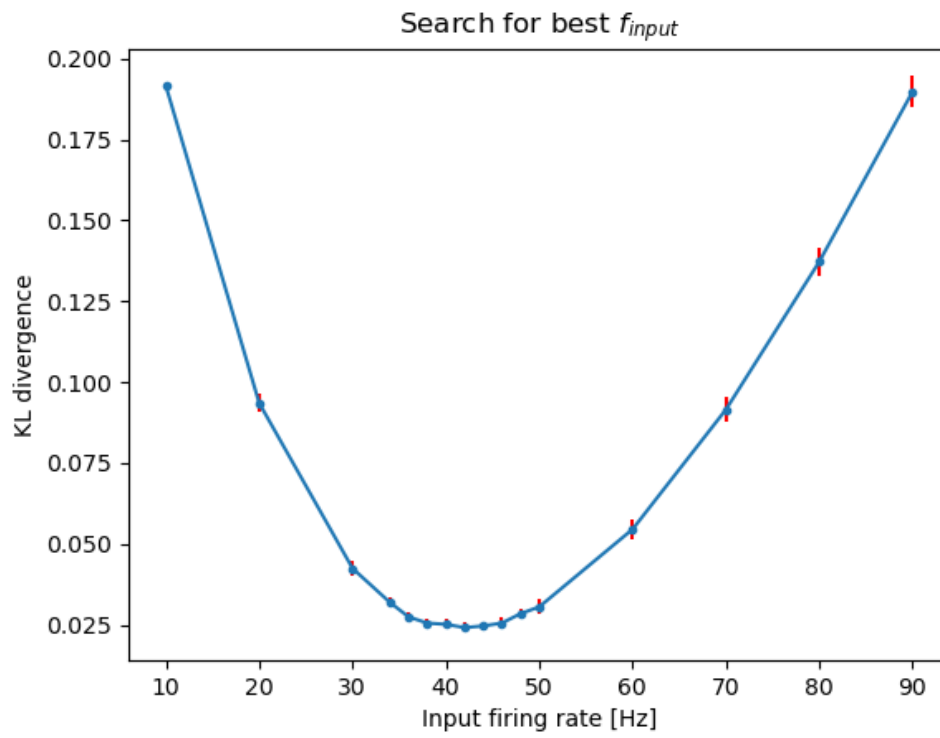


Figure 4.9: KL divergence for different  $f_{input}$  values  $f_{prior} = 0\text{Hz}$ ,  $\tau_{decay} = 15\text{ms}$

## 4 Experiments

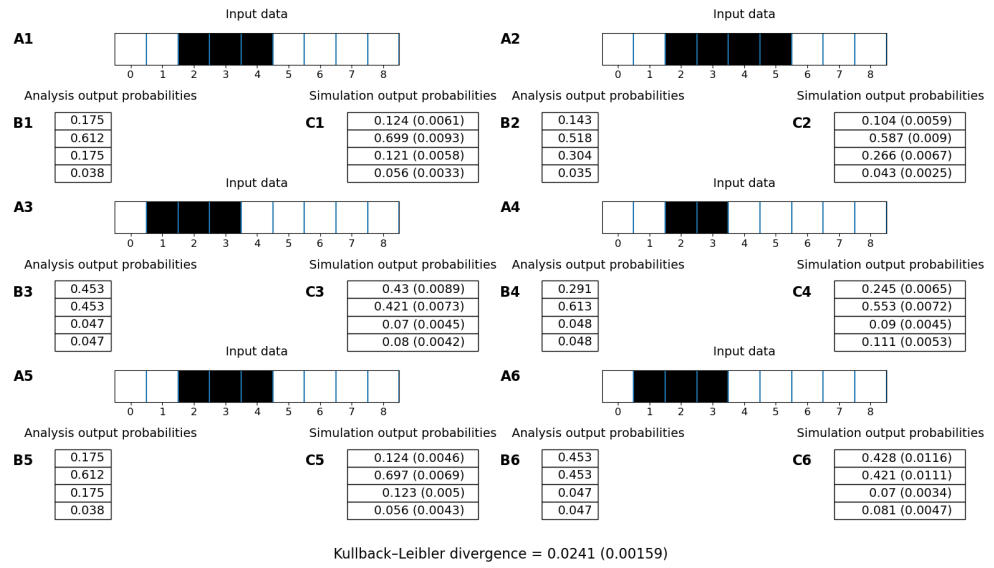


Figure 4.10: **Analysis and simulation result.** Parameters:  $f_{input} = 42\text{Hz}$ ,  $f_{prior} = 0\text{Hz}$ ,  $\tau_{decay} = 15\text{ms}$  **A** Input images with  $9 \times 1$  pixels. **B** Analytically calculated posterior probabilities. **C** Proportions of the spikes of the output neurons during the simulation and their standard deviations in brackets.

## 4.2 Experiment 5: Mathematical analysis and simulation of a 1D network

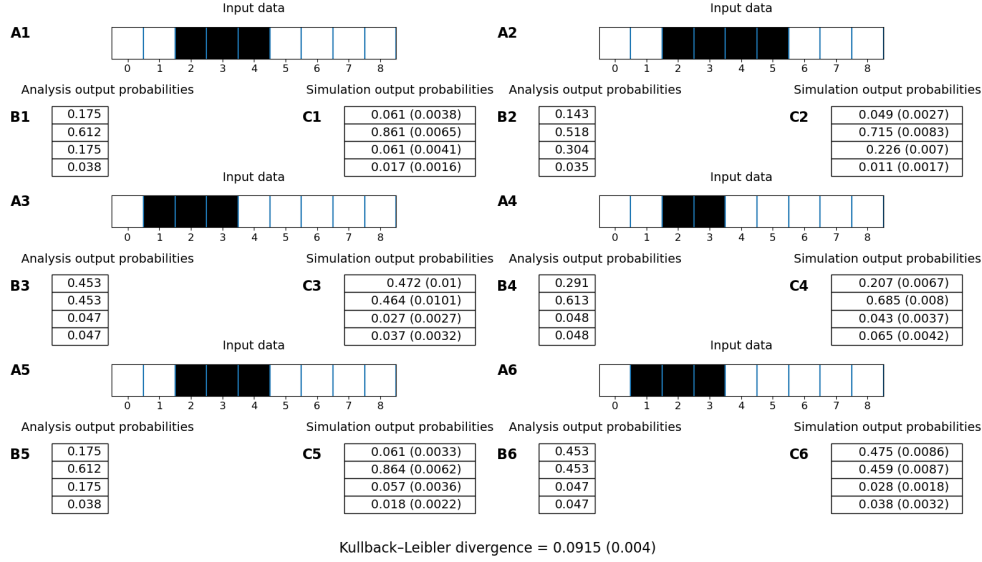


Figure 4.11: **Analysis and simulation result.** Parameters:  $f_{input} = 70\text{Hz}$ ,  $f_{prior} = 0\text{Hz}$ ,  $\tau_{decay} = 15\text{ms}$  **A** Input images with  $9 \times 1$  pixels. The red borders indicate the class of the prior. **B** Analytically calculated posterior probabilities. **C** Proportions of the spikes of the output neurons during the simulation and their standard deviations in brackets.

When  $f_{input}$  was 70 Hz the results of the analysis and the simulation differed more as can be seen in Figure 4.11.

$\tau_{decay} = 0.004\text{seconds}$ ,  $f_{prior} = 0\text{Hz}$  For this parameter combination values between 50 and 150 Hz for  $f_{input}$  in steps of 10 Hz were simulated. Analogously to the previous parameter set after finding the best input firing rate the search was performed in finer steps until the best value was determined as 88 Hz. The result of this search can be seen in Figure 4.12. The result of the simulation with those parameters can be seen in Figure 4.13.

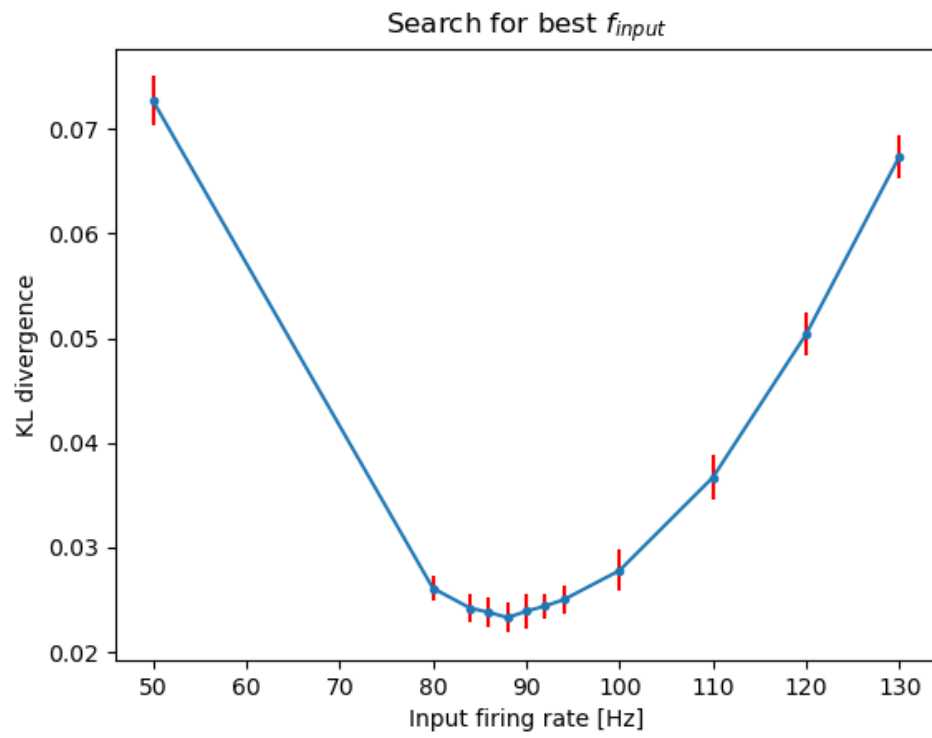


Figure 4.12: KL divergence for different  $f_{input}$  values  $f_{prior} = 0\text{Hz}$ ,  $\tau_{decay} = 4\text{ms}$

## 4.2 Experiment 5: Mathematical analysis and simulation of a 1D network

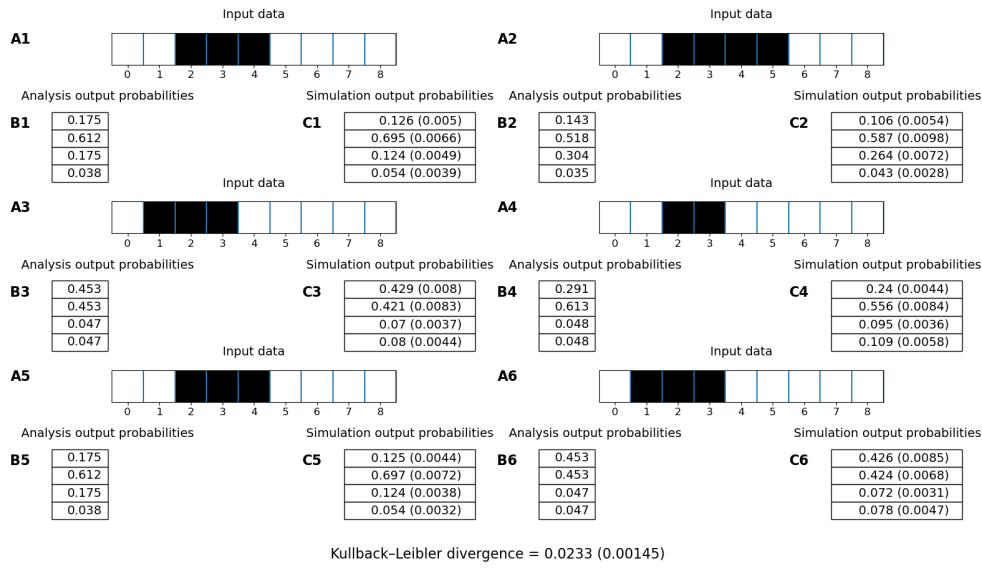


Figure 4.13: **Analysis and simulation result.** Parameters:  $f_{input} = 88\text{Hz}$ ,  $f_{prior} = 0\text{Hz}$ ,  $\tau_{decay} = 4\text{ms}$  **A** Input images with  $9 \times 1$  pixels. **B** Analytically calculated posterior probabilities. **C** Proportions of the spikes of the output neurons during the simulation and their standard deviations in brackets.

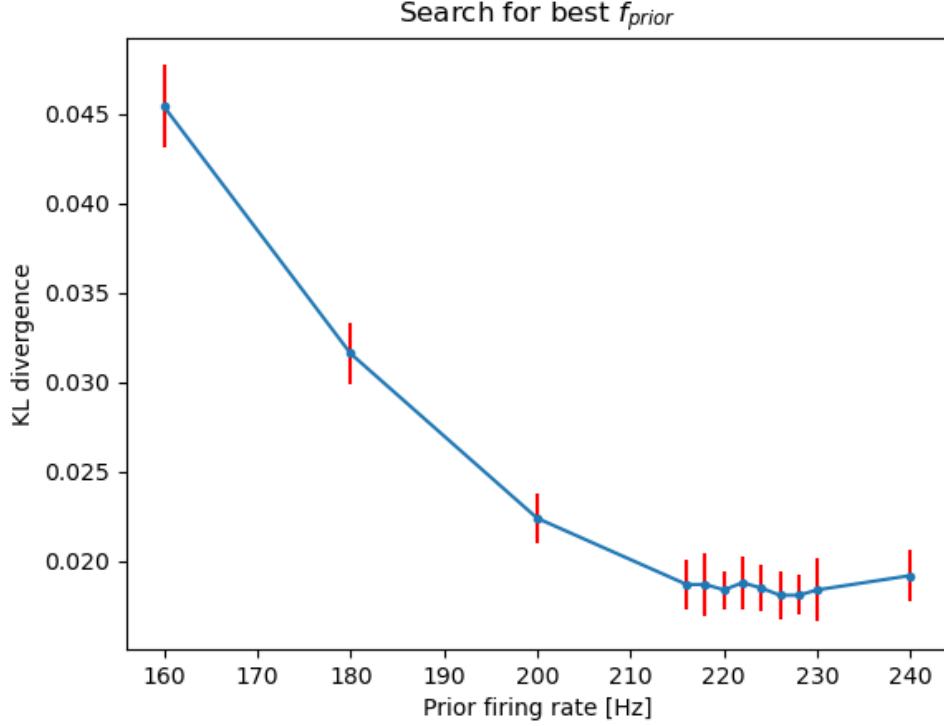


Figure 4.14: KL divergence for different  $f_{prior}$  values  $f_{input} = 42\text{Hz}$ ,  $\tau_{decay} = 15\text{ms}$

**Simulation results with prior** After determining the best input firing rates for two different values of  $\tau_{decay}$ , the prior neurons were activated and the best prior firing rate  $f_{prior}$  was fitted.

$\tau_{decay} = 0.015\text{seconds}$ ,  $f_{input} = 42\text{Hz}$  The search for the best value of  $f_{prior}$  was performed in the same manner as for  $f_{input}$ . Values between 140 and 240 Hz were simulated and a prior firing rate of 222 Hz performed the best. The result of this search can be seen in Figure 4.14. The simulation results can be seen in Figure 4.15. The value of the prior is indicated by the red border which is three pixels wide and centered at the center position of the corresponding output class.

## 4.2 Experiment 5: Mathematical analysis and simulation of a 1D network

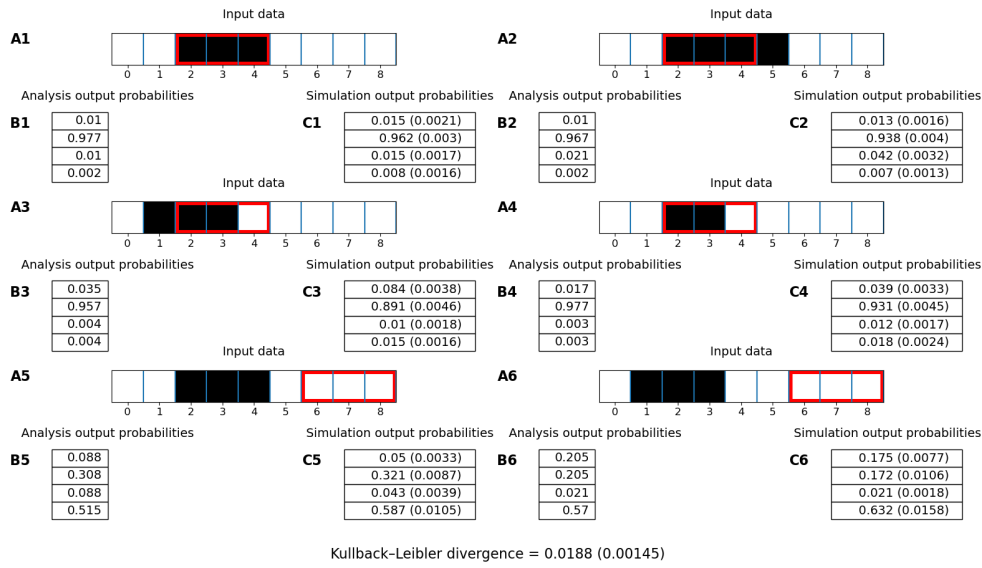


Figure 4.15: **Analysis and simulation result.** Parameters:  $f_{input} = 42\text{Hz}$ ,  $f_{prior} = 222\text{Hz}$ ,  $\tau_{decay} = 15\text{ms}$  **A** Input images with  $9 \times 1$  pixels. **B** Analytically calculated posterior probabilities. **C** Proportions of the spikes of the output neurons during the simulation and their standard deviations in brackets.

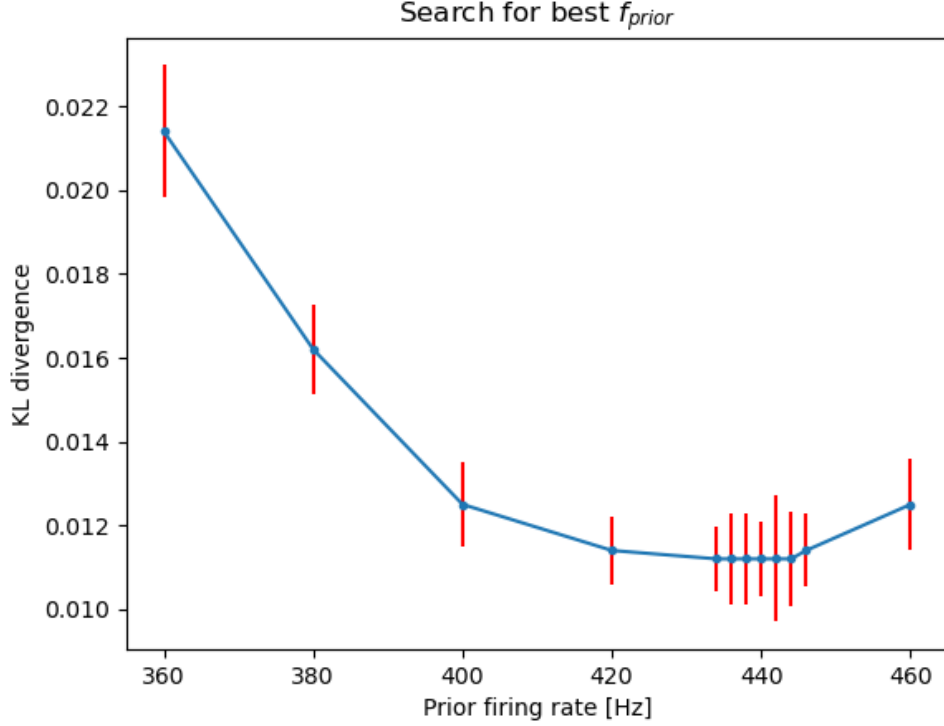


Figure 4.16: KL divergence for different  $f_{prior}$  values  $f_{input} = 88\text{Hz}$ ,  $\tau_{decay} = 4\text{ms}$

$\tau_{decay} = 0.004\text{seconds}$ ,  $f_{input} = 88\text{Hz}$  The search for the best value of  $f_{prior}$  was performed in the same manner as for  $f_{input}$ . Values between 360 and 460 Hz were simulated and a prior firing rate of 440 Hz performed the best. The result of this search can be seen in Figure 4.16. The results of this parameter combination are given in Figure 4.17.

To demonstrate the impact of rising  $f_{prior}$  it was set to 600 Hz and the results can be seen in Figure 4.18.

$\tau_{decay} = 0.004\text{seconds}$ ,  $f_{input} = 98$ ,  $f_{prior} = 440\text{Hz}$  Finally to it was tested if a increase of  $f_{input}$  might decrease the Kullback-Leibler divergence even further. The network was simulated with increasing values of  $f_{input}$  in steps of 2 Hz, beginning from 90 Hz. The result of this search can be seen in



## 4.2 Experiment 5: Mathematical analysis and simulation of a 1D network

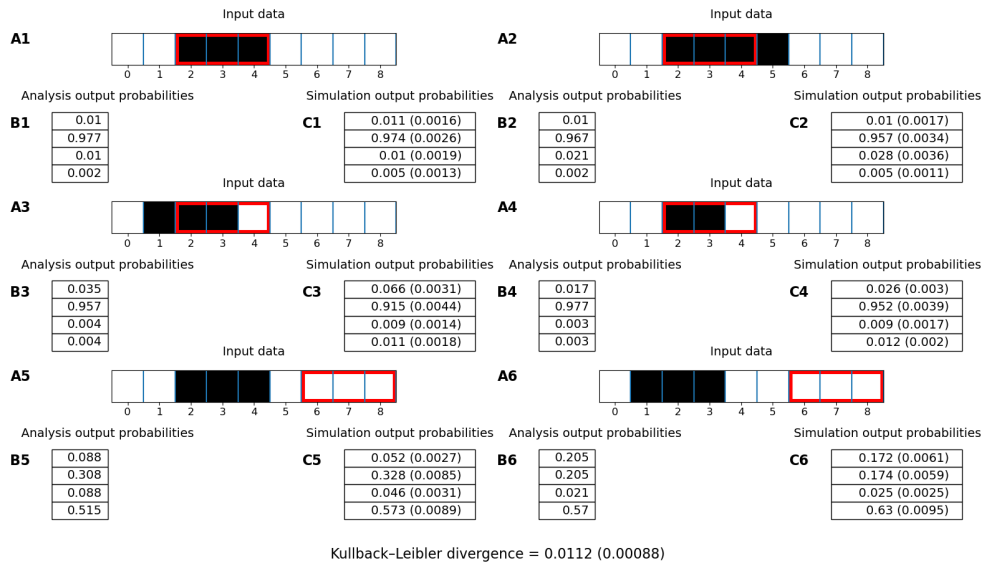


Figure 4.17: **Analysis and simulation result.** Parameters:  $f_{input} = 88\text{Hz}$ ,  $f_{prior} = 440\text{Hz}$ ,  $\tau_{decay} = 4\text{ms}$  **A** Input images with  $9 \times 1$  pixels. **B** Analytically calculated posterior probabilities. **C** Proportions of the spikes of the output neurons during the simulation and their standard deviations in brackets.

## 4 Experiments

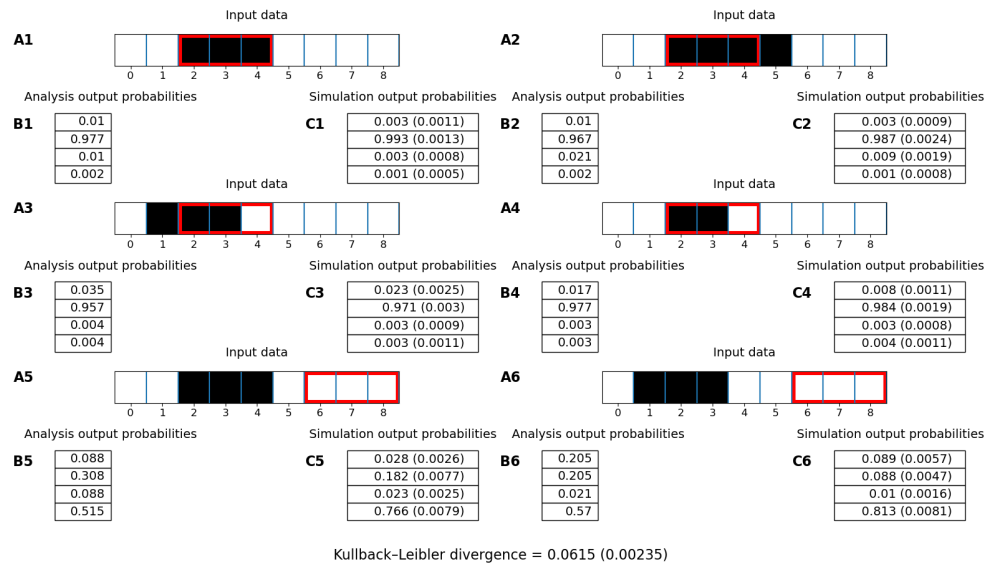


Figure 4.18: Analysis and simulation result. The Kullback-Leibler divergence could not be calculated for this case, as it is not defined for probabilities of 0. Parameters:  $f_{input} = 88\text{Hz}$ ,  $f_{prior} = 600\text{Hz}$ ,  $\tau_{decay} = 4\text{ms}$  A Input images with  $9 \times 1$  pixels. B Analytically calculated posterior probabilities. C Proportions of the spikes of the output neurons during the simulation and their standard deviations in brackets.

## 4.2 Experiment 5: Mathematical analysis and simulation of a 1D network

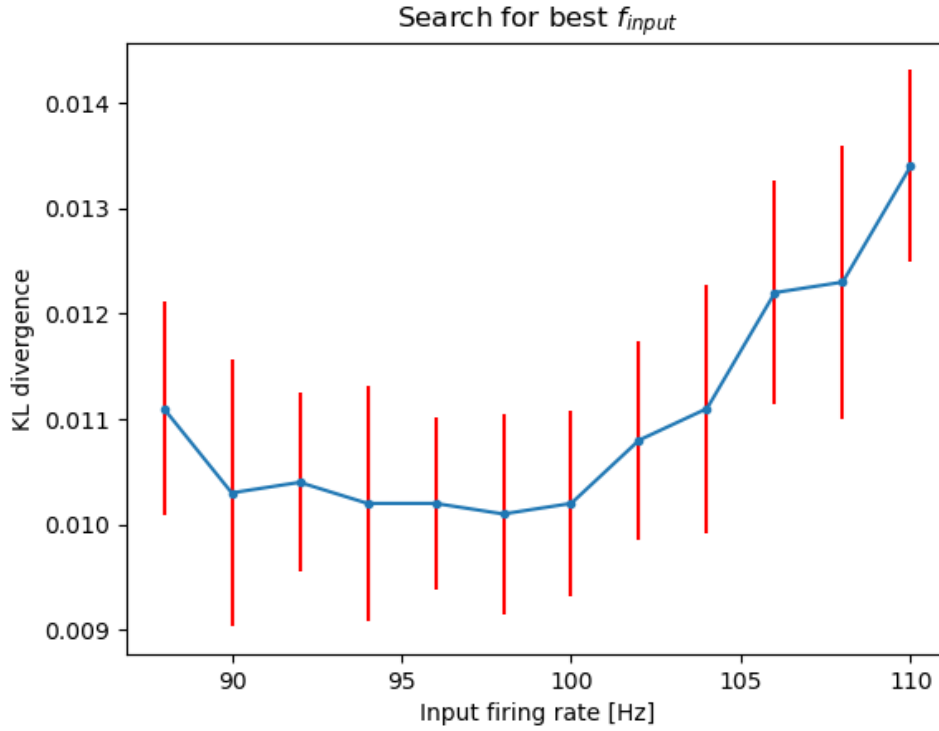


Figure 4.19: KL divergence for different  $f_{input}$  values  $f_{prior} = 440\text{Hz}$ ,  $\tau_{decay} = 4\text{ms}$

Figure 4.19. The best result was obtained with an input firing rate of 98 Hz. The results of that simulation can be seen in Figure 4.20.

### 4.2.4 Discussion

In this experiment the impact of the three network parameters  $f_{input}$ ,  $f_{prior}$  and  $\tau_{decay}$  was analysed.

$f_{input}$  controls how strongly the information of the pixels of the input image is weighed. This means that by raising  $f_{input}$  the impact of the active

## 4 Experiments

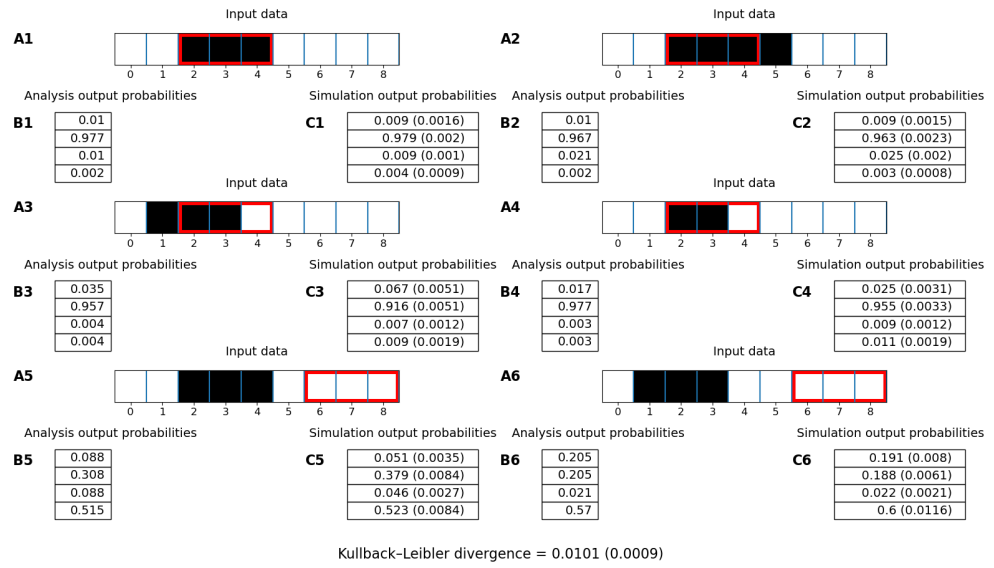


Figure 4.20: **Analysis and simulation result.** Parameters:  $f_{input} = 98\text{Hz}$ ,  $f_{prior} = 440\text{Hz}$ ,  $\tau_{decay} = 4\text{ms}$  **A** Input images with  $9 \times 1$  pixels. **B** Analytically calculated posterior probabilities. **C** Proportions of the spikes of the output neurons during the simulation and their standard deviations in brackets.

pixels increases, while the impact of the prior neuron decreases comparatively. This effect will be shown in the discussion about  $f_{prior}$ . However this is not the only impact this parameter has. When raising  $f_{input}$  it was also observed that the probabilities for output classes adjacent to the active pixels decreased. This can be observed when comparing Figures 4.10 and 4.11 where  $f_{input}$  was raised from 42 Hz to 70 Hz. For example when looking at "C4" in the mentioned figures, it can be seen that for  $f_{input} = 42\text{Hz}$  the simulation output probability for class 1 is 0.245. This high probability is mostly due to the active pixel number 2, which belongs to class 1 and 2 at the same time. When now increasing  $f_{input}$  to 70 Hz one might expect the probabilities for class 1 and 2 to rise. This however does not happen, instead the simulation output probability for class 1 fell to 0.207, while for class 2 it rose. It is assumed that this happens because the membrane potentials of the output neurons are never normalized. As the input neurons spike more quickly the membrane potential of output neuron 1 rises slower than the membrane potential of output neuron 2. This leads to shifted firing rates in favour of output neuron 2. However this behaviour might be expected, as faster spiking input neurons correspond statistically to taking more samples of a probability distribution. This means that the more samples the network takes, the more certain it becomes of the more likely option, which is output class 2.

$f_{prior}$  When increasing the prior firing rate the impact on the result of the prior neurons increases, while the impact of the input neurons decreases comparatively. When comparing the Figures 4.17 and 4.18 which show the results for  $f_{input} = 88\text{Hz}$ ,  $\tau_{decay} = 4\text{ms}$  and  $f_{prior} = 440$  and  $600\text{Hz}$  respectively it can be seen under "C6" how the probability for output class 4 rose, while all other probabilities fell. The opposite behaviour can be observed when raising  $f_{input}$  instead, but no separate figure will be provided for this case.

$\tau_{decay}$  determines for how long and how strongly an input or prior spike contributes to the membrane potentials of the output neurons. The bigger  $\tau_{decay}$  is, the smaller  $f_{input}$  and  $f_{prior}$  need to be, to minimize the Kullback-Leibler divergence. This is represented by the final parameters for  $\tau_{decay}$  of

4 and 15 ms. While for  $\tau_{decay} = 15ms$  the best input firing rate was 42 Hz and the prior firing rate was 222 Hz, for  $\tau_{decay} = 4ms$  they had to be raised to 98 and 440 Hz to minimize the Kullback-Leibler divergence.

**Approximating the analytic solution** After first finding the optimal  $f_{input}$  for disabled prior activity and then finding the optimal  $f_{prior}$  with enabled prior activity for  $\tau_{decay}$  the simulation was not yet approximating the analytical solution perfectly. Because of that it was tried to raise  $f_{input}$  to further decrease the Kullback-Leibler divergence. The further search for a better  $f_{input}$  was performed for  $\tau_{decay} = 0.004ms$  and  $f_{prior} = 440Hz$ , as this set of parameters performed the best overall. When comparing the former optimal result in Figure 4.17 with  $f_{input} = 88Hz$ , to the result with  $f_{input} = 98Hz$  in Figure 4.20, it can be seen that the Kullback-Leibler divergence decreased from 0.0112 to 0.0101. The simulation output probabilities with the higher  $f_{input}$  approximated the analysis output probabilities for example for "B3" and "C3" in the mentioned figures on one hand better, while on the other hand for "B5" and "C5" the output probabilities of the analysis and the simulation of class 2 diverged more. A further increase of  $f_{input}$  started to increase the Kullback-Leibler divergence again, thus the final optimum of the parameter set was reached. It is assumed that increasing  $f_{input}$  after  $f_{prior}$  was fitted was necessary because the proportion of the impact of  $f_{input}$  on the simulation decreased due to the introduction of the prior activity.

### 4.3 Experiment 6: Simulation of the 1D network with double size

#### 4.3.1 Introduction

In this experiment the optimal parameters determined in Experiment 5 were used for a network double in size of the network in Experiment 5. By doing this the applicability of parameters determined for one network to another network was to be examined.

### 4.3.2 Methods

The network of Experiment 5 was doubled in size by increasing the number of input neurons from 18 to 36 neurons. This resulted in input images with 18 pixels. Furthermore the matrix  $P^{X|Y}$  was doubled in size by inserting each value of the matrix to the right of itself. The amount of the prior neurons was kept the same with 4 prior neurons. However this network was simulated once for a prior firing rate of 440 Hz, and once for the double rate of 880 Hz. The rest of the methods were performed analogously to Experiment 5.

### 4.3.3 Results

The expanded matrix  $P^{X|Y}$  was doubled in size, now being  $[18 \times 4]$  yielding

$$P^{X|Y} = \begin{bmatrix} 0.9 & 0.9 & 0.9 & 0.9 & 0.9 & 0.9 & 0.1 & 0.1 & 0.1 & \dots \\ \dots & 0.1 & 0.9 & 0.9 & 0.9 & 0.9 & 0.9 & 0.9 & 0.1 & \dots \\ \dots & 0.1 & 0.9 & 0.9 & 0.9 & 0.9 & 0.9 & 0.9 & 0.1 & \dots \\ \dots & 0.1 & 0.1 & 0.1 & 0.9 & 0.9 & 0.9 & 0.9 & 0.9 & 0.9 \end{bmatrix}. \quad (4.14)$$

The simulation result for  $f_{input} = 98\text{Hz}$ ,  $f_{prior} = 440\text{Hz}$  and  $\tau_{decay} = 4\text{ms}$  can be seen in Figure 4.21. The Kullback-Leibler divergence is infinity in this result, because some simulation output probabilities were zero and the Kullback-Leibler divergence is not defined for probabilities of zero. To circumvent this an approximated Kullback-Leibler divergence was calculated by setting the simulation output probabilities that were 0 to 0.0000001. This yielded a Kullback-Leibler divergence of 0.1411.

Finally the simulation result for  $f_{input} = 98\text{Hz}$ ,  $f_{prior} = 880\text{Hz}$  and  $\tau_{decay} = 4\text{ms}$  can be seen in Figure 4.22. As in the previous result the Kullback-Leibler divergence was approximated and calculated as 0.2391 for this parameter set.

Finally the Kullback-Leibler divergence for the results of the network in Experiment 5 with the parameters  $f_{input} = 98\text{Hz}$ ,  $f_{prior} = 440\text{Hz}$  and

## 4 Experiments

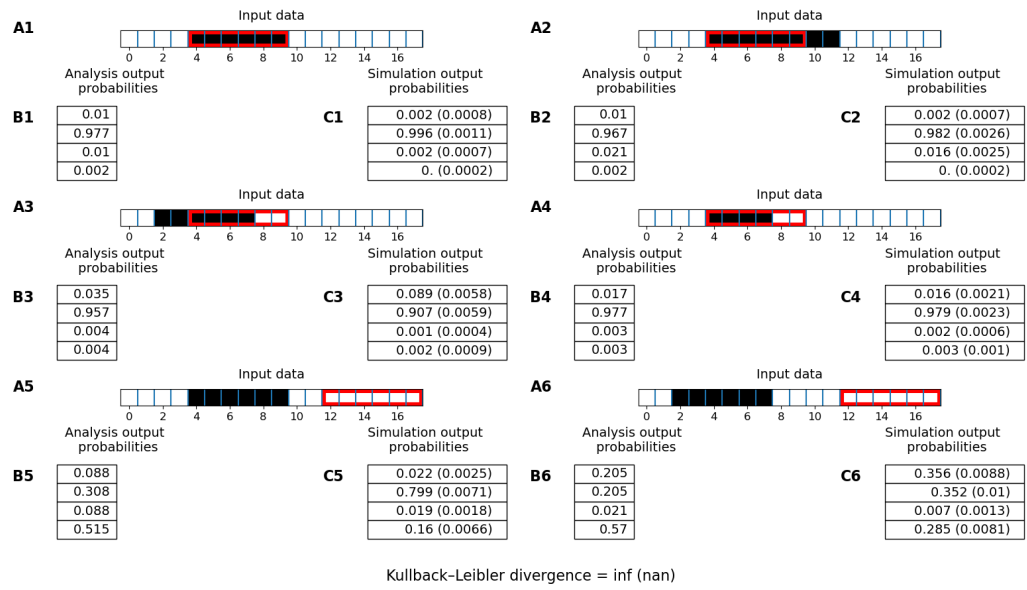


Figure 4.21: **Analysis and simulation result.** Parameters:  $f_{input} = 98\text{Hz}$ ,  $f_{prior} = 440\text{Hz}$ ,  $\tau_{decay} = 4\text{ms}$  **A** Input images with  $18 \times 1$  pixels. **B** Analytically calculated posterior probabilities. **C** Proportions of the spikes of the output neurons during the simulation and their standard deviations in brackets.



### 4.3 Experiment 6: Simulation of the 1D network with double size

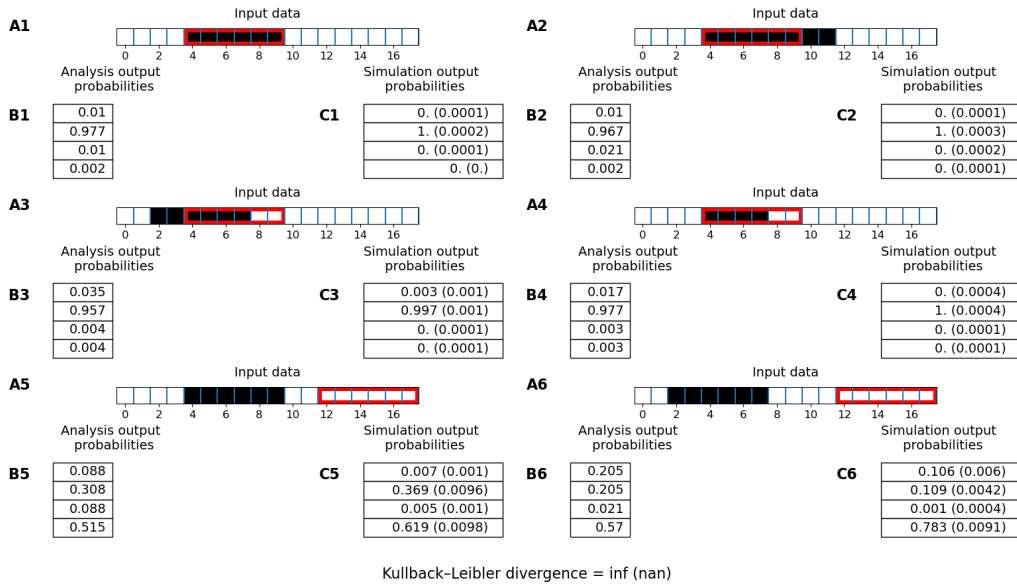


Figure 4.22: Analysis and simulation result. Parameters:  $f_{input} = 98\text{Hz}$ ,  $f_{prior} = 880\text{Hz}$ ,  $\tau_{decay} = 4\text{ms}$  **A** Input images with  $18 \times 1$  pixels. **B** Analytically calculated posterior probabilities. **C** Proportions of the spikes of the output neurons during the simulation and their standard deviations in brackets.

## 4 Experiments

---

$\tau_{decay} = 4ms$  was also approximated in the above mentioned way and resulted in a value of 0.0094.

### 4.3.4 Discussion

When comparing Figures 4.20 and 4.21 it can be seen that the analysis output probabilities stayed the same. This is expected, because by doubling the pixels of the input images the information within it does not change as the areas corresponding to an output class double in size, as do the active pixels shown in black. However when comparing the Kullback-Leibler divergences of the network in Experiment 5 and the network of this experiment with parameters of  $f_{input} = 98Hz$ ,  $f_{prior} = 440Hz$  and  $\tau_{decay} = 4ms$  it can be seen the the network with double size performed worse. The Kullback-Leibler divergence of the network with doubled size was 0.1411 compared to 0.0094 of the network the parameters were fitted to. This clearly indicates that the fitted parameters are not universal to every network size. This might be due to the fact that the membrane potentials of the output neurons are never normalized, which was already discussed in Experiment 5. However if such a normalization was implemented the fitted parameters of one network size could be universal to all other sizes.

## 4.4 Experiment 7: Training of the 1D network with predetermined parameters

### 4.4.1 Introduction

In this Experiment the network of Experiment 5 was used, but the weights of the network were not derived from the matrices  $P^{X|Y}$  and  $P^{Y|Z}$ , but they were learned from the input images.

### 4.4.2 Methods

The network architecture was the same as in Experiment 5 and the training paradigm was the same as in Experiment 4. The used network parameters were  $f_{input} = 98\text{Hz}$ ,  $f_{prior} = 440\text{Hz}$  and  $\tau_{decay} = 4\text{ms}$ . First the weight shifting parameter  $c$  was set to 1. Additionally to improve the results the values 2, 3 and 4 were also tried for  $c$ .

### 4.4.3 Results

The training results can be seen in Figure 4.23.

The evaluation results can be seen in Figure 4.24.

The Kullback-Leibler divergence for different values of  $c$  can be seen in Figure 4.25.

The training and evaluation results for the best value of  $c = 3$  can be seen in Figures 4.26 and 4.27.

### 4.4.4 Discussion

Using the previously determined optimal network parameters for the weight training process was successful. When comparing A with B and C with D in Figure 4.23 it can be seen that the network learned the correct discrimination function. However the size the weights and the prior weights is too small. The Kullback-Leibler divergence also was worse with 0.0625 compared to 0.0101 from Experiment 5 Figure 4.20. To try to improve the similarity of the learned and the calculated probability matrices, and also to minimize the Kullback-Leibler divergence, different values for the weight shifting parameter  $c$  were tried. The lowest Kullback-Leibler divergence was achieved with  $c = 3$ . For this  $c$  the divergence was 0.0342. When comparing the probability matrices in Figure 4.26 it is apparent that the values of the learned  $P^{X|Y}$  are still too small and they could profit from further increasing  $c$ . On the other hand the values in the learned  $P^{Y|Z}$  are already too big and would profit from a smaller  $c$ . If one would want to further minimize the

## 4 Experiments

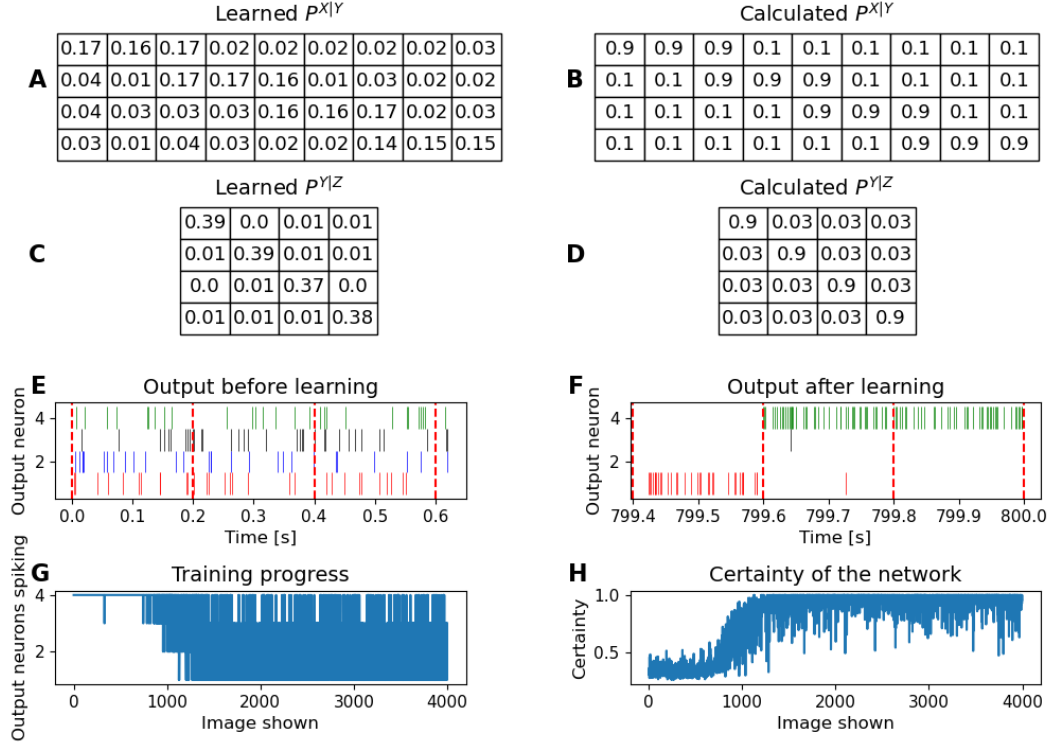


Figure 4.23: **Training result**  $f_{input} = 98\text{Hz}$ ,  $f_{prior} = 440\text{Hz}$ ,  $\tau_{decay} = 4\text{ms}$ ,  $c = 1$  **A** The learned probability matrix  $P^{X|Y}$ . It was determined by taking the weights to the power of e. **B** The calculated probability matrix  $P^{X|Y}$ . **C** The learned prior probability matrix  $P^{Y|Z}$ . **D** The calculated prior probability matrix  $P^{Y|Z}$ . **E**, **F** Spike activity expressed by the output neurons before and after the training of the network. **G** Number of distinct output neurons active during the presentation duration of each training image. **H** Proportion of most active output neuron to activity of all other output neurons during the presentation duration of each training image.

## 4.4 Experiment 7: Training of the 1D network with predetermined parameters

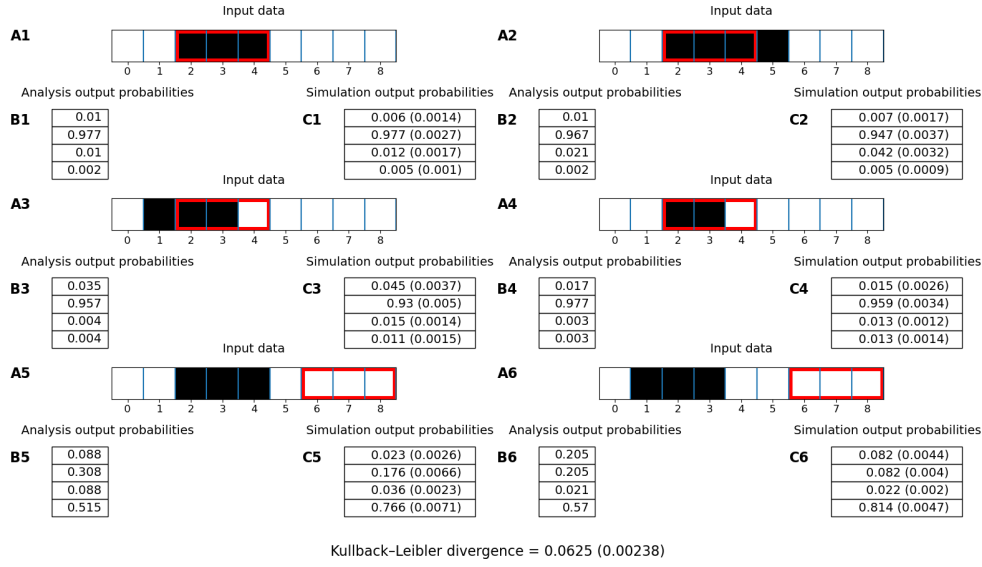


Figure 4.24: **Analysis and simulation result. Parameters:**  $f_{input} = 98\text{Hz}$ ,  $f_{prior} = 440\text{Hz}$ ,  $\tau_{decay} = 4\text{ms}$  **A** Input images with  $9 \times 1$  pixels. **B** Analytically calculated posterior probabilities. **C** Proportions of the spikes of the output neurons during the simulation and their standard deviations in brackets.

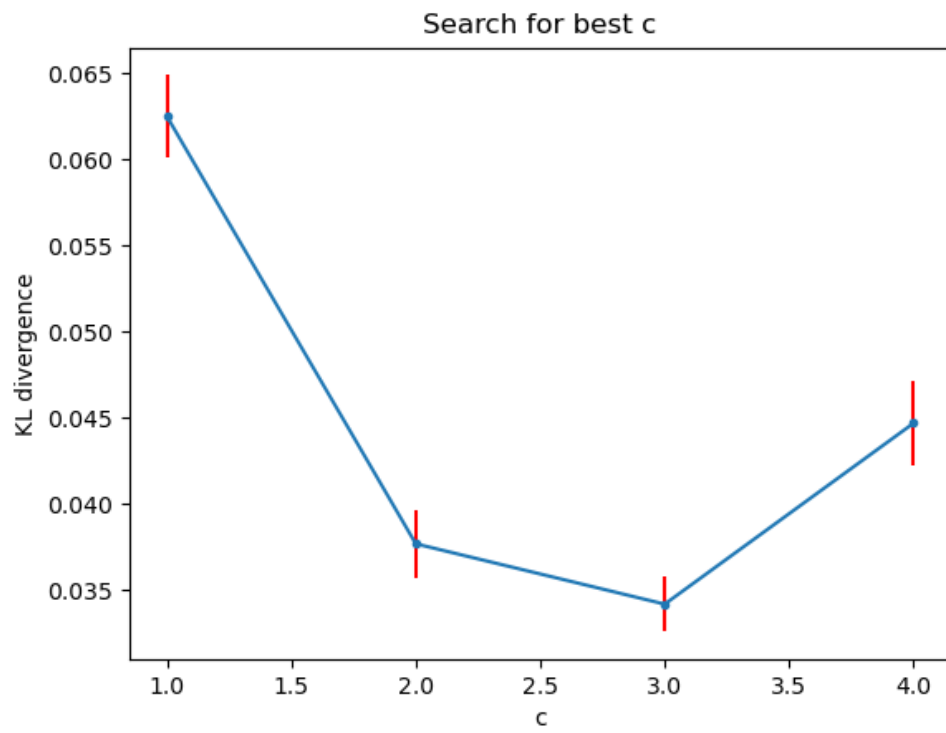


Figure 4.25: **KL divergence for different c values**  $f_{input} = 98\text{Hz}$ ,  $f_{prior} = 440\text{Hz}$ ,  $\tau_{decay} = 4\text{ms}$

#### 4.4 Experiment 7: Training of the 1D network with predetermined parameters

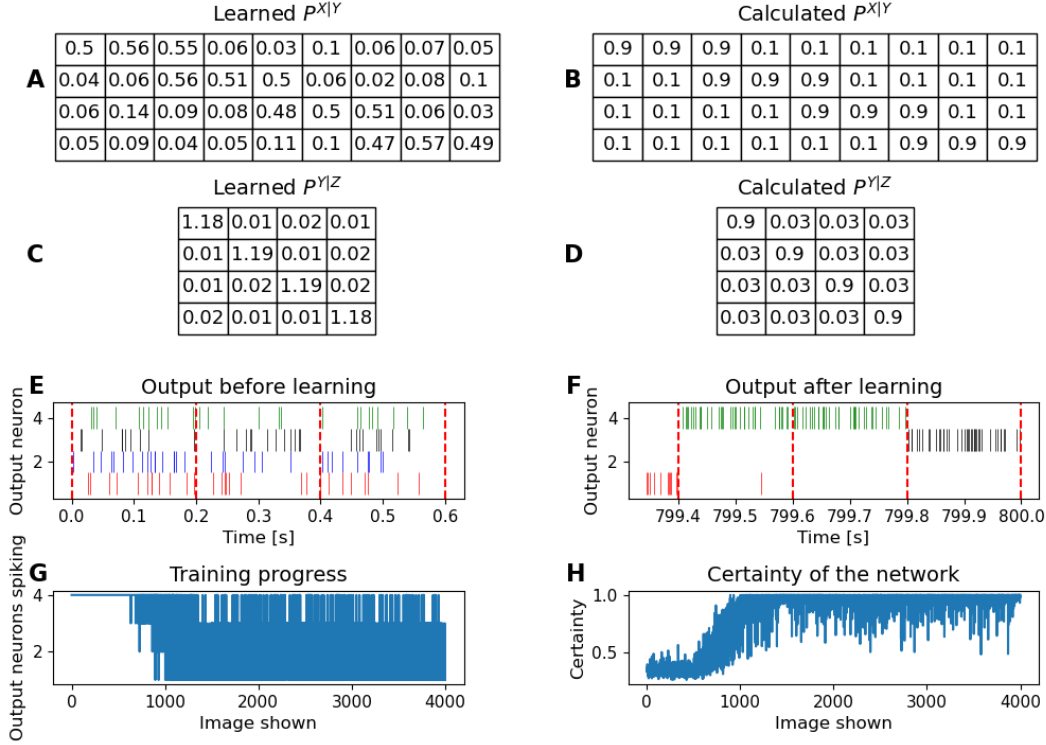


Figure 4.26: **Training result**  $f_{input} = 98\text{Hz}$ ,  $f_{prior} = 440\text{Hz}$ ,  $\tau_{decay} = 4\text{ms}$ ,  $c = 3$  **A** The learned probability matrix  $P^{X|Y}$ . It was determined by taking the weights to the power of e. **B** The calculated probability matrix  $P^{X|Y}$ . **C** The learned prior probability matrix  $P^{Y|Z}$ . **D** The calculated prior probability matrix  $P^{Y|Z}$ . **E, F** Spike activity expressed by the output neurons before and after the training of the network. **G** Number of distinct output neurons active during the presentation duration of each training image. **H** Proportion of most active output neuron to activity of all other output neurons during the presentation duration of each training image.

## 4 Experiments

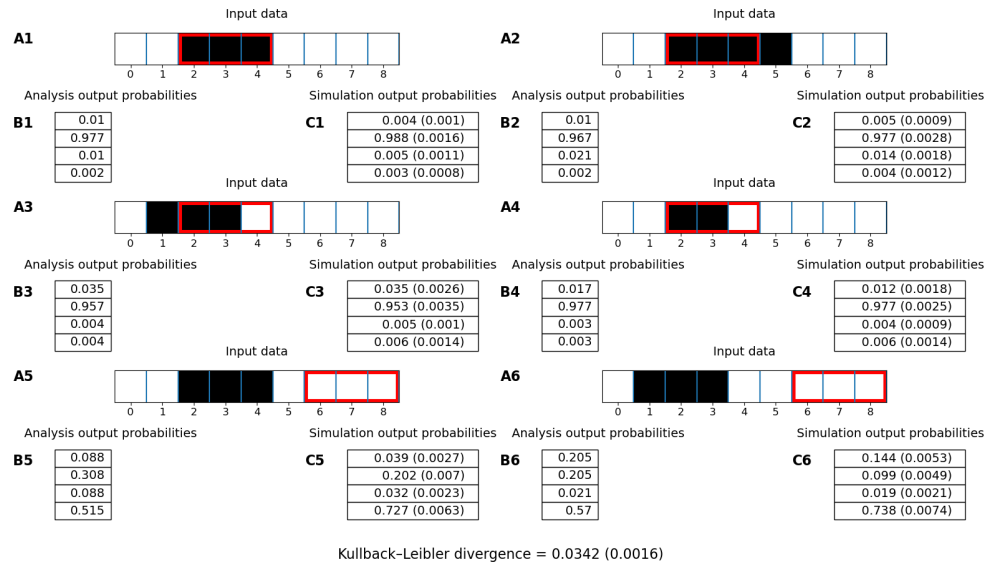


Figure 4.27: **Analysis and simulation result.** Parameters:  $f_{input} = 98\text{Hz}$ ,  $f_{prior} = 440\text{Hz}$ ,  $\tau_{decay} = 4\text{ms}$ ,  $c = 3$  **A** Input images with  $9 \times 1$  pixels. **B** Analytically calculated posterior probabilities. **C** Proportions of the spikes of the output neurons during the simulation and their standard deviations in brackets.



#### 4.4 Experiment 7: Training of the 1D network with predetermined parameters

---

Kullback-Leibler divergence two separate weights shifting parameters for the input weights and the prior weights could be implemented.



## 5 Discussion



# Bibliography

- Arbib, Michael A. (2003). *The handbook of brain theory and neural networks 2nd Edition*. Cambridge, MA, USA: MIT Press, pp. 1228–1231. ISBN: 0–262–01197–2 (cit. on p. 3).
- Contreras, Diego (2004). “Electrophysiological classes of neocortical neurons.” In: *Neural Networks 17.5. Vision and Brain*, pp. 633–646. ISSN: 0893-6080. DOI: <https://doi.org/10.1016/j.neunet.2004.04.003>. URL: <https://www.sciencedirect.com/science/article/pii/S0893608004000863> (cit. on p. 3).
- Dan Yang, Poo Mu-Ming (2004). “Spike timing-dependent plasticity of neural circuits.” In: *Neuron* 44, pp. 23–30. DOI: [10.1016/j.neuron.2004.09.007](https://doi.org/10.1016/j.neuron.2004.09.007) (cit. on p. 2).
- Darlington, Timothy R, Jeffrey M Beck, and Stephen G Lisberger (Oct. 2018). “Neural implementation of Bayesian inference in a sensorimotor behavior.” en. In: *Nat. Neurosci.* 21.10, pp. 1442–1451 (cit. on p. 6).
- Feldman, Daniel E. (2012). “The Spike-Timing Dependence of Plasticity.” In: *Neuron* 75.4, pp. 556–571. ISSN: 0896-6273. DOI: <https://doi.org/10.1016/j.neuron.2012.08.001>. URL: <https://www.sciencedirect.com/science/article/pii/S0896627312007039> (cit. on p. 2).
- Funamizu Akihiro Kuhn Bernd, Doya Kenji (Dec. 2016). “Neural substrate of dynamic Bayesian inference in the cerebral cortex.” In: *Nature Neuroscience* 19. DOI: [doi:10.1038/nn.4390](https://doi.org/10.1038/nn.4390) (cit. on pp. 1, 6).
- Gerstner, Wulfram and Werner M. Kistler (2002). *Spiking Neuron Models: Single Neurons, Populations, Plasticity*. Cambridge University Press (cit. on pp. 2, 6, 9).
- Guo, Shangqi et al. (2019). “Hierarchical Bayesian Inference and Learning in Spiking Neural Networks.” In: *IEEE Transactions on Cybernetics* 49.1, pp. 133–145. DOI: [10.1109/TCYB.2017.2768554](https://doi.org/10.1109/TCYB.2017.2768554) (cit. on p. 2).
- Huff T Mahabadi N, Tadi P. (2024). *StatPearls [Internet]*. StatPearls Publishing. Chap. Neuroanatomy, Visual Cortex. (Cit. on p. 5).

- Jolivet, Renaud et al. (Aug. 2006). "Predicting spike timing of neocortical pyramidal neurons by simple threshold models." In: *Journal of Computational Neuroscience* 21.1, pp. 35–49. ISSN: 1573-6873. DOI: [10.1007/s10827-006-7074-5](https://doi.org/10.1007/s10827-006-7074-5). URL: <https://doi.org/10.1007/s10827-006-7074-5> (cit. on p. 15).
- Jones EG; Hendry, SHC, ed. (1984). *Cerebral cortex: cellular components of the cerebral cortex*. ew York: Plenum Press. Chap. Basket cells, pp. 309–334 (cit. on p. 3).
- Joyce, James (2019). "Bayes' Theorem." In: *The Stanford Encyclopedia of Philosophy*. Ed. by Edward N. Zalta. Spring 2019. Metaphysics Research Lab, Stanford University (cit. on p. 11).
- Lee TS, Mumford D. (July 2003). "Hierarchical Bayesian inference in the visual cortex." In: *J Opt Soc Am A Opt Image Sci Vis*. DOI: [doi:10.1364/josaa.20.001434](https://doi.org/10.1364/josaa.20.001434) (cit. on pp. 1, 6, 8).
- Maass, Wolfgang (Nov. 2000). "On the Computational Power of Winner-Take-All." In: *Neural Computation* 12.11, pp. 2519–2535. ISSN: 0899-7667. DOI: [10.1162/089976600300014827](https://doi.org/10.1162/089976600300014827). eprint: <https://direct.mit.edu/neco/article-pdf/12/11/2519/814328/089976600300014827.pdf>. URL: <https://doi.org/10.1162/089976600300014827> (cit. on pp. 2, 3).
- Meunier, David et al. (2009). "Hierarchical modularity in human brain functional networks." In: *Frontiers in Neuroinformatics* 3. ISSN: 1662-5196. DOI: [10.3389/neuro.11.037.2009](https://doi.org/10.3389/neuro.11.037.2009). URL: <https://www.frontiersin.org/articles/10.3389/neuro.11.037.2009> (cit. on pp. 1, 4).
- Nessler, Bernhard et al. (Apr. 2013). "Bayesian Computation Emerges in Generic Cortical Microcircuits through Spike-Timing-Dependent Plasticity." In: *PLOS Computational Biology* 9.4, pp. 1–30. DOI: [10.1371/journal.pcbi.1003037](https://doi.org/10.1371/journal.pcbi.1003037). URL: <https://doi.org/10.1371/journal.pcbi.1003037> (cit. on pp. 1, 2, 12–14, 17, 23).
- Palmer, Stephen (Jan. 1999). *Vision Science: From Photons to Phenomenology*. Vol. 1, p. 153 (cit. on p. 5).
- Parr, Thomas and Karl J. Friston (2018). "The Anatomy of Inference: Generative Models and Brain Structure." In: *Frontiers in Computational Neuroscience* 12. ISSN: 1662-5188. DOI: [10.3389/fncom.2018.00090](https://doi.org/10.3389/fncom.2018.00090). URL: <https://www.frontiersin.org/articles/10.3389/fncom.2018.00090> (cit. on pp. 1, 6).
- Pouget, Alexandre et al. (Sept. 2013). "Probabilistic brains: knowns and unknowns." In: *Nature Neuroscience* 16.9, pp. 1170–1178. ISSN: 1546-1726.

- DOI: [10.1038/nn.3495](https://doi.org/10.1038/nn.3495). URL: <https://doi.org/10.1038/nn.3495> (cit. on p. 6).
- Riesenhuber, Maximilian and Tomaso Poggio (2002). "Neural mechanisms of object recognition." In: *Current Opinion in Neurobiology* 12.2, pp. 162–168. ISSN: 0959-4388. DOI: [https://doi.org/10.1016/S0959-4388\(02\)00304-5](https://doi.org/10.1016/S0959-4388(02)00304-5). URL: <https://www.sciencedirect.com/science/article/pii/S0959438802003045> (cit. on p. 5).
- Rodney J Douglas, Kevan A C Martin (2004). "Neuronal circuits of the neocortex." In: *Annual review of neuroscience* 27, pp. 419–451. DOI: [10.1146/annurev.neuro.27.070203.144152](https://doi.org/10.1146/annurev.neuro.27.070203.144152) (cit. on pp. 2, 3).
- Taherkhani, Aboozar et al. (2020). "A review of learning in biologically plausible spiking neural networks." In: *Neural Networks* 122, pp. 253–272. ISSN: 0893-6080. DOI: <https://doi.org/10.1016/j.neunet.2019.09.036>. URL: <https://www.sciencedirect.com/science/article/pii/S0893608019303181> (cit. on p. 10).