

\* one can postulate that the posterior is represented by the output of a neural network [cik]. The likelihood can be computed based on the sensory input to the network and the feedback....

## 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 the posterior is represented by the output of a neural network and the likelihood is represented by its input. The feedback from high-level to low-level cortical areas can be modelled as the prior probability.

There are various models for the computational simulation of neural networks (Gerstner and Kistler, 2002). The plasticity of neural networks is often

Discuss

Spiking neurons

First discuss briefly synaptic plasticity.

softWTA took about the occasion.

critical microcircuits

(Douglas & Martin)

Say that WTA was postulated as a

1 Introduction

key computational motif

modelled as Spike-timing-dependent plasticity (STDP), as it agrees with biological experiments (Feldman, 2012; Dan Yang, 2004).

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.

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.

Summarize what we do and the main results.

## 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 deeper layers of the cortex. 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 powerful compared to threshold gates (McCulloch-Pitts neurons) and sigmoidal gates. Furthermore, it was possible to approximate arbitrary continuous function by circuits that only contained 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 nature follows from the complex cell receiving input from many simple cells which is summed and integrated.



property

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 the 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 talked about 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)

then?

discussed



### 2.4 Probabilistic brain

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 TODO) 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).

*What is the connection to your work?*

### 2.5 Feedback in the visual cortex

*shows*

Lee TS (2003) shows 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 show 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 V1 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. ←

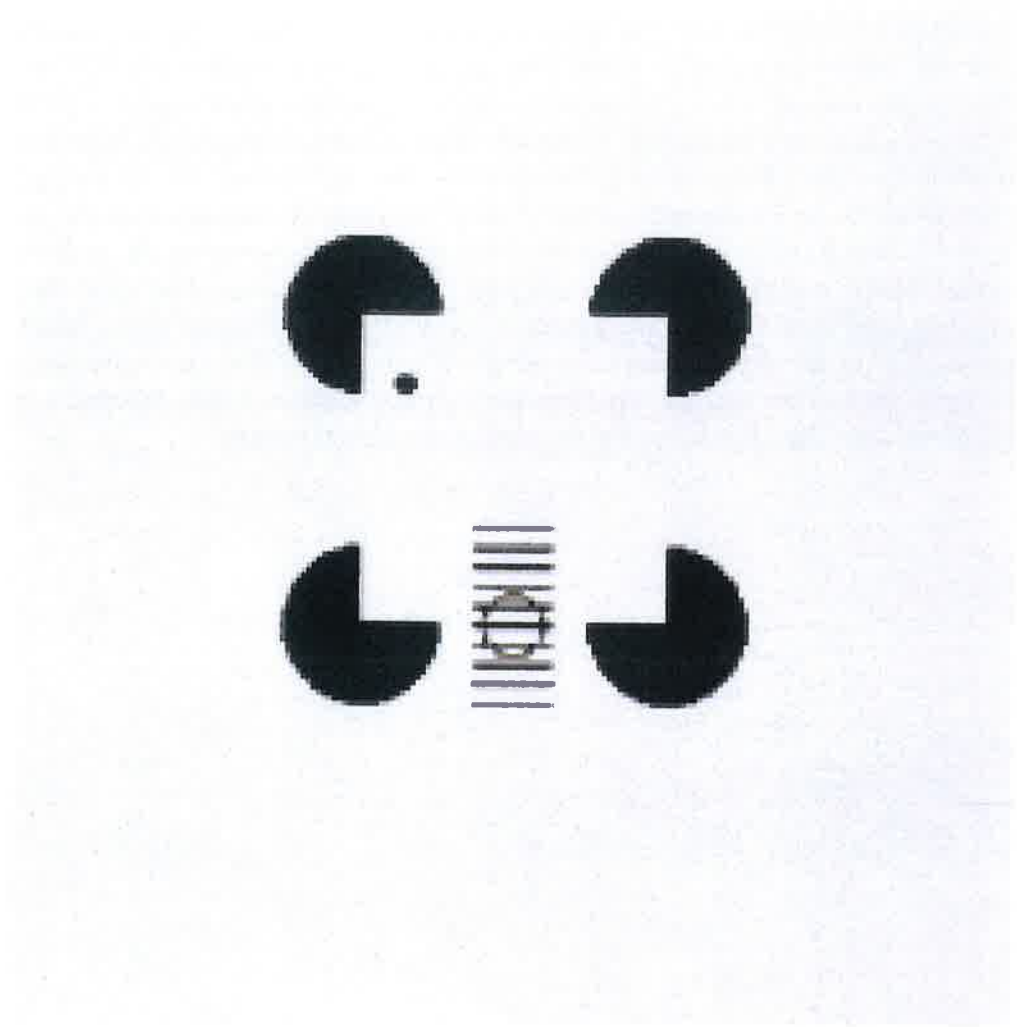


Figure 2.1: Kanizsa square shown to the monkey by Lee TS (2003)