

# Contents

|          |                                                                     |           |
|----------|---------------------------------------------------------------------|-----------|
| <b>1</b> | <b>Introduction</b>                                                 | <b>1</b>  |
| 1.1      | Structure, function and the cerebral cortex . . . . .               | 1         |
| 1.2      | Modularity and hierarchy for neural computation . . . . .           | 3         |
| 1.3      | Modular sensory pathways and topographic maps . . . . .             | 4         |
| 1.4      | Robust state representations from noisy sensory inputs . . . . .    | 5         |
| 1.5      | From discrete representations to sequence processing . . . . .      | 7         |
| 1.6      | Scope and structure of the thesis . . . . .                         | 8         |
| <b>2</b> | <b>Concepts and tools from computational neuroscience</b>           | <b>13</b> |
| 2.1      | Mathematical models of biological neurons . . . . .                 | 13        |
| 2.2      | Network dynamics and mean-field approximations . . . . .            | 15        |
| 2.3      | Neuroplasticity and learning . . . . .                              | 17        |
| 2.3.1    | Correlation-based (Hebbian) plasticity . . . . .                    | 17        |
| 2.3.2    | Neuromodulation, eligibility traces and three-factor learning rules | 18        |
| 2.3.3    | Short-term plasticity . . . . .                                     | 19        |
| 2.4      | Functional benchmarking using reservoir computing . . . . .         | 19        |
| 2.4.1    | End-to-end training . . . . .                                       | 19        |
| 2.4.2    | Transient dynamics and reservoir computing . . . . .                | 20        |
| 2.4.3    | Benchmarking biological neural circuits . . . . .                   | 21        |
| <b>3</b> | <b>Computational models of sequence processing</b>                  | <b>23</b> |
| 3.1      | Sequence complexity and experimental designs . . . . .              | 23        |
| 3.1.1    | Formal language theory and the Chomsky hierarchy . . . . .          | 24        |
| 3.1.2    | Artificial grammar learning . . . . .                               | 24        |
| 3.1.3    | Measures of sequence complexity . . . . .                           | 25        |
| 3.2      | Recurrent neural networks and formal languages . . . . .            | 27        |
| 3.3      | Biologically-constrained models . . . . .                           | 29        |
| 3.3.1    | Reproducing sequential activation patterns . . . . .                | 30        |
| 3.3.2    | Static chains and dynamical trajectories for sequence processing    | 30        |
| 3.3.3    | Processing complex stimulus sequences . . . . .                     | 33        |
| <b>4</b> | <b>Functional Neural Architectures</b>                              | <b>39</b> |
| 4.1      | Description of the toolkit . . . . .                                | 40        |
| 4.2      | Components . . . . .                                                | 42        |
| 4.2.1    | Task definitions as symbolic sequences . . . . .                    | 42        |

|          |                                                                                               |           |
|----------|-----------------------------------------------------------------------------------------------|-----------|
| 4.2.2    | Embeddings . . . . .                                                                          | 44        |
| 4.2.3    | Encoding . . . . .                                                                            | 44        |
| 4.2.4    | Network models . . . . .                                                                      | 45        |
| 4.2.5    | Decoder: state extraction and readouts . . . . .                                              | 45        |
| 4.2.6    | Analysis and visualization . . . . .                                                          | 47        |
| 4.3      | Example use case: simulation, analysis and visualization of a spiking network model . . . . . | 47        |
| 4.4      | Conclusions and scope of the toolkit . . . . .                                                | 50        |
| 4.4.1    | Related work . . . . .                                                                        | 50        |
| 4.4.2    | Limitations . . . . .                                                                         | 53        |
| <b>5</b> | <b>Random and structured connectivity for representation transfer</b>                         | <b>55</b> |
| 5.1      | Introduction . . . . .                                                                        | 56        |
| 5.2      | Network architecture and analysis methods . . . . .                                           | 57        |
| 5.2.1    | Network architecture . . . . .                                                                | 57        |
| 5.2.2    | Structured feedforward connectivity . . . . .                                                 | 59        |
| 5.2.3    | Neuron and synapse model . . . . .                                                            | 59        |
| 5.2.4    | Stimulus input and computational tasks . . . . .                                              | 60        |
| 5.2.5    | State space analysis . . . . .                                                                | 61        |
| 5.2.6    | Numerical simulations and analysis . . . . .                                                  | 62        |
| 5.3      | Simulation results . . . . .                                                                  | 63        |
| 5.3.1    | Sequential transmission of stimulus representation . . . . .                                  | 63        |
| 5.3.2    | Memory capacity and stimulus sensitivity . . . . .                                            | 69        |
| 5.3.3    | Integrating multiple input streams . . . . .                                                  | 71        |
| 5.4      | Discussion . . . . .                                                                          | 76        |
| 5.4.1    | Representation transfer in sequential hierarchies . . . . .                                   | 76        |
| 5.4.2    | Network architecture and input integration . . . . .                                          | 77        |
| 5.4.3    | Degree of mixed selectivity predicts computational performance . . . . .                      | 78        |
| 5.4.4    | Limitations and future work . . . . .                                                         | 79        |
| <b>6</b> | <b>Denoising through topographic modularity</b>                                               | <b>81</b> |
| 6.1      | Introduction . . . . .                                                                        | 81        |
| 6.2      | Numerical simulations and theoretical analysis . . . . .                                      | 82        |
| 6.2.1    | Sequential denoising through structured projections . . . . .                                 | 83        |
| 6.2.2    | Noise suppression and response amplification . . . . .                                        | 84        |
| 6.2.3    | E/I balance and asymmetric effective couplings . . . . .                                      | 86        |
| 6.2.4    | Modulating inhibition . . . . .                                                               | 88        |
| 6.2.5    | A generalizable structural effect . . . . .                                                   | 89        |
| 6.2.6    | Variable map sizes . . . . .                                                                  | 92        |
| 6.2.7    | Modularity as a bifurcation parameter . . . . .                                               | 93        |
| 6.2.8    | Critical modularity for denoising . . . . .                                                   | 96        |

|          |                                                                                                                               |            |
|----------|-------------------------------------------------------------------------------------------------------------------------------|------------|
| 6.2.9    | Input integration and multi-stability . . . . .                                                                               | 100        |
| 6.2.10   | Reconstruction and denoising of dynamical inputs . . . . .                                                                    | 103        |
| 6.3      | Methods . . . . .                                                                                                             | 105        |
| 6.3.1    | Network architecture . . . . .                                                                                                | 105        |
| 6.3.2    | Modular feedforward projections . . . . .                                                                                     | 105        |
| 6.3.3    | Neuron and synapse model . . . . .                                                                                            | 106        |
| 6.3.4    | Signal reconstruction task . . . . .                                                                                          | 107        |
| 6.3.5    | Effective connectivity and stability analysis . . . . .                                                                       | 108        |
| 6.3.6    | Fixed point analysis . . . . .                                                                                                | 109        |
| 6.3.7    | Critical modularity and relation to recurrent connectivity, back-ground input and single-neuron activation function . . . . . | 111        |
| 6.3.8    | Multiple inputs and correlation-based similarity score . . . . .                                                              | 112        |
| 6.3.9    | Numerical simulations and analysis . . . . .                                                                                  | 112        |
| 6.4      | Discussion . . . . .                                                                                                          | 112        |
| <b>7</b> | <b>Overcoming temporal compression during sequence learning</b>                                                               | <b>117</b> |
| 7.1      | Introduction . . . . .                                                                                                        | 117        |
| 7.2      | Methods . . . . .                                                                                                             | 118        |
| 7.2.1    | Network architecture . . . . .                                                                                                | 118        |
| 7.2.2    | Neuron model . . . . .                                                                                                        | 120        |
| 7.2.3    | Eligibility-based learning rule . . . . .                                                                                     | 121        |
| 7.2.4    | Stimulation protocol . . . . .                                                                                                | 122        |
| 7.2.5    | Numerical simulations and analysis . . . . .                                                                                  | 122        |
| 7.3      | Simulation results and reproducibility analysis . . . . .                                                                     | 122        |
| 7.3.1    | Sequence learning and recall . . . . .                                                                                        | 123        |
| 7.3.2    | Learning and recall precision . . . . .                                                                                       | 124        |
| 7.3.3    | Model robustness . . . . .                                                                                                    | 126        |
| 7.3.4    | Model scaling . . . . .                                                                                                       | 129        |
| 7.3.5    | Projections between all columns . . . . .                                                                                     | 131        |
| 7.3.6    | Alternative wiring with local inhibition . . . . .                                                                            | 133        |
| 7.4      | Discussion . . . . .                                                                                                          | 134        |
| 7.4.1    | Reproducibility . . . . .                                                                                                     | 135        |
| 7.4.2    | Learning cross-columnar projections . . . . .                                                                                 | 137        |
| 7.4.3    | Functional and neurophysiological considerations . . . . .                                                                    | 138        |
| <b>8</b> | <b>Benchmarking and critical evaluation of biologically-plausible models of sequence learning</b>                             | <b>141</b> |
| 8.1      | Introduction . . . . .                                                                                                        | 141        |
| 8.2      | Model selection . . . . .                                                                                                     | 142        |
| 8.2.1    | Implementation considerations . . . . .                                                                                       | 142        |

|          |                                                                            |            |
|----------|----------------------------------------------------------------------------|------------|
| 8.3      | Model evaluation and benchmarking . . . . .                                | 144        |
| 8.3.1    | Pattern perception . . . . .                                               | 144        |
| 8.3.2    | Rule learning . . . . .                                                    | 146        |
| 8.3.3    | Task evaluation . . . . .                                                  | 149        |
| 8.4      | Results . . . . .                                                          | 151        |
| 8.4.1    | Pattern perception . . . . .                                               | 151        |
| 8.4.2    | Rule learning . . . . .                                                    | 157        |
| 8.5      | Conclusion . . . . .                                                       | 165        |
| <b>9</b> | <b>Discussion and outlook</b>                                              | <b>169</b> |
| 9.1      | On the role of structured projections and topographic modularity . . . . . | 169        |
| 9.1.1    | Signal representation and denoising . . . . .                              | 170        |
| 9.1.2    | Integrating multiple information streams . . . . .                         | 171        |
| 9.1.3    | Beyond simplified models of cortical processing . . . . .                  | 172        |
| 9.2      | On biologically-plausible models for sequence processing . . . . .         | 174        |
| 9.2.1    | Functional considerations . . . . .                                        | 175        |
| 9.2.2    | Neurophysiological implications . . . . .                                  | 178        |
| 9.3      | On software tools and reproducibility . . . . .                            | 180        |
| 9.4      | On the role and value of computational studies . . . . .                   | 181        |
|          | <b>Bibliography</b>                                                        | <b>183</b> |
| <b>A</b> | <b>Supplementary materials for Chapter 5</b>                               | <b>225</b> |
| A.1      | Supplementary figures . . . . .                                            | 225        |
| A.2      | Supplementary tables . . . . .                                             | 227        |
| <b>B</b> | <b>Supplementary materials for Chapter 6</b>                               | <b>229</b> |
| B.1      | Supplementary figures . . . . .                                            | 229        |
| B.2      | Supplementary tables . . . . .                                             | 238        |
| B.3      | Constraints on feedforward connectivity . . . . .                          | 243        |
| B.4      | Mean-field analysis of network dynamics . . . . .                          | 244        |
| <b>C</b> | <b>Supplementary materials for Chapter 7</b>                               | <b>255</b> |
| C.1      | Supplementary figures . . . . .                                            | 255        |
| C.2      | Parameters of the baseline model . . . . .                                 | 257        |
| C.3      | Parameters of the scaled model . . . . .                                   | 260        |
|          | <b>List of Figures</b>                                                     | <b>263</b> |
|          | <b>List of Tables</b>                                                      | <b>265</b> |