

# NEUR0016

## Neural computation: Models of brain function

### 2021 timetable.

Module organisers: Prof. Caswell Barry & Prof. Neil Burgess

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#### **Contact details**

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Further course information available on Moodle.

# NEUR0016 – 15 credit

## Module aims and objectives

### Aims

1. To introduce the consideration of neurons and synapses in terms of their computational properties and interpretation of their action in terms of information processing.
2. To introduce the analysis of an animal's ability to learn, remember or act in terms of the action of neurons and synapses within the animal's nervous system.
3. To understand several examples of how the action of individual neurons and synapses in various parts of the central nervous system contribute to the learning, memory or behaviour of an organism.

### Method of assessment

#### NEUR0016 is a 15 credit module

Undergraduate BSc and 4<sup>th</sup> year MSci students: *Coursework essay* analysing a research paper, max. 2000 words. Papers for your essay available on the Moodle site and listed at the end of this booklet. You will make a 5 min presentation about a paper to get feedback (not marked) in weeks 12, 13 or 14. The essay mark constitutes 10% of the final mark for the course.

*Final assessment* constitutes the remaining 90% of the mark for the course. This was a 3 hour exam (pre-covid) or an open book essay (2500 words) for 3<sup>rd</sup> year BSc or 4<sup>th</sup> year MSci students.

MSc students, and affiliate students (leaving before May): One 3,000 word essay, chosen from these titles:

Can a mechanistic neuron-level understanding of some aspects of cognition be attained?

Discuss the approximations made in computational approaches to understanding the functional properties of networks of neurons, including when and how they have proved to be useful.

Describe examples where understanding of the electrophysiological behaviour of neurons allows increased understanding of the behaviour of the organism.

The deadline for essays is 2.00pm Tuesday January 11<sup>th</sup> 2022.

# NEUR0016 Neural computation: Models of brain function

## Provisional Timetable Autumn 2021

3 hours/week. 2 hrs for watching recorded lectures on Moodle 9-11 Fridays (and Weds 6/10).

1 hr (11 or 12) Wednesdays: Live Q&A or student presentations, face to face (will be recorded).

Day	Time	Subject	Lecturer	Location	Week
Wed 6 Oct	11:00– 12:00	Intro to artificial neural networks & unsupervised learning.	Prof Neil Burgess	Moodle <recorded>	6
Fri 8 Oct	9:00– 10:00	Intro to artificial neural networks & unsupervised learning.	Prof Neil Burgess	Moodle <recorded>	6
	10:00– 11:00	Intro to artificial neural networks & unsupervised learning, cont.	Prof Neil Burgess	Moodle <recorded>	
Wed 13 Oct	11:00– 12:00	Q&A (group 1)	Prof Neil Burgess	F2F: Archaeology G6 LT (will be recorded)	7
	12:00– 13:00	Q&A (group 2)	Prof Neil Burgess		
Fri 15 Oct	9:00– 10:00	Simple supervised learning in artificial neural networks.	Prof Neil Burgess	Moodle <recorded>	7
	10:00– 11:00	More advanced learning algorithms in artificial neural networks.	Prof Neil Burgess	Moodle <recorded>	
Wed 20 Oct	11:00– 12:00	Q&A (group 1)	Prof Neil Burgess	F2F: Archaeology G6 LT (will be recorded)	8
	12:00– 13:00	Q&A (group 2)	Prof Neil Burgess		
Fri 22 Oct	9:00– 10:00	More advanced learning algorithms in artificial neural networks, cont.	Prof Neil Burgess	Moodle <recorded>	8
	10:00– 11:00	Computational properties of individual neurons	Prof David Attwell	Moodle <recorded>	
Wed 27 Oct	11:00– 12:00	Q&A (group 1)	Prof Neil Burgess	F2F: Archaeology G6 LT (will be recorded)	9
	12:00– 13:00	Q&A (group 2)	Prof Neil Burgess		
Fri 29 Oct	9:00– 10:00	The hippocampus and spatial representation	Prof Caswell Barry	Moodle <recorded>	9
	10:00– 11:00	Hippocampal and striatal navigation.	Prof Caswell Barry	Moodle <recorded>	
Wed 3 Nov	11:00– 12:00	Q&A (group 1)	Prof Caswell Barry	F2F: Archaeology G6 LT (will be recorded)	10
	12:00– 13:00	Q&A (group 2)	Prof Caswell Barry		

Fri 5 Nov	9:00– 10:00	Reinforcement learning.	Prof Neil Burgess	Moodle <recorded>	10
	10:00– 11:00	Reinforcement learning, cont.	Prof Neil Burgess	Moodle <recorded>	

**Week 11 = Reading Week.**

Wed 17 Nov	11:00– 12:00	Q&A (group 1)	Prof Neil Burgess	F2F: Archaeology G6 LT (will be recorded)	12
	12:00– 13:00	Q&A (group 2)	Prof Neil Burgess		
Fri 19 Nov	9:00– 10:00	Path integration, continuous attractors and grid cells.	Prof Caswell Barry	Moodle <recorded>	12
	10:00– 11:00	Learning, performing & remembering serially ordered actions.	Prof Caswell Barry	Moodle <recorded>	
Wed 24 Nov	11:00– 12:00	Student presentation of essay papers (group 1)		F2F: various locations or Zoom <live>	13
	12:00– 13:00	Student presentation of essay papers (group 2)			
Fri 26 Nov	9:00– 10:00	Hippocampus and associative memory	Prof Caswell Barry	Moodle <recorded>	13
	10:00– 11:00	Hippocampus and associative memory, cont.	Prof Caswell Barry	Moodle <recorded>	
Wed 1 Dec	11:00– 12:00	Student presentation of essay papers (group 1)		F2F: various locations or Zoom <live>	14
	12:00– 13:00	Student presentation of essay papers (group 2)			
Fri 3 Dec	9:00– 10:00	Spatial processing in the spine and motor cortex.	Prof Caswell Barry	Moodle <recorded>	14
	10:00– 11:00	Model(s) of conscious awareness	Prof Neil Burgess	Moodle <recorded>	
Wed 8 Dec	11:00– 12:00	Q&A (group 1)	Prof Caswell Barry	F2F: Archaeology G6 LT (will be recorded)	15
	12:00– 13:00	Q&A (group 2)	Prof Caswell Barry		
Fri 10 Dec	9:00– 10:00	Temporal processing in audition and olfaction.	Prof Caswell Barry	Moodle <recorded>	15
	10:00– 11:00	Computing with spike timing and delays.	Prof Neil Burgess	Moodle <recorded>	
Wed 15 Dec	11:00– 12:00	Q&A (group 1)	Prof Caswell Barry	F2F: Archaeology G6 LT (will be recorded)	16
	12:00– 13:00	Q&A (group 2)	Prof Caswell Barry		

## **General reading list**

**General:** Fundamentals of Computational Neuroscience by Thomas Trappenberg (OUP, 2002)

### **Artificial Neural Networks:**

1. An Introduction to Neural Networks, James A. Anderson (MIT Press, 1995);
2. An Introduction to Neural Networks, Kevin Gurney (UCL Press, 1997);
3. Parallel Distributed Processing I: Foundations, Rumelhart, DE and McClelland, JL (Eds.) (MIT Press, 1986).
4. Parallel Distributed Processing II: Psychological and Biological Models. McClelland, JL and Rumelhart, DE (Eds.) (MIT Press, 1986).
5. Neural Networks for Control Miller W, Sutton R, Werbos P, (MIT Press, 1995)
6. Reinforcement Learning: An Introduction, Sutton & Barto 2<sup>nd</sup> Ed. (2018)
7. Genetic programming : on the programming of computers by means of natural selection. Koza JR (MIT press, 1992).
8. Self-Organisation and Associative Memory. Kohonen T (Springer Verlag, 1989).

### **Biological neural networks:**

9. The synaptic organisation of the brain. Shepard GM (Oxford University Press, 1979).
10. The computational brain. Churchland PS and Sejnowski TJ (MIT press, 1994)
11. The computing neuron. Durbin R, Miall C and Mitchison G (Addison Wesley, 1989).

### **Models of brain systems/ systems neuroscience:**

12. The handbook of brain theory and neural networks. Arbib MA (ed) (MIT Press 1995)
13. The cognitive neurosciences. Gazzaniga MS (ed) (MIT Press 1995)
14. The hippocampal and parietal foundations of spatial cognition. Burgess N, Jeffery KJ and O'Keefe J (eds) (OUP 1999).

### **Computational Neuroscience** (includes most things, but v. v. mathematical)

15. Theoretical Neuroscience: Computational and Mathematical Modeling of Neural Systems. Peter Dayan and L. F. Abbott (MIT, 2001).
16. Introduction to the Theory of Neural Computation. Hertz J, Krogh P and Palmer RG, (Addison Wesley, 1991).

## Specific reading lists

For students interested in the details of a particular lecture (lecturers may also give additional references during the lecture).

### Introduction to artificial neural networks and unsupervised learning.

- Books 1,2,8.
- Rumelhart DE & Zipser D (1986) 'Feature discovery by competitive learning', in: Rumelhart D E and McClelland J L (Eds.) *Parallel Distributed Processing* 1 151-193 MIT Press.
- Sharp P E (1991) 'Computer simulation of hippocampal place cells', *Psychobiology* 19 103-115.
- Kohonen T (1982) 'Self-organised formation of topologically correct feature maps' *Biological Cybernetics* 43 59-69.

### Simple supervised learning in artificial neural networks

- Books 1,2,5.

### More advanced learning algorithms in artificial neural networks

- Books 1,2,4,6
- Rumelhart D E, Hinton G E & Williams R J, (1986) 'Learning internal representations by error propagation', In Rumelhart, D. E. and McClelland, J. L. (Eds.) *Parallel Distributed Processing*, 1 151-193 MIT Press.
- Patarnello S & Carnevali P (1989) 'A neural network model to simulate a conditioning experiment' *Int. J. Neural Systems* 1 47-53.
- Barto A G & Sutton R S (1981) 'Landmark learning: an illustration of associative search', *Biological Cybernetics* 42 1-8.

### Computational properties of neurons

- Books 8,9,10.

### Spatial processing in the spine and motor cortex

- Bizzi E, Giszter S F, Loeb E, MussaIvaldi F A, Saltiel P (1995) 'Modular organization of motor behavior in the frogs spinal-cord' *Trends in Neurosciences* 18 442-446.
- Georgopoulos A P, Kettner R E & Schwartz A B (1988) 'Primate motor cortex and free arm movements to visual targets in three-dimensional space. II. Coding of the direction of movement by a neuronal population', *J. Neurosci.* 8 2928-2937.
- Lukashin A V, Amirikian B R, Georgopoulos A P (1996) 'A simulated actuator driven by motor cortical signals' *Neuroreport* 7 2597-2601.

### The hippocampus and spatial representation

- Book 13
- Sharp P E (1991) 'Computer simulation of hippocampal place cells', *Psychobiology* 19 103-115.
- Hartley T., Burgess N., Lever C., Cacucci F., O'Keefe J. (2000) Modeling place fields in terms of the cortical inputs to the hippocampus. *Hippocampus* 10 369-379.

### Path integration, continuous attractors & grid cells

- Etienne & Jeffery 2004 Path integration in mammals. *Hippocampus*. 14:180-92.
- Zhang 1996 Representation of spatial orientation by the intrinsic dynamics of the head-direction cell ensemble: a theory. *J Neurosci* 16: 2112-2126.
- Samsonovich and McNaughton 1997 Path integration and cognitive mapping in a continuous attractor neural network model. *J Neurosci* 17: 5900-5920.
- Hafting et al., 2005 Microstructure of a spatial map in the entorhinal cortex. *Nature* 436: 801-806.
- Jeffery and Burgess 2006 A Metric for the Cognitive Map: Found at last? *Trends in Cognitive Science* 10 1-3.

### Hippocampal and striatal navigation

- Brown M A & Sharp P E (1995) 'Simulation of spatial-learning in the morris water maze by a neural-network model of the hippocampal-formation and nucleus-accumbens' *Hippocampus* 5 171-188.
- Burgess N, Donnett J G, Jeffery K J & O'Keefe J (1997) 'Robotic and neuronal simulation of the hippocampus and rat navigation', *Philosophical Transactions of the Royal Society, B* 352 1535-1543.

#### The hippocampus and associative memory

- Willshaw D J & Buckingham J T (1990) 'An assessment of Marr's theory of the hippocampus as a temporary memory store', *Phil. Trans. Roy. Soc. Lond. B*, 329 205-215.
- McNaughton B L & Morris R G M (1987) 'Hippocampal synaptic enhancement and information storage in a distributed memory system' *Trends in Neurosciences* 10 408-414.
- Wills et al. (2005) 'Attractor dynamics in the hippocampal representation of the local environment.' *Science* 308 873-876.

#### Reinforcement learning

- Barto A G & Sutton R S (1981) 'Landmark learning: an illustration of associative search', *Biological Cybernetics* 42 1-8.
- Schultz W, Dayan P & Montague PR (1997) 'A neural substrate of prediction and reward' *Science* 275 1593-1599.
- See also Book 14, chapter 9.
- Mnih et al "Human-level control through deep reinforcement learning" *Nature* (2015)  
*doi:10.1038/nature14236*

#### Learning, performing and remembering serially ordered actions

- Elman J L (1990) 'Finding structure in time', *Cognitive Science* 14 179-211.
- G Houghton & T Hartley (1996) 'Parallel Models of Serial Behaviour: Lashley Revisited' *PSYCHE*, 2(25). <http://psyche.cs.monash.edu.au/v2/psyche-2-25-houghton.html>
- Houghton G & Tipper S P (1996) 'Inhibitory mechanisms of neural and cognitive control: application to selective attention and sequential action' *Brain and Cognition* 30 20-43.
- Burgess N & Hitch G J (1999) 'Memory for Serial Order: A Network Model of the Phonological Loop and its Timing', *Psychological Review*, 106 551-581.
- D Bullock (2004) 'Adaptive neural models of queuing and timing in fluent action' *Trends Cog. Sci.* 426-33

#### Temporal processing: Models of audition and olfaction

- Konishi M 'Neural mechanisms of auditory image formation' in: *The Cognitive Neurosciences* Ed: M S Gazzaniga (MIT press, 1995)
- Gerstner W, Kempter R, Van Hemmen J L, Wagner H (1996) 'A neuronal learning rule for submillisecond temporal coding' *Nature* 383 76-78.
- Ambros-Ingerson J, Granger R, Lynch G (1990) 'Simulation of paleocortex performs hierarchical-clustering' *Science* 247 1344-1348

#### Model(s) of conscious awareness

- Mathis, D.W. and Mozer, M.C. (1995), "On the computational utility of consciousness", *Neural Information Processing Systems*, Volume 7, pages 11-18. (<https://papers.nips.cc/paper/1994>)
- Lamme VAF (2006) "Towards a true neural stance on consciousness" *Trends in Cognitive Sciences*, 10: 494-501

#### Computing with spike timing and delay

- Sejnowski TJ (1995) 'Pattern recognition - time for a new neural code'. *Nature* 376 21-22.
- Hopfield J J (1995) 'Pattern-recognition computation using action-potential timing for stimulus representation' *Nature* 376 33-36.

# Objectives

*By the end of the following lectures the students should be able to:*

*Introduction to artificial neural networks and unsupervised learning (3hrs)*

- Understand simple mathematical models of how a neuron's firing rate depends on the firing rates of the neurons with synaptic connections to it.
- Describe how Hebbian learning rules relate change in synaptic weights to the firing rates of the pre- and post-synaptic neurons.
- Describe how application of these rules can lead to self-organisation in artificial neural networks.
- Relate self-organisation in artificial neural networks to organisation of the brain, such as in topographic maps.
- Explain how Hebbian learning in recurrent connections between neurons can create an associative memory.

*Artificial neural networks, simple supervised learning (1 hr)*

- Describe how a set of examples of stimuli and correct responses can be used to train an artificial neural network to respond correctly via changes in synaptic weights governed by the firing rates of the pre- and post-synaptic neurons and the correct post-synaptic firing rate.
- Describe how this type of learning rule is used to perform pattern classification in a Perceptron.

*More advanced learning algorithms in artificial neural networks (2 hrs)*

- Discuss the limitation of simple supervised learning algorithms such as the Perceptron, and the use of multi-layered networks to overcome them.
- Explain the problems posed to learning by the credit assignment problems caused by correct responses not being provided for each neuron, or for each stimulus.
- Discuss how reinforcement learning and genetic algorithms overcome the problems of temporal credit assignment and how error back-propagation and the use of forward models can overcome the problem of credit assignment for neurons contributing indirectly to the network's output.
- Discuss the relative biological plausibility of these learning algorithms

*Computational properties of neurons (1 hr)*

- Discuss how information can be coded by a neuron's membrane potential as graded potentials or action potentials.
- Explain how processing of synaptic signals as graded potentials allows the operations of addition, subtraction, multiplication and division to be carried out by an individual neuron.

*Spatial processing in the spine and motor cortex (1 hr).*

- Explain the idea of a 'convergent force field' and how the combination of a small number of these could be used to control limb movements to an arbitrary end point.
- Understand how a large number of broadly tuned neurons can provide an accurate code via their net 'population vector'.
- Discuss how the spine and motor cortex together could control movement, with motor cortex providing a population vector of reaching direction and the spine solving the complex transformation to muscle tensions by producing convergent force fields.

*The hippocampus and associative memory (2 hrs)*

- Understand how an associative memory matrix stores information by switching synapses on such that a pattern of activation in the output is reproduced by representation of the pattern of

activation in the inputs.

- Explain what is meant by the terms content-addressable, pattern completion, error correction, interference, hetero-association and auto-association.
- Describe how the Chadwick of the hippocampal region CA3 is consistent with a role as an associative memory matrix.

#### *The hippocampus and spatial representation (1 hr)*

- Explain how unsupervised competitive learning could lead to the formation of location-specific firing in hippocampal 'place cells', and how the rat's movement during learning would determine the effect the rat's orientation has on their firing rates (Sharp, 1991).
- Discuss Sharp's model & subsequent expts. Inputs sensitive to the distance of landmarks appear to be present (O'Keefe & Burgess, 1996), but place cell firing is probably non-directional to start with (not learned) & a fixed feed-forward model is sufficient to model the firing of cells (Hartley et al., 2000; Zipser, 1986). Synaptic plasticity may be required, but for stability and robustness of place cell representation (Kentros et al., 2000; Nakazawa et al., 2002).

#### *Path integration, continuous attractors & grid cells (1 hr)*

- Understand the idea of path integration, and how it might contribute to navigation and place cell firing.
- Discuss the continuous attractor model of place cell firing
- Describe the firing pattern of grid cells in entorhinal cortex and why they might be suitable to produce the path integration input to place cells.

#### *Hippocampal and striatal navigation (1 hr)*

- Describe how place cells could be used as a spatial memory for the proximity of a goal by synaptic change at the goal location.
- Describe how routes to a goal could be learned by modifying connections between the hippocampus and nucleus accumbens (Brown & Sharp, 2000), including the relevance of the limitations of perceptrons to linearly-separable functions and the problem of temporal credit-assignment

#### *Reinforcement learning (2 hrs)*

- Discuss formal models of classical and instrumental conditioning in animals
- Describe how reinforcement learning (e.g. using the temporal difference learning rule) solves the 'temporal credit assignment' problem in learning to act from infrequent reward.
- Describe how the involvement of neuromodulators, such as dopamine, in reward and punishment learning is included in these models.

#### *Learning, performing and remembering serially ordered actions (1 hr)*

- Explain how asymmetric recurrent connections can be used to learn a chain of association.
- Discuss the limitation of associative chaining as a model for response selection.
- Describe the competitive queuing model of response selection, and how it applies to human short-term memory for serial order.

#### *Temporal processing: Models of audition and olfaction (1 hr)*

- Understand how delay lines and coincidence detection can be used to produce responses tuned to inputs with specific time differences.
- Explain how the auditory system of the Barn Owl can detect inter-aural time differences and use this information to determine the azimuthal angle of a sound
- Describe how the rat olfactory system solves the problem of detecting weak odours masked by the presence of strong odours.

*Model(s) of conscious awareness (1 hr)*

- Understand the different temporal durations required for stimuli to enter consciousness.
- Discuss some examples of the detection of information in the brain that is not available for conscious report (e.g. subliminal priming, skin conductance responses, blindsight).
- Explain how a model of modules with fast feed-forward processing and slower relaxation to attractor states could explain some of the differences between unconscious and conscious processing.

*Using spike timing and delays (1 hr)*

- Discuss the problems of the standard models using firing-rates and synaptic weights have encoding both absolute and relative sizes of stimuli.
- Describe the alternative model of using spike timing with respect to an oscillatory potential and delay lines to encode information.
- Discuss the biological plausibility and functional advantages and disadvantages of this model.

## **Essay subject matter:**

1. Evolution of Artificial Neural Networks, by S. Nolfi & D. Parisi (p. 418-421), and Evolution and Learning in neural networks, by S. Nolfi (p.418-418) in *The Handbook of Brain Theory and Neural Networks* 2<sup>nd</sup> ed (Ed: MA Arbib) MIT Press (2002).
2. The Upstart Algorithm: a method for constructing and training feed-forward neural networks. M Freat (1990) *Neural Computation* 2 189-209.
3. Population coding of shape in area V4. A Pasupathy & CE Connor (2003) *Nature Neuroscience* 5 1332-1338.
4. Simulations of neuromuscular control in lamprey swimming. O Ekeberg and S Grillner (1999) *Phil.Trans. R. Soc. Lond. B* 354, 895-902.
5. The timing game. L. F. Abbott (2001) *Nature Neuroscience* 4 115-116.
6. Synaptic Learning Models of Map Separation in the Hippocampus. Mark C. Fuhs, David S. Touretzky (2000) *NeuroComputing* 32 379-384.
7. Storage of 7+-2 short-term memories in oscillatory sub-cycles. J E Lisman M A P Idiart (1995) *Science* 267 1512-1515.
8. A back-propagation programmed network that simulates response properties of a subset of posterior parietal neurons, Zipser D & Andersen RA (1988) *Nature* 331 679-684.
9. A model of spatial recall, mental imagery and neglect. Becker S., Burgess N. (2001) *Neural Information Processing Systems* 13 96-102.