NEUR0016
Neural computation: Models of brain function
2019 timetable.

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

-

Contact details

Prof. Caswell Barry: caswell.barry@ucl.ac.uk

Prof. Neil Burgess: n.burgess@ucl.ac.uk

Further course information available on:

https://www.ucl.ac.uk/icn/neur0016-neural-computation-models-brain-function

Please note that up to date (i.e. not provisional) room assignments are provided on the common timetable – you would be wise to check rooms have not changed prior to each lecture:

https://timetable.ucl.ac.uk/tt/moduleTimet.do?firstReq=Y&moduleId=NEUR0016

NEUR0016 – 15 credit (formerly a 'half unit' course).

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 4th year MSci students: There is a course essay and a 3 hour exam. The course essay consists of analysing a research paper, max. 2,000 words. Papers for essay available on: https://www.ucl.ac.uk/icn/neur0016-neural-computation-models-brain-function. The essay constitutes 10% of the final mark for the course. The exam constitutes the remaining 90% of the final mark for the course.

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 14th 2020.

NEUR0016 Neural computation: Models of brain function

Provisional Timetable Autumn 2019

Lectures: Wednesday 11-1 and Friday 10-11. NB the order/topic of lectures may change.

Day	**Time**	**Subject**	**Lecturer**	**Venue**	**Week**
11 Oct	10:00 – 11:00	Introduction to artificial neural networks & unsupervised learning.	Prof. Neil Burgess	Drayton House B03 Ricardo LT	7
16 Oct	11:00 – 12:00	Intro to artificial neural networks & unsupervised learning, cont.	Prof. Neil Burgess	Taviton (16) 347	8
	12:00 – 13:00	Intro to artificial neural networks & unsupervised learning, cont	Prof. Neil Burgess		
18 Oct	10:00 – 11:00	Artificial neural networks, feedback & simple supervised learning.	Prof. Neil Burgess	Drayton House B03 Ricardo LT	8
23 Oct	11:00 – 12:00	More advanced learning algorithms in artificial neural networks.	Prof. Neil Burgess	Taviton (16) 347	9
	12:00 – 13:00	More advanced learning algorithms in artificial neural networks, cont.	Prof. Neil Burgess		
25 Oct	10:00 – 11:00	The hippocampus and spatial representation	Dr Andrej Bicanski	Drayton House B03 Ricardo LT	9
30 Oct	11:00 – 12:00	Computational properties of individual neurons	David Attwell	Taviton (16) 347	10
	12:00 – 13:00	Neural bases of sensory decision making.	Prof Peter Latham		
1 Nov	10:00 – 11:00	Hippocampal and striatal navigation.	Prof Caswell Barry	Drayton House B03 Ricardo LT	10
		Reading Week			11

13 Nov	11:00 – 12:00	Hippocampus and associative memory	Dr Andrej Bicanski	Taviton (16) 347	12
	12:00 – 13:00	Hippocampus and associative memory	Dr Andrej Bicanski		
15 Nov	10:00 – 11:00	Path integration, continuous attractors and grid cells.	Dr Daniel Bush	Drayton House B03 Ricardo LT	12
20 Nov	11:00 – 12:00	Reinforcement learning.	Prof. Neil Burgess	Taviton (16) 347	13
	12:00 – 13:00	Reinforcement learning, cont.	Prof. Neil Burgess		
22 Nov	10:00 – 11:00	Learning, performing and remembering serially ordered actions.	Prof Caswell Barry	Drayton House B03 Ricardo LT	13
27 Nov	11:00 – 12:00	Spatial processing in the spine and motor cortex.	Prof Caswell Barry	Taviton (16) 347	14
	12:00 – 13:00	Temporal processing in audition and olfaction.	Prof Caswell Barry		
29 Nov	10:00 – 11:00	Filtering and normalization in sensory systems.	Prof Matteo Carandini	Drayton House B03 Ricardo LT	14
4 Dec	11:00 – 12:00	Theories of the cerebellum	Dr Peter Gilbert	Taviton (16) 347	15
	12:00 – 13:00	Models of prefrontal cortex.	Dr Sam Gilbert		
6 Dec	11:00 – 12:00	Computing with spike timing and delays; course review.	Prof. Neil Burgess	Drayton House B03 Ricardo LT	15

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. Perceptrons Minsky M, Papert S (MIT Press, 1969).
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.
- Udin S B, Fawcett J W (1988) `Formation of topographic maps' Annual Review of Neuroscience 11 289-327
- Linsker R (1986) `From basic network principles to neural architecture' Proc. Nat. Acad. Sci. USA 83 7508-7512.

Artificial neural networks, feedback & simple supervised learning

- Books 1,2,5.

Computational properties of neurons

- Books 8,9,10.

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.

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.

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

Models of prefrontal cortex

- Cohen, J.D. Braver, T.S., & O'Reilly, R.C. (1996). A computational approach to prefrontal cortex, cognitive control and schizophrenia: recent developments and current challenges. Philosophical Transactions of the Royal Society of London B: Biological Sciences, 351(1346):1515-27.

(This is also reprinted as chapter 14 of: Roberts, A.C., Robbins, T.W., & Weiskrantz, L. (1998). The Prefrontal Cortex: Executive and Cognitive Functions. OUP.)

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

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.

Filtering and normalization in sensory systems

- Carandini M (2012) From circuits to behavior: a bridge too far? Nat Neurosci 15:507-509.
- Carandini M & Heeger DJ (2012) Normalization as a canonical neural computation. Nature Reviews Neuroscience, 13: 51-62.

Theories of the cerebellum

- Dean P, Porrill J, Ekerot C and Jörntell H (2010) "The cerebellar microcircuit as an adaptive filter: experimental and computational evidence" Nature Reviews Neuroscience 11 30-43

Neural bases of sensory decision making

- Gold JI and Shadlen MN (2001) Neural computations that underlie decisions about sensory stimuli. TRENDS in Cognitive Sciences 5 10-16.
- Shadlen MN and Newsome WT (2001) Neural Basis of a Perceptual Decision in the Parietal Cortex (Area LIP) of the Rhesus Monkey. J Neurophysiol 86 1916-36.

Objectives

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

Introduction to artificial neural networks and unsupervised learning (2hrs)

- 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.

Artificial neural networks, feedback & simple supervised learning (2 hr)

- Explain how Hebbian learning in recurrent connections between neurons can create an associative memory.
- 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 recognition in a perceptron.

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.

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

- 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

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

- Explain the idea of a 'convergent force field' and how the combination of a small number of these could 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 (1hr)

- 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 wt 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

Models of prefrontal cortex (1 hr)

- Discuss computational and behavioral studies of contextual control deficits in Schizophrenia and frontal lobe patients, e.g. in the Stroop task.
- Explain a computational hypothesis for the impairment of Schizophrenics and frontal lobe patients in override automatic but inappropriate response tendencies.

Reinforcement learning (2hrs)

- Discuss formal models of classical and instrumental conditioning in animals
- 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 (1hr)

- 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 (1hr)

- 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.

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.

Filtering and normalization in sensory systems (1 hr)

- Describe the concept of linear receptive fields in multiple sensory modalities.
- Describe the concept of divisive normalization in multiple sensory modalities.
- Describe the advantages and disadvantages of thinking about sensory processing in computational terms.

Theories of the cerebellum (1hr)

- <u>Cerebellar circuitry</u>: Parallel and climbing fibre inputs to Purkinje cells. Influence on movement via cerebellar nuclei.
- <u>Marr's theory and motor learning</u>: Purkinje cells receive cerebral teaching signals for movements via climbing fibres; contexts via parallel fibres. Parallel fibre synapses on P-cells modifiable when climbing fibre fires. Memory capacity of P-cells.
- <u>Albus</u> LTD at parallel fibre synapses on P-cells, basket cells and stellate cells.
- <u>Gilbert</u> Group of P-cells as the memorizing unit. Variable frequencies learned by P-cells (as opposed to binary outputs of Marr and Albus). How muscular actions are coordinated. Potential second teaching input to P-cells via the noradrenergic input.
- <u>D'Angelo and De Zeeuw</u> Granular layer plasticity: potential role in cerebellar learning.
- <u>Rhythmic activity in the cerebellum</u>: possible role in "binding" of complex contexts and in temporal sequencing of movements.
- <u>Experimental testing of the theories</u>. LTD in cerebellum. Output of P-cells during learning of movements. On-beam synchrony in parallel fibres of cerebellum.

Neural bases of sensory decision making (1 hr)

- Describe the experiment of Shadlen and Newsome (2001) and how it sheds light on sensory decision making such as the direction of motion of a visual stimulus.
- Understand how the neural responses in the lateral intraparietal area (LIP) appear to be weighing the evidence behind a decision about sensory stimuli.

Essay subject matter:

1. Evolution and Learning. S. Nolfi; Evolution of Artificial Neural Networks S. Nolfi & D Parisi (2002) Handbook of Brain Theory and Neural Networks 2nd edition (Ed: MA Arbib) MIT press.
2. The Upstart Algorithm: a method for constructing and training feed-forward neural networks. M Frean (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. Zipser D & Andersen R A (1988) A back-propagation programmed network that simulates response properties of a subset of posterior parietal neurons, Nature 331 679-684.