Syllabus — Final Version
Computational Models of Neural Systems
15-880(B) Spring '95
Version of 4 May 1995 00:57

David S. Touretzky

Daggers † signify required readings; bulleted items • are lecture summaries or optional readings.

1. Introduction to Computational Neuroscience

1.1 What is Computational Neuroscience? [Tue. January 17]

† Barinaga, M. (1990) Neuroscience models the brain. *Science* **247**:524-526.

† Sejnowski, T. J., Koch, C., and Churchland, P. S. (1990) Computational neuroscience. In S. J. Hanson and C. R. Olson (eds.), *Connectionist Modeling and Brain Function,* chapter 2, pp. 5–35. MIT Press. (An earlier version appeared in *Science* **241**:1299–1306.)

† Churchland, P. S. and Sejnowski, T. J. (1988) Perspectives on cognitive neuroscience. *Science* **242**:741-745.

1.2 Brains and Computation [Thu. January 19]

• Lecture: summary of Churchland and Sejnowski's *The Computational Brain*, chapters 2-3.

What physical processes qualify as "computation"?
What are the distinctive features of brains as computing devices?

† Churchland, P. S. (1986) *Neurophilosophy: Toward a Unified Science of the Mind-Brain*. Chapter 3, Functional Neuroanatomy, sections 3.1 and 3.2, pp 99–107. MIT Press.

† Crick, F. and Asanuma, C. (1986) Certain aspects of the anatomy and physiology of the cerebral cortex. In J. L. McClelland and D. E. Rumelhart (eds.), *Parallel Distributed Processing*: *Explorations in the Microstructure of Cognition*, vol. II, chapter 20, pp. 333–371. MIT Press.

****Note: The above two readings are not required for anyone who has had Neuroscience 3.*

• Cherniak, C. (1990) The bounded brain: toward quantitative neuroanatomy. *Journal of Cognitive Neuroscience* **2**:58-68.

1.3 Neurophysiology for Computer Scientists [Tue. January 24]

† Churchland, P.S. (1986) *Neurophilosophy: Toward a Unified Science of the Mind-Brain.* Chapter 2, Modern Theory of Neurons, pp 48-77. MIT Press.

The above reading (and the lecture) are not required for anyone who has taken Neuroscience 1. The following paper is still worth reading, though, as an illustration of how information processing within a dendritic tree can be far more complex than linear summation of inputs.

† Shepherd, G. M., Woolf, T. B., and Carnevale, N. T. (1989) Comparison between active properties of distal dendritic branches and spines: Implications for neuronal computations. *Journal of Cognitive Neuroscience* **1**:273-286.

2. The Hippocampus

2.1 Vectors, Matrices, and Associative Memory [Thu. January 26]

- Jordan, M. I. (1986) An introduction to linear algebra in parallel distributed processing. In D. E. Rumelhart and J. L. McClelland (eds.), *Parallel Distributed Processing*: *Explorations in the Microstructure of Cognition*, vol. I, chapter 9, pp. 365–422. MIT Press.

  The above is for those of you who would like a quick review of dot products and eigenvectors. It also contains some material on why linear algebra is relevant to neural network models.

† Kohonen, T., Oja, E., and Lehtiö, P. (1981) Storage and processing of information in distributed associative memory systems. In G. E. Hinton and J. A. Anderson (eds.), *Parallel Models of Associative Memory*, chapter 4, pp. 105–143. Lawrence Erlbaum Associates.

2.2 Anatomy of the Hippocampal System [Tue. January 31]

† Brown, T. H. and Zador, A. M. (1990) Hippocampus. In G. M. Shepherd (ed.), *The Synaptic Organization of the Brain*, chapter 11, pp. 346–388. Oxford University Press. *[Read pages 346–364 and 383–388. Skim the rest if you like.]*

† Amaral, D. G. (1993) Emerging principles of intrinsic hippocampal organization. *Current Opinion in Neurobiology* **3**:225–229.

- Witter, M. P. (1993) Organization of the entorhinal–hippocampal system: a review of current anatomical data. *Hippocampus* **3**(special issue):33-44. *[Very technical, but Figure 2 is worth looking at.]*

2.3 Associative Memory Models of Hippocampus [Thu. February 2]

† Marr, D. (1971) Simple memory: A theory for archicortex, In L. M. Vaina (ed.), *From the Retina to the Neocortex: Selected papers of David Marr*, pp. 59–128. Includes commentaries by D. Willshaw and B. McNaughton. Paper originally appeared in *Philosophical Transactions of the Royal Society of London B,* **262**:23–81. ***[Note: you might want to read the commentaries first, then the paper.]***

† Willshaw, D. J. and Buckingham, J. T. (1990) An assessment of Marr's theory of the hippocampus as a temporary memory store. *Philosophical Transactions of the Royal Society of London B*, **329:**205–215.

2.4 Hippocampus as a Cognitive Map, Part 1 [Tue. February 7]

† McNaughton, B. L. and Nadel, L. (1990) Hebb-Marr networks and the neurobiological representation of action in space. In M. A. Gluck and D. E. Rumelhart (eds.), *Neuroscience and Connectionist Theory*, chapter, 1, pp. 1–63. Hillsdale, NJ: Lawrence Erlbaum Associates.

† Macphail, E. M. (1993) *The Neuroscience of Animal Intelligence*, pp. 405–421. New York: Columbia University Press.

† O'Keefe, J. (1989) Computations the hippocampus might perform. In L. Nadel, L. A. Cooper, P. Culicover, and R. M. Harnish (eds.), *Neural Connections, Mental Computation,* chapter 8, pp. 225–284. MIT Press.

- O'Keefe, J. and Nadel, L. (1978) *The Hippocampus as a Cognitive Map.* Oxford University Press.

2.5 Hippocampus as a Cognitive Map, Part 2 [Thu. February 9]

† Burgess, N., Recce., M., and O'Keefe, J. (1994) A model of hippocampal function. *Neural Networks* **7***(6/7):1065-1081.*

† Redish, A. D. and Touretzky, D. S. (in press) Navigating with landmarks: computing goal locations from place codes. In K. Ikeuchi and M. Veloso (eds.), *Symbolic Visual Learning.* Oxford University Press, to appear in 1995.

- Shapiro, M. L. and Hetherington, P. A. (1993) A simple network model simulates hippocampal place fields: I. Parametric analyses and physiological predictions. *Behavioral Neuroscience **107**(1):34–50.*
- Hetherington, P. A. and Shapiro, M. L. (1993) A simple network model simulates hippocampal place fields: II. Computing goal-directed trajectories and memory fields. *Behavioral Neuroscience* **107**(3):434-443.

2.6 Hippocampus and Memory Recoding [Tue. February 14]

† Rolls, E. T. (1989) The representation and storage of information in neural networks in the primate cerebral cortex and hippocampus. In R. Durbin, C. Miall, and G. Mitchison (eds.), *The Computing Neuron,* chapter 8, pp. 125–159. . Addison-Wesley.

† Myers, C. E., Gluck, M. A., and Granger, R. (in press) Dissociation of hippocampal and entorhinal function in associative learning: a computational approach. *Psychobiology*, in press.

- Eichenbaum, H. and Buckingham, J. (1990) Studies on hippocampal processing: experiment, theory, and model. In M. Gabriel and J. Moore (eds.), *Learning and Computational Neuroscience: Foundations of Adaptive Networks,* chapter 5, pp. 171–231. MIT Press.

2.7 Pattern Completion/Separation [Thu. February 16]

† O'Reilly R. C. and McClelland, J. L. (1994) Hippocampal conjunctive encoding, storage and recall: avoiding a tradeoff. *Hippocampus* **4**(6):661–682.

† Hasselmo, M. E. and Schnell, E. (1994) Laminar selectivity of the cholinergic suppression of synaptic transmission in rat hippocampal region CA1: computational modeling and brain slice physiology. *Journal of Neuroscience* **14**(6):3898-3914.

- Brown, M. (1990) Why does the cortex have a hippocampus? In M. Gabriel and J. Moore (eds.), *Learning and Computational Neuroscience: Foundations of Adaptive Networks,* chapter 6, pp. 233–282. MIT Press.

3. Neural Basis of Learning and Memory

3.1 LTP and the NMDA receptor [Tue. February 21]

† Malenka, R. C. (1995) LTP and LTD: dynamic and interactive processes of synaptic plasticity. *The Neuroscientist* **1**(1):35–42.v

† Baxter, D. A. and Byrne, J. H. (1993) Learning rules from neurobiology. In D. Gardner (ed.), *The Neurobiology of Neural Networks,* chapter 4, pp. 71–105.. MIT Press.

- Sejnowski, T., Chatarji, S., and Stanton, P. (1989) Induction of synaptic plasticity by Hebbian covariance in the hippocampus. In R. Durbin, C. Miall, and G. Mitchison (Eds.), *The Computing Neuron,* chapter 7, pp. 105–124. Addison-Wesley.

† Hertz, J., Krogh, A., and Palmer, R. G. (1991) *Introduction to the Theory of Neural Computation*. Chapter 8, Unsupervised Hebbian Learning, sections 8.1–8.3 (pp. 197–210.) Addison-Wesley.

3.2 The Clusteron; Volume Learning [Thu. February 23]

† Mel, B. W. (in revision) Memory capacity of an excitable dendritic tree. *Neural Computation*, to appear.

† Mel, B. W. (1992) NMDA-based pattern discrimination in a modeled cortical neuron. *Neural Computation* **4**:502–517.

- Mel, B. W. (1993) Synaptic integration in an excitable dendritic tree. *Journal of Neurophysiology* **70**:1086–1101.

† Montague, P. R. and Sejnowski, T. J. (1994) The predictive brain: Temporal conincidence and temporal order in synaptic learning mechanisms. *Learning and Memory* **1**(1):1–33.

- Montague, P. R., Gancayco, C. D., Winn, M., Marchase, R. B., and Friedlander, M. J. (1994) Nitric oxide production links NMDA receptor activation to transmitter release. *Science* **263:**973-977.

4. Olfactory Bulb and Pyriform Cortex

4.1 Overview of Bulbar/Cortical Anatomy, and Theory of Competitive Learning [Tue. February 28]

† Shepherd, G. M. and Greer, C. A. (1990) Olfactory bulb. In G. M. Shepherd (ed.), *The Synaptic Organization of the Brain,* 3rd edition, chapter 5, pp. 133–169. Oxford University Press.

† Haberly, L. (1990) Olfactory Cortex. In G. M. Shepherd (ed.), *The Synaptic Organization of the Brain,* 3rd edition, chapter 10, pp. 317–345. Oxford University Press.

Note: you can skim the less interesting portions of the above two chapters.

† Hertz, J., Krogh, A., and Palmer, R. G. (1991) *Introduction to the Theory of Neural Computation*. Chapter 9, Competitive Learning, first two sections (pp. 217–228.) Addison-Wesley.

4.2 Granger-Lynch Competitive Learning Model [Thu. March 2]

† Lynch, G., Granger, R., Larson, J., and Baudry, M. (1989) Cortical encoding of memory: hypotheses derived from analysis and simulation of physiological learning rules in anatomical structures. In L. Nadel, L. A. Cooper, P. Culicover, and R. M. Harnish (eds.), *Neural Connections, Mental Computation,* chapter 7, pp. 180–224. MIT Press.

† Granger, R., Ambros–Ingerson, J., and Lynch, G. (1989) Derivation of encoding characteristics of layer II of cerebral cortex. *Journal of Cognitive Neuroscience* **1**(1):61–87,

- Barnard, E. (1989) Analysis of the Lynch–Granger model for olfactory cortex. *Biological Cybernetics* **62:**151–155.
- Granger, R., Ambros-Ingerson, J., Antón, P., and Lynch, G.(1990) Unsupervised perceptual learning: a paleocortical model. In S. J. Hanson and C. R. Olson (eds.), *Connectionist Modeling and Brain Function,* chapter 5, pp. 105–131. MIT Press.

4.3 Oscillation Model of Piriform Cortex [Tue. March 7]

† Bower, J. M. (1995) Reverse engineering the nervous system: an an *in vivo, in vitro,* and *in computo* approach to understanding the mammalian olfactory system. In S. F. Zornetzer, J. L. Davis, and C. Lau (eds.), *An Introduction to Neural and Electronic Networks,* 2nd edition, chapter 1, pp. 3–29. New York: Academic Press.

† Wilson, M. and Bower, J. M. (1992) Cortical oscillations and temporal interactions in a computer simulation of piriform cortex. *Journal of Neurophysiology* **67**(3):981–995.

- Protopapas, A. and Bower, J. M. (1995) Dynamics of cerebral cortical networks. In J. M. Bower and D. Beeman, *The Book of GENESIS: Exploring Realistic Neural Models with the GEneral NEural SImulation System,* chapter 9, pp. 159–179. Springer-Verlag.

4.4 Chaos in the Olfactory Bulb [Thu. March 9]

† Skarda, C. A. and Freeman, W. J. (1987) How brains make chaos in order to make sense of the world. *Behavioral and Brain Sciences* **10:**161-195. Reprinted in J. A. Anderson, A. Pellionisz, and E. Rosenfeld (eds.), *Neurocomputing 2: Directions for Research*, pp.383–420; includes editors' commentary. MIT Press, 1990.

† Baird, B. (1990) Bifurcation and category learning in network models of oscillating cortex. *Physica D* **42:**365-384. Reprinted in S. Forrest (ed.), *Emergent Computation: Self-Organizing, Collective, and Coop-*

erative Phenomena in Natural and Artificial Computing Networks. MIT Press, 1991.

5. Models of Classical Conditioning

5.1 Conditioning in Vertebrates: Rabbit Eye Blink Response [March 14]

† Thompson, R. F. (1990) Neural mechanisms of classical conditioning in mammals. *Philosophical Transactions of the Royal Society of Landon, Series B* **329:**161–170.

† Moore, J. W., Berthier, N. E., and Blazis, D. E. J. (1990) Classical eye-blink conditioning: brain systems and implementation of a computational model. In M. Gabriel and J. Moore (eds.), *Learning and Computational Neuroscience: Foundations of Adaptive Networks,* chapter 8, pp. 360–387.

† Sutton, R. S. and Barto, A. G. (1990) Time-derivative models of Pavlovian reinforcement. In M. Gabriel and J. Moore (eds.), *Learning and Computational Neuroscience: Foundations of Adaptive Networks,* chapter 12, pp. 497–537.

- Interview with Randy Gallistel. (1994) *Journal of Cognitive Neuroscience* **6**(2):174-179.

5.2 Invertebrate Learning [March 16]

† MacPhail, E. (1993) *The Neuroscience of Animal Intelligence: From the Sea Hare to the Seahorse*, pp. 101–146. Columbia University Press.

† Hawkins, R. D. and Kandel, E. R. (1984) Is there a cell-biological alphabet for simple forms of learning? *Psychological Review* **91**(3)375–391.

† Gluck, M. A. and Thompson, R. F. (1987) Modeling the neural substrates of associative learning and memory: a computational approach. *Psychological Review* **94**(2):176–191.

5.3 Error Minimization Learning [March 28]

- Lecture on the derivation of the backpropagation learning rule, and its applications.

6. Vision

6.1 Neuroanatomy of the Visual System [March 30]

† Van Essen, D. C. and Anderson, C. H. (19??) Information processing strategies and and pathways in the primate retina and visual cortex. In S. F. Zornetzer, J. L. Davis and C. Lau (Eds.), *An Intorduction to Neural and Electronic Networks*, pp. 43–72. San Diego, CA: Academic Press.

† Van Essen, D. C., and DeYoe, E. A. (1995) Concurrent processing in the primate visual cortex. In M. S. Gazzaniga (Ed.), *The Cognitive Neurosciences*, pp. 383–400.

- Kaas, J. H. (1989) Why does the brain have so many visual areas? *Journal of Cognitive Neuroscience* **1**:121-135.

6.2 Motion Detection in the Fly Retina [April 4]

- Reichardt, W. and Poggio, T. (1979) Figure-ground discrimination by relative movement in the visual system of the fly. Part I. Experimental results. *Biological Cybernetics* **35:**81–100.

† Reichardt, W. and Poggio, T. (1983) Figure-ground discrimination by relative movement in the visual system of the fly. Part II. Towards the neural circuitry. *Biological Cybernetics* **46:** Suppl. 46, pp. 1–30.

† Franceschini, N., Riehle, A., and Le Nestour, A. (1989) Directionally selective motion detection by insect neurons. In Stavenga and Hardie (Eds.), *Facets of Vision*, ch.17, pp. 360–390. Berlin: Springer-Verlag.

- Pichon, J.-M., Blanes, C., and Fraceschini, N. (1990) Visual guidance of a mobile robot equipped with a network of self-motion sensors. *SPIE Vol. 1195 Mobile Robots IV (1989),* pp. 44–53..

6.3 Stereo [April 6]

† Marr, D. and Poggio, T. (1979) A computational theory of human stereo vision. *Proceedings of the Royal Society of London, Series B* **204:**301–328.

† Qian, N. (1994) Computing stereo disparity and motion with known binocular cell properties. *Neural Computation* **6**(3):390–404.

6.4 Ocular Dominance and Orientation Columns in V1 [April 11]

† Miller, K. D., and Stryker, M. P. (1990) The development of ocular dominance columns: mechanisms and models. In S. J. Hanson and C. R. Olson (eds.), *Connectionist Modeling and Brain Function,* chapter 9, pp. 255–350. MIT Press.
[Read parts I and III. Skim part II if you like. Pages ???]

- Miller, K. D., Keller, J. B., and Stryker, M. P. (1986) Ocular dominance column development: Analysis and simulation. *Science* **245:**605–615.

† Swindale, N. V. (1992) A model for the coordinated development of columnar systems in primate striate cortex. *Biological Cybernetics* **66:**217–230.

† Erwin, E., Obermayer, K., and Schulten, K. (in press) A critical comparison of models for orientation and ocular dominance columns in the striate cortex. In G. Tesauro, D. S. Touretzky, and T. K. Leen (eds.), *Advances in Neural Information Processing Systems 7.* MIT Press.

- Obermayer, K., Blasdel, G. G., and Schulten, K. (1992) Statistical-mechanical analysis of self-organization and pattern formation during the development of visual maps. *Physica Review A* **45:**7568–7589.
- Linsker, R. (1990) Self-organization in a perceptual system: How network models and information theory may shed light on neural organization. In S. J. Hanson and C. R. Olson (eds.), *Connectionist Modeling and Brain Function,* chapter 10, pp. 351–392. MIT Press.

6.5 Motion Processing in Primates [April 13]

† Adelson, E. H. and Bergen, J. R. (1985) Spatiotemporal energy models for the perception of motion. *Journal of the Optical Society of America* ***2**:284.*

† Nowlan, S. J. and Sejnowski, T. J. (1995) A selection model for motion processing in area MT of primates. *Journal of Neuroscience* **15**(2):1195-1214.

6.6 Curvature/Shape from Shading [April 18]

† Lehky, S. R. and Sejnowski, T. J. (1988) Network model of shape-from-shading: neural function arises from both receptive and projective fields. *Nature* **333:**452–454.

† Dobbins, A., Zucker, S. W., and Cynader, M. S. (1989) Endstopping and curvature. *Vision Research* **29**(10):1371–1387.

7. Spatial Representations

7.1 Coordinate Transformations in Parietal Cortex [April 20]

† D. Zipser and R.A. Andersen (1988) A back-propagation programmed network that simulates response properties of a subset of posterior parietal neurons. *Nature* **331**: 679-684.

† Pouget, A. and Sejnowski, T. J. (manuscript) Representing spatial transformation in the parietal cortex with basis functions.

7.2 Superior Colliculus and Saccade Generation [April 25]

- † van Opstal, A. J. and Kappen, H. (1993) A two-dimensional ensemble coding model for spatial temporal transformation of saccades in monkey superior colliculus. *Network* **4**: 19-38.
- † Lefevre, P. and Galiana, H. L. (1992) Dynamic feedback to the superior colliculus in a neural network model of the gaze control system. *Neural Networks* **5**: 871-890.
- • Arai, K., Keller, E. L., and Edelman, J. A. (1994) Two-dimensional neural network model of the primate saccadic system. *Neural Networks* **7**(6/7): 1115-1135.

7.3 Visuomotor Coordination in Frogs [April 27]

Special lecture: Jim-Shih Liaw of USC will present his work with Michael Arbib on modeling visuomotor behavior (looming avoidance and prey catching) of frogs. The talk will take place at the usual time, 1:30 PM, but in Wean Hall 4623.

- † Liaw, J.-S. and Arbib, M. A. (1993) Neural mechanisms underlying direction-selective avoidance behavior. *Adaptive Behavior* **1**(3):227–261.
- † Liaw, J.-S., Weerasuriya, A., and Arbib, M. A. (1994) Snapping: a paradigm for modeling coordination of motor synergies. *Neural Networks* **7**(6/7):1137–1152.

7.4 Population Vector Models [May 2]

- † Georgopoulos, A. P., Kettner, R. E., and 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**(8): 2913-2927.
- † Redish, A. D. and Touretzky, D. S. (1994) The reaching task: Evidence for vector subtraction in the motor system? *Biological Cybernetics* **71**(4): 307-317.
- • Sanger, T. D. (1994) Theoretical considerations for the analysis of population coding in motor cortex. *Neural Computation* **6**(1):29-37.

8. Cerebellum

8.1 Motor Control [May 4]

- † Glickstein, M. and Yeo, C. (1990) The cerebellum and motor learning. *Journal of Cognitive Neuroscience* **2:**69-80.
- † Tyrrell, T. and Willshaw, D. (1992) Cerbellar cortex: its simulation and the relevance of Marr's theory. *Philosophical Transaction of the Royal Society of London, Series B*, **336**:239–257.
- • Buckingham, J. T., Barto, A. G., and Houk, J. C. (in press) Adaptive predictive control with a cerebellar model. Proceedings of the 1995 World Congress on Neural Networks.
- • Marr, D. (1969) A theory of cerebellar cortex. *Journal of Physiology (London),* **202:**437–470.

Take-Home Final Exam

- Distributed on Monday, May 8. Open book, open notes. The exam will be available in the file `/afs/cs/academic/class/15880b-s95/handouts/exam.ps`. Or you can pick it up in hard-copy form from Cary Lund in Wean Hall 8106 from 1:30 PM onward.
- Due back by 3pm on Monday, May 15. Drop off with Cary Lund, or stick the envelope under Dave Touretzky's door. Or you can email your answers to `dst@cs.cmu.edu`.