

MATHEMATICAL TRIPOS Part III

Tuesday 13 June, 2006 1.30 to 3.30

PAPER 84

COMPUTATIONAL NEUROSCIENCE

*Attempt **FOUR** questions.*

*There are **FIVE** questions in total.*

The questions carry equal weight.

STATIONERY REQUIREMENTS

*Cover sheet
Treasury Tag
Script paper*

SPECIAL REQUIREMENTS

None

**You may not start to read the questions
printed on the subsequent pages until
instructed to do so by the Invigilator.**

1 (a) Describe the Hopfield model for the encoding of long term memories. Include details of the architecture, a learning rule for the connections, and how the dynamics evolve given an input.

(b) If you were explaining a Hopfield network to an experimental neuroscientist, what would you say to describe its usefulness and limitations in understanding how the brain functions?

(c) Consider a network of 3 neurons with firing rate x_i ($i = 1, 2, 3$), connected in a ring:

$$\tau \frac{dx_i}{dt} = -x_i + W_{i,i-1} f(x_{i-1}), \quad f(x) = \tanh(\beta x)$$

where $\beta > 0$, $W_{10} \equiv W_{13}$ and $x_0 \equiv x_3$. Let \mathbf{J} be the Jacobian matrix of the system at the origin. Show that the eigenvalues of \mathbf{J} satisfy the characteristic equation:

$$(1 + \tau\lambda)^3 = \Gamma, \quad \Gamma = W_{13}W_{32}W_{21}\beta^3$$

(d) When the number of inhibitory weights is *even*, find the eigenvalues and thus derive the constraint on Γ for the origin to be stable.

(e) When the number of inhibitory weights is *odd*, find the eigenvalues and thus derive the constraint on Γ for the origin to be stable. What happens when $|\Gamma|^{1/3} = 1/\cos(\pi/3)$?

2 The back propagation algorithm can be used to learn the association between inputs z_i and desired outputs t_k . (In this question, subscripts denotes the layer of neurons: i for input, j for hidden, k for output.) Unit activations, x_j, x_k , and outputs, z_j, z_k , are calculated by:

$$\begin{array}{ll} \text{Hidden layer} & x_j = \sum_i w_{ij} z_i, \quad z_j = g_j(x_j) \\ \text{Output layer} & x_k = \sum_j w_{jk} z_j, \quad z_k = g_k(x_k) \end{array}$$

where $g_j(\cdot)$ and $g_k(\cdot)$ are the activation functions for hidden and output units.

(a) Given the error function $E = \frac{1}{2} \sum_k (t_k - z_k)^2$, derive the back-propagation rule for weight updates in the form:

$$\begin{aligned} \Delta w_{jk} &= \delta_k z_j \\ \Delta w_{ij} &= \delta_j z_i \end{aligned}$$

where δ_k and δ_j are to be derived. Why is this algorithm called back-propagation?

(b) Describe, with suitable examples, why hidden units are useful in networks. How is the computational ability of the network affected if the activation function for hidden units is given by $g(x_j) = x_j$?

(c) Briefly describe two reasons in favour and two reasons against using the back-propagation algorithm to study learning in the nervous system.

(d) Specify suitable weight values and thresholds of a network with four binary input units, one hidden layer and one output unit that can solve the parity problem (i.e. the activity of the output unit should be 1 iff an odd number of inputs are 1). Describe how your network solves the problem. Explain briefly whether this would be a difficult problem for back-propagation to learn.

3 (a) Explain the ionic basis of the action potential. In particular, what happens at rest, and during an action potential, to the distribution of ions, and their ion channels? Describe how the dynamics of subunit gate opening and closing influence the conductance of a channel. (You may assume that the opening and closing rates of a gate X (either m, n, or h) as a function of membrane voltage are given by $\alpha_X(V)$, $\beta_X(V)$.)

(b) Describe the dynamic clamp technique. Give two examples of its use.

(c) The sub-threshold response of an integrate and fire neuron is given by:

$$C_m \frac{dV}{dt} = -g_L(V - V_L) - g_E(V - V_E) + I_e$$

Describe these terms, along with the threshold voltage V_θ and reset voltage, V_0 . What happens to V over time? In what situations would you use such a model?

(d) For the integrate and fire model in (c), when $g_E = 0$, find the critical value of I_e that causes an action potential, and show how the firing rate varies as I_e increases above this critical value. Use the approximation $\log(1 + x) \approx x$ for small x to show that the firing rate grows linearly with I_e for large I_e .

4 (a) You are given a time-varying stimulus $s(t)$ and a spike train t_i recorded from a neuron when presented with that stimulus. Describe in detail a method that uses $s(t)$ and t_i to create a model neuron that generates synthetic spike trains with similar characteristics. How would you compare your synthetic spike trains with the real spike train? What differences might you expect?

(b) Describe the receptive field of a complex cell in primary visual cortex. Describe and compare two models for simulating such receptive fields.

5 Write a brief essay, with examples, on how theoretical models have aided our understanding of development of the visual system. In particular, describe the motivation for building networks, their weight modification rules, the biological phenomena being modelled and results and conclusions from modelling work.

END OF PAPER