MATHEMATICAL TRIPOS Part III

Tuesday 12 June 2007 9.00 to 11.00

PAPER 73

COMPUTATIONAL NEUROSCIENCE

Attempt **THREE** questions. There are **FOUR** 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) Write a short review of how neurons use action potentials ("spikes") to encode information. You should describe what an action potential is and how information flows from one neuron to another. Give examples to demonstrate the difference between *rate coding* and *temporal coding*.

(b) Assuming that a neuronal spike train can be characterized by a Poisson process, derive the cumulative distribution function (CDF) of the interspike interval. Describe a method for simulating a spike train using this CDF to create a spike train with time-varying firing r(t).

[Hint: under the Poisson process, the probability of n spikes occuring in a trial of duration T with constant rate r is:

$$P[n] = \frac{(rT)^n}{n!} \exp(-rT) \,. \quad]$$

(c) A white-noise time-varying stimulus s(t) is presented to a neuron which generates a spike train t_i . Describe a technique for computing a model neuron that will generate spike trains with similar statistics. How would you compare the real spike train against the simulated spike trains? Why would building such a model be useful?

(d) A neuron receives two stimuli, + and -, with equal frequency. The ideal response of the neuron is r_+ when stimulus + is presented, and r_- to the - stimulus. However, since the neuron is noisy, there is a probability P_x that the neuron will respond incorrectly. What is the mutual information between the stimulus and the response? Briefly interpret the cases when the mutual information is (a) maximised and (b) minimised.

[Hints: The definition of noise entropy, H_{noise} , is:

$$H_{noise} = \sum_{s} p(s)H_{s},$$
$$H_{s} = -\sum_{r} p(r|s)\log p(r|s).$$

Bayes rule is: p(s|r)p(r) = p(r|s)p(s).]

2 Write a brief essay *critically evaluating* the role of computational models in neuroscience. Do models help us understand the development and functioning of nervous systems, or should we perform more biological experiments? Give examples of computational models to support your argument.

3 The activities, x(t) and y(t), of two neurons evolve using the following system:

$$\begin{aligned} \tau \frac{dx}{dt} &= -x + s(ay) ,\\ \tau \frac{dy}{dt} &= -y + s(ax) ,\\ s(p) &= \frac{mp^2}{\sigma^2 + p^2} . \end{aligned}$$

(a) Explain briefly what each term and equation means in the context of a neural circuit.

(b) Determine the condition for the network to have three unique steady states. Draw the nullclines of the system and indicate typical flow patterns.

(c) Evaluate the stability of the three steady states when $\tau = 10$, m = 10, $\sigma = 12$, a = 3. Interpret these steady states in a biological context.

(d) Describe the architecture of a Hopfield network, and how you would use it to store memories. Provide details of how the weights are determined in the network and how neuron activities are updated.

(e) An energy function for the Hopfield network is given by:

$$E = -1/2 \sum_{ij} w_{ij} x_i x_j \,,$$

where x_i is the activity of node *i* and w_{ij} is the connection strength between unit *i* and unit *j*. Show that *E* always decreases to a minimum.

(f) Describe two limitations of the standard Hopfield network, and how they can be addressed in extensions to the standard network.

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4 The Oja rule for unsupervised learning is given by:

$$\begin{aligned} y &= \mathbf{w}^T \mathbf{x} \,, \\ \tau \frac{d \mathbf{w}}{d t} &= y \mathbf{x} - \alpha y^2 \mathbf{w} \end{aligned}$$

(a) Explain briefly each of the terms above and how the network might be used. What happens to the network during learning?

(b) Show that when $\langle \frac{d\mathbf{w}}{dt} \rangle = \mathbf{0}$, the weight vector is an eigenvector of \mathbf{C} , where \mathbf{C} is to be defined.

(c) Show that $\langle y^2 \rangle$ is maximised when **w** is the maximal eigenvector of **C**. What does this mean biologically? [Hint: rewrite **w** in terms of the eigenvectors of **C**.]

(d) Show that only the maximal eigenvector is stable, and hence that the Oja rule finds the maximal eigenvector of \mathbf{C} .

Hint: let $\mathbf{w} = \mathbf{v}_i + \mathbf{u}$, where \mathbf{v}_i is a unit-length eigenvector of \mathbf{C} and \mathbf{u} is a small displacement from the eigenvector. Evaluate $\langle \frac{d\mathbf{u}}{dt} \rangle$, ignoring $O(u^2)$ terms.

(e) Define the concept of a receptive field (RF) for a visual neuron. Sketch the RF of a simple cell from primary visual cortex as an example. Describe examples of how unsupervised learning rules can account for different aspects of development of the visual cortex.

END OF PAPER