# Gatsby Computational Neuroscience Unit
# Theoretical Neuorscience 2006

## Written Examination
## 12 Feb 2007

## Part I

This part has 20 short questions arranges in blocks of 4. Answer any 3 questions in each block. Each is worth 5 marks. No reference materials are allowed.

This part should take 1 hour. You may continue to work for another 30 minutes once that time is up, but indicate clearly which answers (or parts of answers) were written afterward.

**Biophysics.** Answer any 3 questions.

1. Provide a biophysical explanation for synaptic depression.
2. Consider an experiment in which you hold a cell at -60 mV for a long time, then suddenly inject hyperpolarizing current current into it. When you do that, you see a fast drop in voltage, followed by a slow increase with eventual saturation slightly below -60 mV. Sketch the activation and inactivation curves, and give the reversal potential, of a current that could lead to this behavior.
3. A 100 M$\Omega$ neuron exhibits an EPSP that instantaneously rises to 1 mV and then decays exponentially with a time constant of 10 ms. How much charge flows into the cell?
4. What is the quantal hypothesis, and how was it verified?

**Coding.** Answer any 3 questions.

1. The early auditory system analyses sounds using an array of narrowband filters. At high sound levels, cells are sensitive to rapid onsets of power in one of these bands. How might you expect this to change at lower sound levels?

2. A cell has a tuning curve for a parameter $\theta \in [0, 2\pi)$ given by:

$$f(\theta) = 100 \sin^2(\omega\theta).$$

   The actual number of spikes is Poisson-distributed around the tuning curve value. Calculate the average Fisher information (as a function of $\omega$) for a uniformly distributed $\theta$. Are larger or smaller values of $\omega$ likely to give effective coding schemes?

3. Consider a population code with radially symmetric, identical (up to location) tuning curves for a 2-dimensional stimulus feature. Explain intuitively why the Fisher information in the code about the stimulus feature does not depend on the tuning width.

4. Under what conditions (on the stimulus, and the nonlinearity) will the spike-triggered covariance method yield consistent (i.e. correct for infinite data) estimates of the linear filters of an LNP cell?

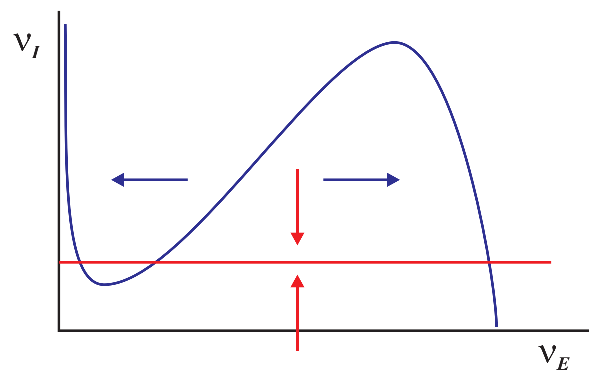
**Networks.** Answer any 3 questions.

1. Consider the differential equation

$$\begin{aligned} \frac{dx}{dt} &= -\frac{(x^2+y^2)x}{2} \\ \frac{dy}{dt} &= -\frac{(x^2+y^2)y}{2}\,. \end{aligned}$$

   Find $x^2+y^2$ as a function of time. Initial conditions are $x(t=0)=1$ and $y(t=0)=2$.

2. For the nullclines given below, the direction of the trajectories at fixed $\nu_E$ or $\nu_I$ are given by the arrows. Sketch the set of points that asymptote to the unstable fixed point.




3. Why are line attractors structurally unstable?

4. Consider a one-memory Hopfield network that evolves according to

$$x_i(t+1) = \text{sign}\left[\frac{\beta}{N}\sum_{j=1}^{N}\xi_i\xi_j x_j(t) + \eta_i\right]$$

   where $\xi_i$ is either $+1$ or $-1$, both with probability $1/2$, and $\eta_i$ is a random variable uniformly distributed between $-1$ and 1. Lext $x_i(t) = \xi_i$. What is the probability that $x_i(t+1)$ is equal to $x_i(t)$? Express your answer in terms of $\beta$.

**Learning.** Answer any 3 questions.

1. What statistical characteristic(s) of an environment should induce fast learning?
2. In a spike-time dependent plasticity rule, what happens if the area devoted to depression is greater than the area devoted to excitation? Consider the case of an isolated pair of neurons. Assume that, when unconnected, both the presynaptic and postsynaptic neurons fire with approximately Poisson statistics.
3. Ken Miller, in his Hebbian model of ocular dominance development in the face of monocular deprivation, imposed pre-synaptic normalization. Why do you think he needed this?
4. What is secondary conditioning? Why does it pose a challenge to the Rescorla-Wagner rule?

**Systems.** Answer any 3 questions.

1. How efficient is the V1 representation of a visual scene compared with that of the output of the retina?
2. What are Marr's three levels of organization for models of the brain?
3. What anatomical characteristics distinguish feedforward and feedback cortical connections?
4. What relationships have been postulated between the fMRI BOLD signal and neural activity?

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## Part II

This part contains 4 questions, of which you only need answer 3. You may consult your texts or notes, but **not** online resources.

This part should take 2 hours. You may continue to work for another 2 hours once this time is up, but indicate clearly which answers (or parts of answers) were written afterward.

1. **Biophysics.**

Consider a simplified Hodgkin-Huxley type model,

$$\begin{aligned} C\frac{dV}{dt} &= -g_L(V-\mathcal{E}_L) - g_0\Theta(V-V_t)h(t)(V-\mathcal{E}_0) + I(t) \\ \tau_h\frac{dh}{dt} &= \Theta(V_t-V) - h \end{aligned}$$

where $\Theta$ is the Heaviside step function: $\Theta(x) = 1$ if $x > 0$ and 0 if $x \le 0$. The parameters are:

$$\begin{aligned} C &= 0.1 \text{ nF} \\ g_L &= 10^{-8} \text{ Siemens} \\ g_0 &= 10^{-7} \text{ Siemens} \\ \mathcal{E}_L &= -65 \text{ mV} \\ \mathcal{E}_0 &= 0 \text{ mV} \\ V_t &= -50 \text{ mV} \\ \tau_h &= 5 \text{ ms}\,. \end{aligned}$$

(a) For $I(t) = 0$, sketch $V(t)$ and $h(t)$ for the following two initial conditions (note that $V(0)$ and $h(0)$ are shorthand for $V(t=0)$ and $h(t=0)$):

i. $V(0) = V_t - 0.001, h(0) = 1$. (3 marks)

ii. $V(0) = V_t + 0.001, h(0) = 1$. (7 marks)

(b) Let $I(t) = I_0\sin(\omega t)$, $V(0) = \mathcal{E}_L$, and assume that $I_0$ is small. Compute voltage, $V(t)$, as a function of time. (10 marks)

(c) Let $I(t)$ consist of action potentials spaced by $t_0$,

$$I(t) = I_0\sum_{n=0}^{\infty}\delta(t-nt_0)\,.$$

Assume that the cell is initially at rest ($V = \mathcal{E}_L$).

i. What is the minimum value of $I_0$ such that the first action potential causes a post-synaptic spike (i.e., causes the voltage to exceed $V_t$)? (3 marks)

ii. What is the minimum value of $I_0$ such that the postsynaptic neuron emits at least one spike in the long run (“Long run” means after many presynaptic action potentials.) (7 marks)

(d) Let $I(t) = I_0$. Show that there is no value of $I_0$ for which the neuron can spike repetitively. (10 marks)

2. **Coding.**

Consider a cell whose firing (viewed as a point process) in the absence of stimulation can be modelled by a conditional intensity function:

$$\lambda(t|t_n, t_{n-1}, ..., t_1) = \lambda(t|t_n) = \nu^2(t - t_n).$$

That is, the intensity depends only on the time of the most recent spike, and increases linearly from that time.

(a) What are the dimensions of the constant $\nu$? (2 marks)

(b) Assuming the model is correct, what is the cell's ISI distribution? (8 marks)

(c) Show that the mean firing rate under this model is $\overline{\lambda} = \sqrt{\frac{2}{\pi}}\nu$ (assuming $\nu \geq 0$). (5 marks)

(d) Assume that we started recording from the cell (i.e. $t = 0$) a random time after the stimulus was turned off. Consider a small interval of time $[t, t + dt)$. What is the entropy $H_t$ of the spiking process in this interval? (5 marks)

(e) What is the entropy rate $\mathcal{H}$ of the process? [Treat it as a binary discrete-time stochastic process in discretised bins of size $dt$. You may leave the answer in integral form.] (5 marks)

Now, suppose that a stimulus $s(t)$ modulates the cell's intensity, so that

$$\lambda(t|s(t), t_n, t_{n-1}, ..., t_1) = \lambda(t|s(t), t_n) = (\nu s(t))^2(t - t_n)$$

and that $s(t)$ is white noise with power $\langle s(t)^2 \rangle = \rho^2$.

(f) What is the new ISI distribution (collected over an infinitely long period of stimulation)? (8 marks)

(g) What is the spike-triggered-average stimulus (again, based on an infinitely long stimulus sequence)? (7 marks)

3. **Network dynamics.**

Consider a population of neurons whose mean firing rate, $\nu$, evolves according to

$$\tau \frac{d\nu}{dt} = (J_0 F D - 1)\nu$$

where $J_0$ is the raw strength of the synapses and $F$ and $D$ are dynamical variables that govern facilitation and suppression, respectively. These evolve according to

$$\begin{aligned} \frac{dF}{dt} &= \frac{1-F}{\tau_F} + (F_0 - F)\nu \\ \frac{dD}{dt} &= \frac{1-D}{\tau_D} - D\nu\,. \end{aligned}$$

where $\tau_F$, $\tau_D$ and $F_0$ are constants.

(a) Suppose that $F$ and $D$ do *not* evolve in time, and instead are fixed at some constant values. What are the three possible behaviors of $\nu(t)$? (5 marks)

(b) For fixed $\nu$, find the equilibrium values of $F$ and $D$. (5 marks)

(c) Show that both of the equilibria you found in part (b) are stable, again assuming that $\nu$ is fixed. (5 marks)

(d) Find conditions on $\tau_F$, $\tau_D$, $F_0$ and $J_0$ that allow bistability – that is, conditions such that there are two stable equilibria. Hint: take the equilibrium values you found in part (b) and insert them into the firing rate equation. (15 marks)

(e) Assume that the time constants are ordered so that $\tau < \tau_F \ll \tau_D$; i.e., facilitation is fast compared to depression, and both are slower than the neuron's time constant. Assume also that $J_0 F_0 > 1$. Suppose that you set $D$ to 1 and then rapidly increased the firing rate to a value much larger than $1/\tau_F$. Sketch the subsequent evolution of the firing rate. (10 marks)

4. **Learning**

Consider a recurrent model of visual processing with random input $\mathbf{u}$ (with zero mean and correlation matrix $\mathcal{U}$), *fixed* full rank feedforward weights $\mathbf{W}$ and *plastic* recurrent intra-cortical weights $\mathbf{M}$.

(a) If cortical dynamics are linear:

$$\tau_v \dot{\mathbf{v}} = -\mathbf{v} + \mathbf{M} \cdot \mathbf{v} + \mathbf{W} \cdot \mathbf{u}$$

what are the equilibrium output activities $\mathbf{v}$ for a single fixed input $\mathbf{u}$? What conditions on $\mathbf{W}$ and $\mathbf{M}$ are necessary and sufficient for them to be stable? (5 points)

(b) Goodall suggested the anti-Hebbian learning rule

$$\mathbf{M}_{n+1} = \mathbf{M}_n + \frac{1}{\tau_M} \left( -(\mathbf{W} \cdot \mathbf{u})\mathbf{v} + \mathbf{I} - \mathbf{M}_n \right)$$

where $\mathbf{I}$ is an appropriately-dimensioned identity matrix, and where we might imagine presenting a single input $\mathbf{u}$, waiting for the output $\mathbf{v}$ to settle, changing $\mathbf{M}$ a very small amount ($\tau_M \gg 1$), and then repeating. If $\mathbf{W} = 0$, what happens to $\mathbf{M}$ as $n \to \infty$? (2 points).

(c) If the rule converges over presentations of the whole set of $\mathbf{u}$ for $\mathbf{W} \neq 0$ having full rank (convergence means $\mathbf{M}_{n+1} = \mathbf{M}_n$), to what will correlation $\langle \mathbf{v}\mathbf{v}^T \rangle$ converge? What is the relationship between this rule and efficient coding of the input $\mathbf{u}$? (10 points)

(d) How would your answers to part (c) (note: *both* answers) change if the *input* $\mathbf{u}$ was corrupted by additive Gaussian white noise with covariance $\sigma^2\mathbf{I}$? (5 points)

(e) How would your answers to part (c) change if the *dynamics* were corrupted by additive Gaussian white noise:

$$\tau_v \dot{\mathbf{v}} = -\mathbf{v} + \mathbf{M} \cdot \mathbf{v} + \mathbf{W} \cdot \mathbf{u} + \boldsymbol{\epsilon}$$

where $\boldsymbol{\epsilon}$ is Gaussian with mean 0 and covariance $\sigma^2\mathbf{I}$? (8 points)

(f) How would your answers to part (c) change if $\mathbf{u}$ does not have mean 0? What about if $\mathbf{W}$ does not have full rank? (10 points)