EGT2
ENGINEERING TRIPOS PART IIA

Monday 9 May 2022 9:30 to 11:10

## Module 3G3

## INTRODUCTION TO NEUROSCIENCE

Answer not more than three questions.
All questions carry the same number of marks.
The approximate percentage of marks allocated to each part of a question is indicated in the right margin.

Write your candidate number not your name on the cover sheet.

## STATIONERY REQUIREMENTS

Single-sided script paper

## SPECIAL REQUIREMENTS TO BE SUPPLIED FOR THIS EXAM

CUED approved calculator allowed
Engineering Data Book
Supplementary page: one extra copy of Fig. 2.

10 minutes reading time is allowed for this paper at the start of the exam.

You may not start to read the questions printed on the subsequent pages of this question paper until instructed to do so.

You may not remove any stationery from the Examination Room.

## Version GH/3

1 This question is about multisensory integration, in the context of the monkey 2AFC heading discrimination task discussed during lectures. The experimental setup is depicted in Fig. 1. A monkey sits on a motion platform which can be translated in any direction at (small) angle $\alpha$ relative to straight heading. A sophisticated virtual reality setup involving a 3D dot cloud allows the simulation of the visual flow consistent with any translation of the platform, whether or not this translation actually occurs physically. Here, we suppose that in any trial where the true heading is $\alpha$, the visual and vestibular inputs to the monkey's brain can be statistically summarised by two quantities, $\hat{\alpha}_{\text {vis. }}$ and $\hat{\alpha}_{\text {vest. }}$, drawn independently from two normal distributions with identical means $\alpha$ and standard deviations $\sigma_{\text {vis. }}$ and $\sigma_{\text {vest. }}$ respectively.
(a) Explain why it is reasonable to assume that $\hat{\alpha}_{\text {vis. }}$ and $\hat{\alpha}_{\text {vest. }}$ are independent given $\alpha$.
(b) Suppose the platform is physically translated, but no visual feedback is provided. Explain why $\hat{\alpha}_{\text {vest. }}$ is also called the "maximum-likelihood estimate" of the heading direction in this case.
(c) Suppose the plaform is physically translated, and consistent visual feedback is provided. Derive expressions for the multisensory maximum likelihood estimate $\hat{\alpha}_{\text {mult }}$. and its variance $\sigma_{\text {mult. }}^{2}$.
(d) Suppose you wish to show that, when combining visual and vestibular sensory cues, monkeys form statistically optimal internal estimates of the heading direction. Describe the experimental protocol you would use, and the associated analysis you would perform. Provide reasons for your choices.
(e) Derive a condition on the visual and vestibular likelihood precisions, $\sigma_{\text {vis. }}^{-2}$ and $\sigma_{\text {vest. }}^{-2}$, such that they together yield the largest percentage increase in multimodal precision $\sigma_{\text {mult. }}^{-2}$ over the best of the two single-modality precisions.
(f) Based on your answer to the previous question, explain why a clever experimenter would in fact corrupt the visual flow feedback (e.g. by introducing noise, as done in Gu et al., Nature Neuroscience, 2008).


Fig. 1

## Version GH/3

2 (a) Write short notes on the following:
(i) The resting membrane potential: in particular, how it arises, and what determines its value;
(ii) The action potential: in particular, what triggers it, and what terminates it; [15\%]
(iii) The sources of uncertainty that may limit performance in perceptual decision making: in particular, explain why making optimal decisions requires adequate treatment of such uncertainty.
(b) A Hodgkin-Huxley model neuron is injected with a step of depolarizing current, sufficiently large to elicit firing (Fig. 2, solid black line, reproduced in each panel to facilitate comparisons in part (ii) below).
(i) Sketch the corresponding time course of the sodium and potassium gate variables.
(ii) The very same current injection is performed in the following variants of the model neuron:

A: Lower reversal potential for sodium channels;
B: Larger peak potassium conductance;
C: Faster kinetics for the $m$ and $h$ gates;
D: Slower kinetics for the $n$ gate.
The membrane potential time courses arising in these four scenarios are shown as dashed lines in the four panels of Fig. 2, in arbitrary order. On the additional copy of Fig. 2 provided at the end of this paper, complete the legend in each panel by circling the correct scenario label (A, B, C, or D). Provide a justification for your choices. Do not forget to hand in your completed copy of Fig. 2 with your answer to this question.


Fig. 2

## Version GH/3

3 (a) This part is about Dale's principle.
(i) What does the principle state?
(ii) Explain how Dale's principle arises from specific regularities governing the production of neurotransmitters and their binding to receptors.
(b) Figure 3, from Bliss \& Lømo 1973, shows the evolution of the population EPSP amplitude in the granule cells of the dentate gyrus area of Hippocampus, evoked by stimulation of the perforant pathway (PP) axons. The PP is stimulated at a frequency of $0.5 \mathrm{~s}^{-1}$, except during the epoch marked by a black bar (bottom) during which the frequency is increased to $15 \mathrm{~s}^{-1}$. Explain why high-frequency stimulation but not lowfrequency stimulation leads to long-term potentiation of the EPSP amplitude. Identify the specific synaptic mechanism involved.


Fig. 3
(c) This part is about the Inhibitory Conditioning (IC) paradigm in reinforcement learning and the Rescorla-Wagner model.
(i) Describe the experimental protocol for the IC paradigm.
(ii) Let $u$ denote the binary $0 / 1$ indicator for the unconditioned stimulus, and $s_{i}$ denote the $0 / 1$ indicator for the $i^{\text {th }}$ conditioned stimulus (CS); there will be as many $s_{i}$ as there are CS's in the IC paradigm. Write the Rescorla-Wagner update rules for all the weights, $w_{i}$, of that model. Provide simplified expressions that only involve $u$ and $w_{i}$.
(iii) To which steady-state values will the weights of the Rescorla-Wagner model converge over time (assuming they will converge), in this paradigm? State the answer for the weights of all CS's used in the IC paradigm.

## Version GH/3

4 (a) This part is about classical conditioning of the gill-withdrawal reflex in Aplysia.
(i) Describe the experimental procedure for this classical conditioning.
(ii) Describe the two types of coincidence detection mechanisms involved in the induction of synaptic plasticity underlying this kind of learning. Describe each:
A. in terms of a coincidence of different stimuli and/or the behavioral response (i.e., gill-withdrawal);
B. in terms of a coincidence of cellular or molecular events and variables, explaining how/why this translates to the corresponding coincidence among stimuli and/or motor response.
(b) This part is about the effect of the learning rate, $\epsilon$, on the function and behavior of the Rescorla-Wagner (RW) model.
(i) Describe the qualitative difference in the time evolution of the RW model's stimulus weight, $w$, during training in the Partial Reinforcement paradigm, for large $(\epsilon \sim 1)$ vs. small $(\epsilon \ll 1)$ learning rates.
(ii) Explain conceptually what is learned by the model in each of the two cases in the previous part (for large learning rate, assume $\epsilon=1$ for concreteness).
(iii) Explain why a large learning rate $(\epsilon \sim 1)$ is typically problematic for learning in the natural environment.
(iv) Consider a modification to the RW model which has an adaptable learning rate. Suppose the environment switches from a low volatility state to a high volatility one. Should $\epsilon$ adapt to a higher or lower value to improve performance? Explain why.

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