

Introduction

These notes are about decision making in cortex. I offer an error bounty of between 20p and 2 pounds for mistakes. Contact me at conor.houghton@bristol.ac.uk or come up after a lecture.

Decision making in cortex

We saw in the case of memory how memories are originally laid down in hippocampus, exploiting the potential for rapid plastic change presented by that part of the brain; we noted also that longer-term memories are formed in the neocortex, the slower learning involved in the neocortex allowed for the formation of connections between different related memories; this contrasted with the hippocampus where pre-processing in the dentate gyrus had the opposite purpose, to separate similar memories. Something similar is thought to occur with decision making, the basal ganglia makes decisions during reinforcement learning based on rapidly changing probable rewards. It is known, however, that the cortex is also involved in decision making and it is hypothesised that there is some sort of similar division of labor, with the basal ganglia involved in decision making during conditioning and the cortex in more rapid, or more accurate, decision making when the structure is better established [1].

Forced choice task

Here we will look at two alternative forced choice tasks when the subject has to make a choice between two alternative possibilities even if the signal is sometimes ambiguous. One example is the one described in [2], a screen is covered with a number of asterisks drawn from one of two distributions, a 'high' distributions with mean 56 and a 'low' distribution with mean 38; the standard deviation is 14.4 so the distributions overlap and values 47 are ambiguous. The subjects are nonetheless required to decide which distribution the results came from. There were four subjects and their reaction times are shown in Fig. 1.

In fact, reaction time distributions are distinctive enough to suggest a model of decision making called the drift-diffusion model [3, 4]. In the drift-diffusion model a decision is the sum of many quasi-random micro-decisions so that the 'decision state' wanders with some tendency to go one way rather than the other. The state is sandwiched between two threshold corresponding to the two alternatives and it wanders until one is reached, this corresponds to a decision. This is illustrated in Fig. 2.

In the drift diffusion model the *drift* measures the tendency to go one way or the other and will correspond to how clear the decision is; another variable, the bias, measures where the process starts, it might start nearer one alternative than the other. If there is more ambiguous evidence, if, in the asterisk task the number of asterisks is close to 47, the drift rate will be lower and the number of wrong decisions will increase, as will the reaction times; this matches experiment. Finally the distance to the decision boundaries controls a play-off between speed and accuracy. If the boundaries are a long way away then the decision state will only get to the boundaries after the drift has acted for a while, averaging out the randomness of the motion, in this case the decision will be slow but accurate. Conversely, if the decision boundaries are nearby the decision will be quick, but sometimes the decision state might stray over the wrong boundary, the one other than the one the drift is pushing it towards, by mistake, because of the randomness.

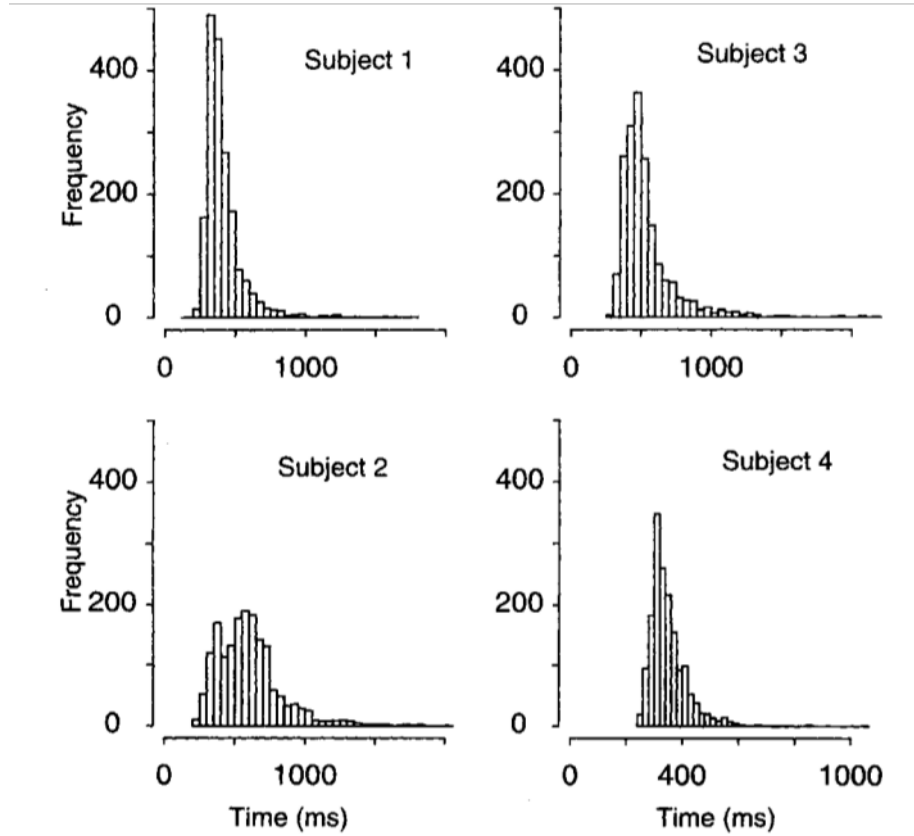


Figure 1: Reaction times for the two alternative forced decision task. [Image from [2]].

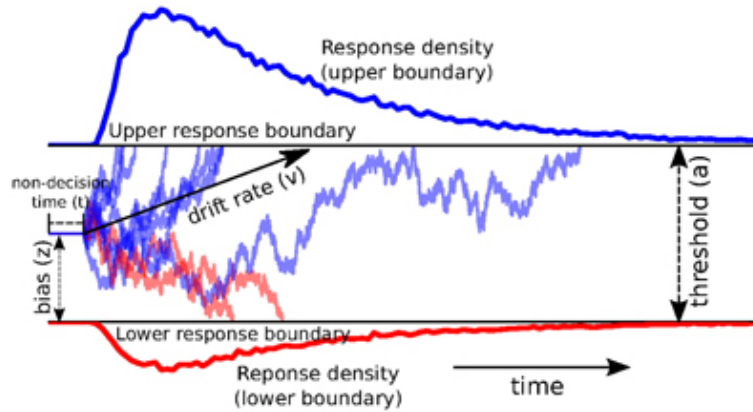


Figure 2: The drift-diffusion model. The state of the system wanders but with a greater tendency to go up than down, this is the drift, marked v . Eventually it reaches one of the decision boundaries, the resulting reaction times distributions are plotted, in blue above for the correct choice, below in red for incorrect. [Image from [5]].

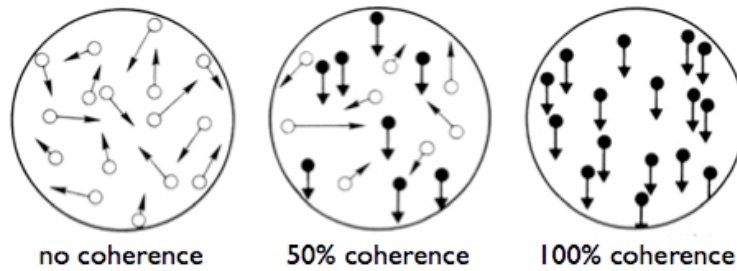


Figure 3: Moving dot task. The dots move, some move randomly and some move in the same direction, which varies from presentation to presentation; it might be up, down, left or right, for a two alternative forced choice task left and right are usually chosen. The monkey is trained to indicate which direction the coherent dots are moving, the difficulty of the task can be varied by varying the fraction that are coherent, if 0% are coherent all the dots move randomly and the task is impossible, if 100% move coherently all the dots move the same way and the task should be easy. [Image taken from <http://www.cns.nyu.edu/~david/courses/perception/>].

Moving dots again

The problem with the drift diffusion model is that, as stated, it is a purely psycho-physical model: it doesn't describe a neuronal process. In fact, decision making appears to be visible in cortex. As an example, we will consider an experiment we have looked at before in the lecture on spike train analysis: as illustrated in Fig. 3 a screen shows moving dots, some of which move in the same direction; a monkey has to select which direction they are moving, the selection is indicated with a saccade, an eye movement.

There are neurons that are sensitive to the direction of motion in an area called MT, or middle temporal. These neurons have receptive fields corresponding to different directions of motion. During the moving dot task in monkey information from MT appears to get integrated by neurons in the Lateral Intraparietal Cortex (LIP); in humans this is part of the cortex located just behind the tip of the ear. Figure 4, taken from [6], shows the activity of neurons in LIP during the moving dot task; some rise and some fall as the decision is being made. It certainly looks as if these neurons are accumulating evidence based on the MT output; ideas about how this accumulation is done are presented next.

Race model

In the race model, [7], there is a race between different LIP neurons; in terms of the moving dot experiment each neuron integrates a MT neuron corresponding to a different direction and the one that reaches the threshold first wins. This is illustrated in Fig. 5. If y_1 and y_2 are the activity levels of the two LIP neurons, and x_1 and x_2 the activity for the two MT neurons, we have

$$y_i = \int_0^t x_i(s) ds \quad (1)$$

with the decision made if the denoised signal y_1 or y_2 exceeds Z . The problem with the race model is that all the neurons increase their activity, it is just that the losing neuron increases

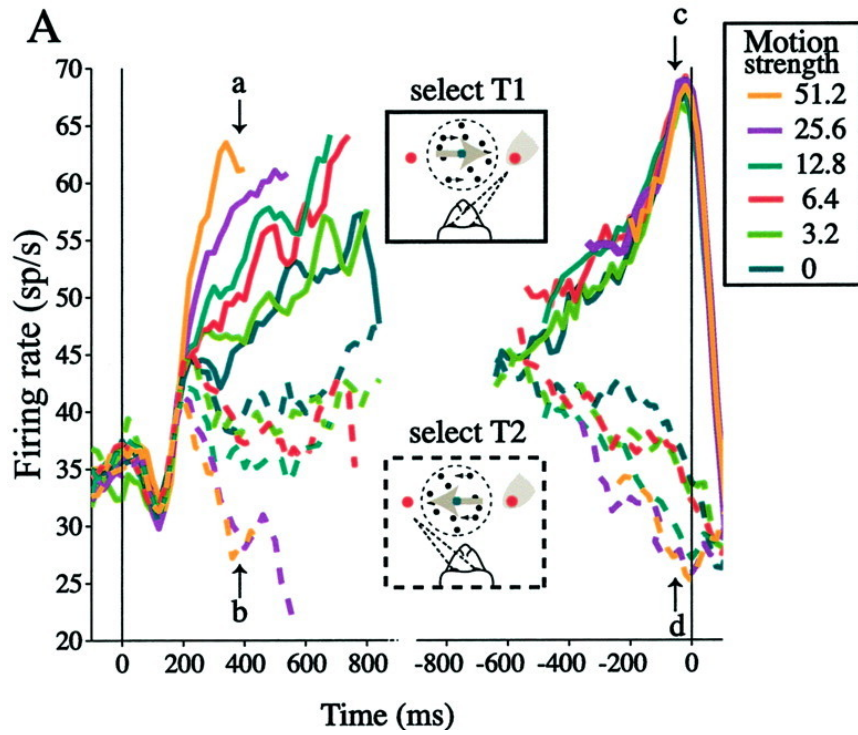


Figure 4: This shows the average response of LIP neurons to different coherence levels of the moving dot task, on the left aligned to stimulus onset and on the right to the time the decision was made; the left ones are clipped 100ms before the eye movement, the right ones are clipped to exclude the first 200ms after the stimulus. The different colors indicate the different levels of coherence, the solid and dashed lines correspond to different choices. [Image from [6]].

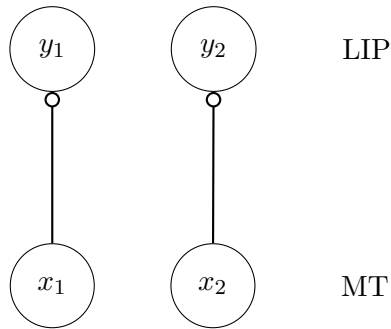


Figure 5: The race model. Each direction in MT feeds forward to be integrated in LIP; the nodes here might correspond to neurons or to collections of neurons, but either way the LIP nodes sum up the activity of the different noisy direction signals recorded at MT.

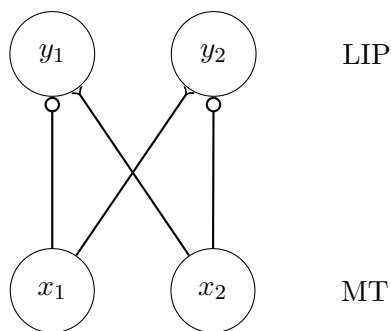


Figure 6: The feedforward inhibition model. Each direction in MT feeds forward to be integrated in LIP, adding to some neurons and inhibiting others.

slower. That isn't what is seen in experiment, in Fig. 4 some neurons increase, some decrease.

Feedforward inhibition model

The feedforward inhibition model is like the race model except the MT neurons excite their own neuron and inhibit the other, giving one neuron with rising activity and one with falling [8]. This is illustrated in Fig. 6. This time we have

$$\begin{aligned} y_1 &= \int_0^t [x_1(s) - x_2(s)] ds \\ y_2 &= \int_0^t [x_2(s) - x_1(s)] ds \end{aligned} \quad (2)$$

with the decision made if the denoised signal y_1 or y_2 exceeds Z , this time we should think of the y_i as starting at some intermediate value, so they can fall as well as rise. This fits the data well and is not dissimilar from the drift diffusion model; $\langle x_1 - x_2 \rangle$ should depend on how unambiguous the task is, Z controls the pay-off between speed and accuracy and variations in the initial values of the y_i reflect the bias.

Sequential probability ratio test

In fact, it is possible to argue that the feedforward inhibition model implements an optimal strategy for dealing with this problem. To see this we need to reformulate the problem statistically [9]. Say $x_i(t)$ is the firing rate of MT neurons selective for i at time t . The goal is to decide whether x_1 or x_2 has the highest mean. Now, imagine x_1 and x_2 are normally distributed with the same variance and that there are two possibilities, x_1 has mean μ_1 and x_2 has mean μ_2 , or visa versa, with $\mu_1 > \mu_2$. Thus, one hypothesis, H_1 , is that

$$x_1 \sim \mathcal{N}(\mu_1, \sigma), \quad x_2 \sim \mathcal{N}(\mu_2, \sigma) \quad (3)$$

and the other, H_2 , is that

$$x_1 \sim \mathcal{N}(\mu_2, \sigma), \quad x_2 \sim \mathcal{N}(\mu_1, \sigma) \quad (4)$$

The challenge is to decide as quickly as possible which of x_1 and x_2 has the higher mean by measuring them.

The optimal solution to this problem is actually known and is provided by the sequential probability ratio test (SPRT) [10]. After each sample the quantity

$$R = \frac{P(\mathbf{x}(t_1), \dots, \mathbf{x}(t_n) | H_1)}{P(\mathbf{x}(t_1), \dots, \mathbf{x}(t_n) | H_2)} \quad (5)$$

where $\mathbf{x}(t_i)$ is the value of the x_i at the sample time t_i and t_n is the most recent sample time. Now, if $R > Z_1$ decide H_1 is true, if $R < Z_2$ decide H_2 is, otherwise continue sampling.

Now, if the sample points are independent

$$P(\mathbf{x}(t_1), \dots, \mathbf{x}(t_n) | H_a) = \prod_{i=1}^n P(\mathbf{x}(t_i) | H_a) \quad (6)$$

for $a = 1$ or $a = 2$ and, in the usual way, this product is turned into a sum by taking the logarithm:

$$\log P(\mathbf{x}(t_1), \dots, \mathbf{x}(t_n) | H_a) = \sum_{i=1}^n \log P(\mathbf{x}(t_i) | H_a) \quad (7)$$

In fact, we know

$$P(\mathbf{x}(t_i) | H_1) = \frac{1}{2\pi\sigma^2} e^{-(x_1(t_i) - \mu_1)/2\sigma^2} e^{-(x_2(t_i) - \mu_2)/2\sigma^2} \quad (8)$$

and so on, so we can substitute explicitly into the formula for $\log R$, in fact, lots of stuff cancels and we get

$$\log R = \frac{\mu_1 - \mu_2}{\sigma^2} \sum_{i=1}^n [x_1(t_i) - x_2(t_i)] \quad (9)$$

This model is clearly implemented by feedforward inhibition. It is also optimal, it is shown in [11] that given level of error the SPRT arrives quickest at an answer. Thus, if the parameters are chosen appropriately the race model and feedforward inhibition model can be chosen to have the same chance of error but the feedforward inhibitory model will be quicker.

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