

## NETWORKS OF NEURONS

In this module we will consider the emergent states of networks of neurons, in particular; two-state networks and short-term memory, inhibitory feedback with delay and oscillations and also touch on the construction of spatial models and their use.

### • SELF-CONSISTENT APPROACH

We consider a network of  $N \gg 1$  neurons (of identical type, i.e. all excitatory or all inhibitory) which are receiving the same form of external drive (treated in the section on populations of neurons) as well as synaptic input from neurons in the network. The synaptic input from within the network is treated purely as a current for simplicity. Thus the equation for the voltage fluctuations can be written

$$\tau_0 \frac{dV}{dt} = E_0 - V + \sqrt{2\tau_0}\sigma_V \xi(t) + \tau_0 r A \quad (1)$$

where the first 3 terms on the RHS come from the external drive and the last term from the internal, recurrent drive. The quantity  $A = aN$  is the strength of the input (proportional to the number of neurons, but finite as the individual amplitude  $a$  of the voltage amplitudes is assumed small) and is positive for an excitatory network and negative for an inhibitory network. The average firing rate of a single neuron in the network is  $r$ . The strategy is to calculate the firing rate with  $r$  as an unknown parameter and then find the solution self consistently. To this end, an effective equilibrium voltage  $\tilde{E}_0$  can be defined

$$\tilde{E}_0 = E_0 + \tau_0 r A \quad (2)$$

which has the firing rate

$$r_1 = \Phi(\tilde{E}_0) = \frac{1}{\tau_{ref} + \tau_0 I(\tilde{x}_{th}, \tilde{x}_{re})} \quad (3)$$

where  $I$  is the integral calculated previously for the firing rate of the leaky IF neuron with its arguments evaluated as  $\tilde{x}_{th} = (V_{th} - \tilde{E}_0)/\sigma_V$  and the same for  $\tilde{x}_{re}$ .

$$I(\tilde{x}_{th}, \tilde{x}_{re}) = \int_0^\infty \frac{dz}{z} e^{-z^2/2} (e^{z\tilde{x}_{th}} - e^{z\tilde{x}_{re}}). \quad (4)$$

A refractory period  $\tau_{ref}$  has also been included to give a maximum firing rate  $1/\tau_{ref}$ . Thus  $r_1$  has a sigmoidal-like shape. However, by rearranging equation (2) another formula for the firing rate can be found in terms of  $\tilde{E}_0$

$$r_2 = \frac{1}{\tau_0} \frac{\tilde{E}_0 - E_0}{A}. \quad (5)$$

The intersection of  $r_1$  and  $r_2$  on a rate versus  $\tilde{E}_0$  graph gives the fixed points of the network. For an excitatory network  $A > 0$  and there can be 1 or 3 fixed points. For an inhibitory network  $A < 0$  and there is only one fixed point.

### • STABILITY OF FIXED POINTS

To correctly evaluate fixed-point stability it is necessary to perturbatively solve the time-dependent Fokker-Planck equation. This is beyond the scope of this course, so we will now use an approximation of the dynamics

$$\tau \frac{dr}{dt} = \Phi(E_0 + rA\tau_0) - r. \quad (6)$$

This equation has the correct fixed points, and a simple exponential dynamics, governed by the (arbitrary) time constant  $\tau$ . We now write  $r = r_{ss} + \delta r$ , and keeping terms to first order in  $\delta r$  we get

$$\tau \frac{d\delta r}{dt} = - \left( 1 - \frac{d\Phi}{d\tilde{E}_0} \frac{d\tilde{E}_0}{dr} \right) \delta r \quad (7)$$

where the derivatives are evaluated at the fixed point in question. For stability it must be that the term in parenthesis on the RHS be greater than zero. Identifying the different functions of  $r$  involved, and that  $d\tilde{E}_0/dr_2 > 0$  for excitation  $d\tilde{E}_0/dr_2 < 0$  for inhibition we have the stability conditions

$$\frac{dr_2}{\tilde{E}_0} > \frac{dr_1}{\tilde{E}_0} \quad \text{for excitation} \quad (8)$$

$$\frac{dr_2}{\tilde{E}_0} < \frac{dr_1}{\tilde{E}_0} \quad \text{for inhibition.} \quad (9)$$

Excitation: the inequality states that for a single fixed point, there is stability and for three fixed points the two outer ones are stable (low and high firing rates) whereas the fixed point inbetween these two is unstable. This bistability for a network with excitatory feedback provides the basis for a particular kind of short-term memory seen in experiment. Inhibition: because the gradient of  $r_2$  is  $A\tau_0$ , and negative for inhibition, we see that the inhibitory fixed point is always stable because the gradient of  $r_1$  is positive.

• INHIBITORY INSTABILITY WITH DELAY

There are many sources of delay in the loop from the triggering of the action potential near the soma, travel along the axon, transmission via the synapse and then current flowing down the dendrite to the soma. For inhibition the synapses are relatively slow:  $\tau_i = 10\text{ms}$ . We will now examine the effects of this delay, by lumping all the delays into a single time difference  $d$ , and writing a delay-differential equation:

$$\tau \frac{dr(t)}{dt} = \Phi(E_0 + r(t-d)A\tau_0) - r(t). \quad (10)$$

Following the same perturbative approach, we get:

$$\tau \frac{d\delta r(t)}{dt} = \left( \frac{d\Phi}{d\tilde{E}_0} A\tau_0 \delta r(t-d) - \delta r(t) \right). \quad (11)$$

On substituting for the trial solution  $\delta(r) \sim e^{\lambda t}$  we get can re-arrange the result into the form

$$d\lambda = \frac{d}{\tau} \left( \alpha e^{-\lambda d} - 1 \right) \quad \text{where } \alpha = \frac{d\Phi}{d\tilde{E}_0} A\tau_0. \quad (12)$$

Oscillations will emerge when the eigenvalue becomes purely imaginary (the real part must vanish). We set  $d\lambda = iu$  and by separating real and imaginary parts we find the equations

$$\begin{aligned} \alpha_1 &= \frac{1}{\cos(u)} \\ \alpha_2 &= -\frac{u}{\delta \sin(u)} \end{aligned} \quad (13)$$

where  $\delta = d/\tau$  is the dimensionless delay. For  $\delta \gg 1$  these curves intercept near  $u \sim \pi$  and  $\alpha^* \simeq -1$ . For  $\delta \ll 1$  the curves intercept near  $u \sim \pi/2$  and so  $\alpha^* \simeq -\pi/(2\delta)$ .

• SPATIAL EFFECTS: PROPAGATION OF A FRONT

We now consider a generalisation of the excitatory network to a one-dimensional array of neurons with position measured by  $X$  and a length of interaction  $\lambda$ . We use  $T$  as the time variable, though this will be rescaled.

$$\tau \frac{dr}{dT} = \lambda^2 \frac{d^2r}{dX^2} + \Phi - r \quad (14)$$

A bistable case is considered in which there is a low firing rate  $r_l$  and  $r_h$  with an unstable rate  $r_i$  inbetween

$$\Phi - r \simeq F(r) = -\kappa^2(r - r_l)(r - r_i)(r - r_h). \quad (15)$$

A convenient rescaling maps the low and high rates onto 0 and 1 respectively,  $\rho = (r - r_l)/(r_h - r_l)$ . We also rescale time  $T = t/\tau$  and space  $X = x\lambda$

$$\frac{d\rho}{dt} = \frac{d^2\rho}{dx^2} + f(\rho) \quad (16)$$

where

$$f(\rho) = -\kappa^2(r_h - r_l)^2\rho(\rho - \alpha)(\rho - 1) \quad \text{where } \alpha = (r_i - r_l)/(r_h - r_l). \quad (17)$$

A scenario is considered where for  $x \rightarrow -\infty$  we have  $\rho \rightarrow 1$  and for  $x \rightarrow \infty$  we have  $\rho \rightarrow 0$ . Between these two limits there must be a front - the question is whether the front is moving forwards or backwards. We assume that the front has a constant shape, though its position changes with constant velocity. Hence we look for a solution  $\rho(x - ct) = \rho(z)$  with  $c$  the velocity of the front. The aim is to find what conditions fix the sign of the velocity. Converting the derivatives in equation (16) to those with respect to  $z$  yields

$$-c \frac{d\rho}{dz} = \frac{d^2\rho}{dz^2} + f(\rho) \quad (18)$$

writing  $w = d\rho/dz$  and multiplying both sides by  $w$  yields

$$-cw^2 = \frac{1}{2} \frac{d(w^2)}{dz} + wf(\rho). \quad (19)$$

We now integrate between  $-\infty, \infty$  to give

$$c \int_{-\infty}^{\infty} w^2 dz = \int_0^1 d\rho f(\rho) \quad (20)$$

where the fact that  $w^2 \rightarrow 0$  on either side of the limits has been used and also that  $w dz = d\rho$ . From this last equation it is seen that the sign of the velocity depends on the integral of the function  $f$ . In this cubic approximation the higher rate state is more stable and propagates to the right if  $\alpha < 1/2$ , whereas the converse is true if  $\alpha > 1/2$ .