Imperial College London

Computational Neurodynamics

Topic 2
Neurons

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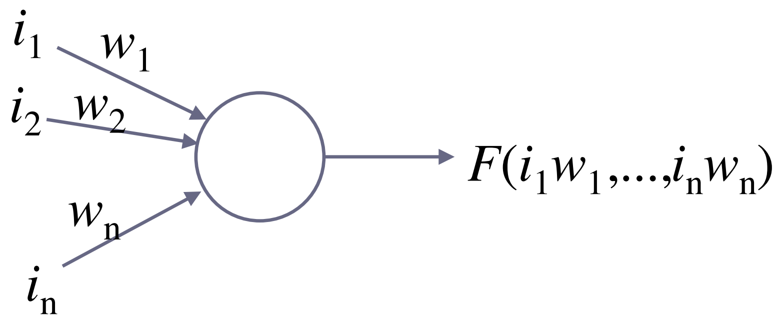
Overview

- Artificial and real neurons
- Axons and dendrites
- Neuron behaviour
- The Hodgkin-Huxley model

Artificial Neurons 1

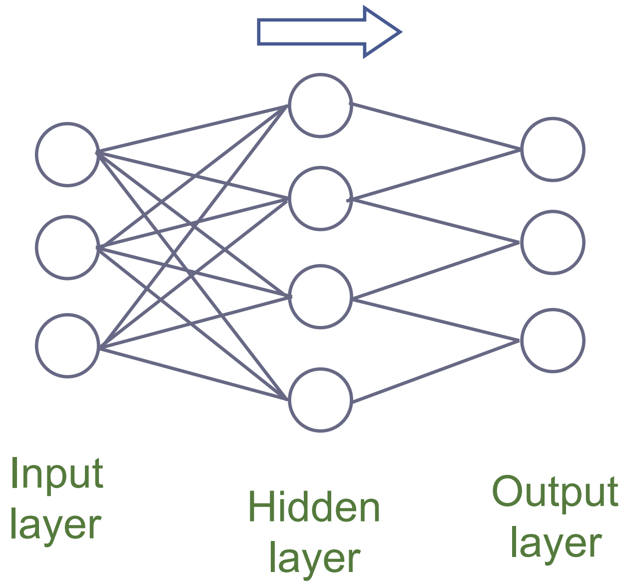
- The kind of artificial neuron traditionally used for neural network applications in computer science is very useful, but has little biological plausibility
- The type of artificial neuron on the right is very common. It computes a weighted sum (F) of its inputs i_1 to i_n



- Each connection has an associated weight (w_i), and a neuron's output is a function of all its weighted inputs
- Many useful applications have been built out of such simple artificial neurons

Artificial Neurons 2

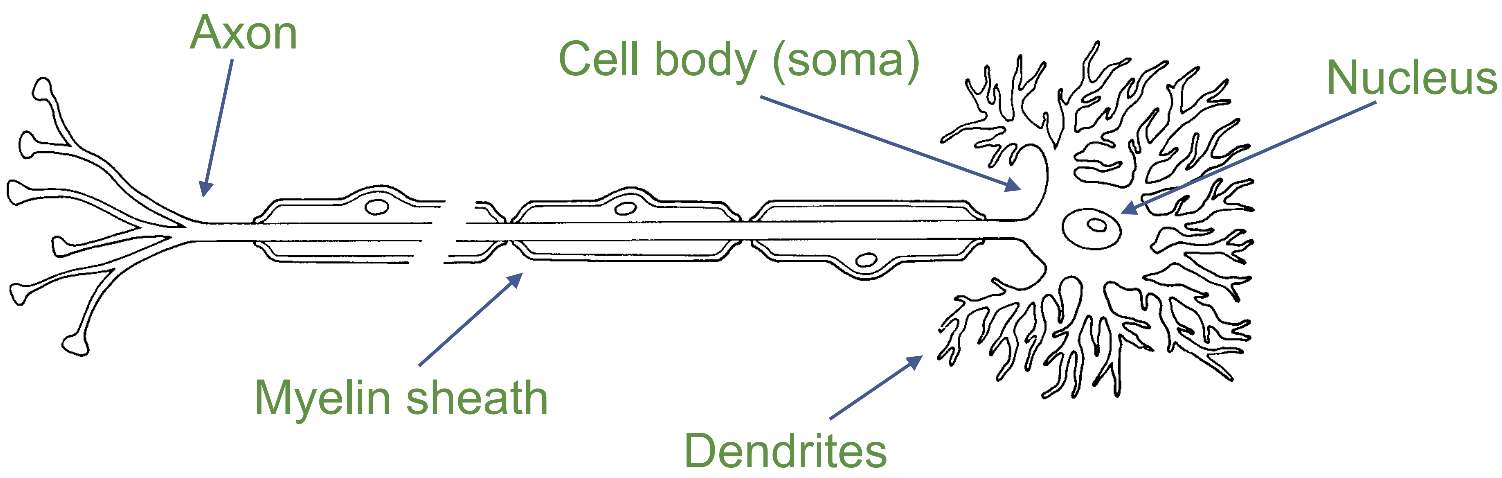
- They are often organised into *feed-forward* networks, comprising an input layer, a hidden layer (or, in *deep learning*, many hidden layers), and an output layer
- A learning algorithm such as *back propagation* is applied to train the network



- Some applications use *recurrent neural networks* (RNNs) with a loop of feedback from the output back the input layer
- But this course is NOT about neural network applications

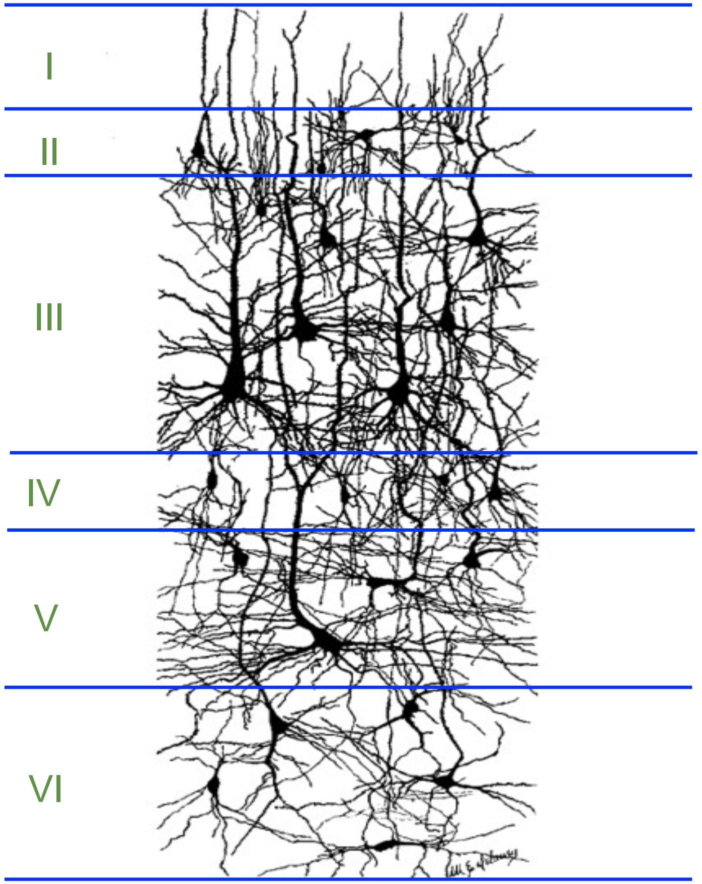
Real Neurons

- A real neuron comprises a *cell body*, a tree of *dendrites* and an *axon*. The dendrites carry incoming electrical signals, and the axon delivers the neuron's electrical output



- Long (white matter) axons are covered in a *myelin sheath*, which increases the speed of electrical conduction

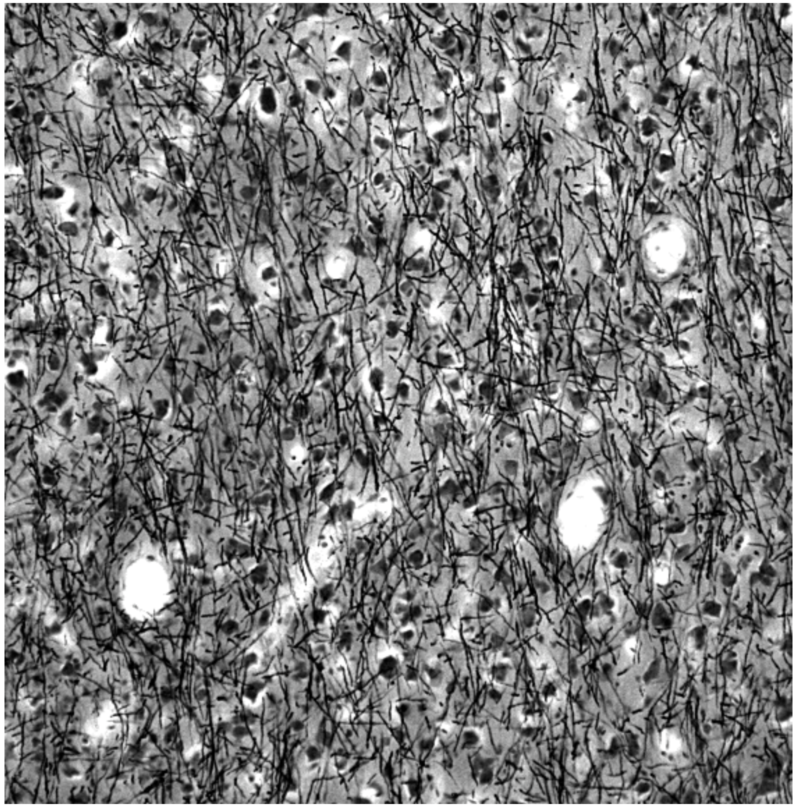
Dendrites and Axons



From Elston (2003), Cereb. Cortex 13:1124-1138

- Human cerebral cortex contains 20 billion neurons, with a variety of morphological (shape) and signalling properties, organised into *six layers*
- This image is of a “vertical” slice through cortex. Only a few of the densely connected neurons that would be found in an area of this size are shown
- Each neuron’s *dendritic tree* ramifies widely
- A single neuron can project to as many as 10,000 other neurons

Brains without Layers

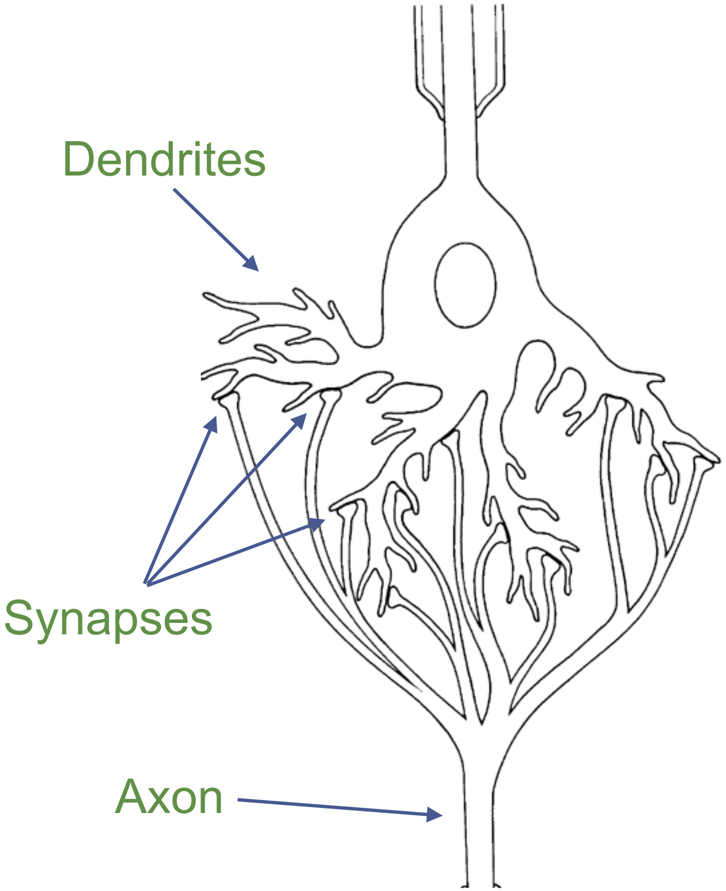


Neurons in the nidopallium of a pigeon

- Not all animals have a layered cortex as mammals do
- The avian brain doesn't have layers, but is nucleated
- The region of the avian brain that is analogous to the prefrontal cortex of the mammalian brain is part of the nidopallium (shown here)
- This area is likely to contribute to the intelligence of clever bird species, such as crows and rooks

Synapses 1

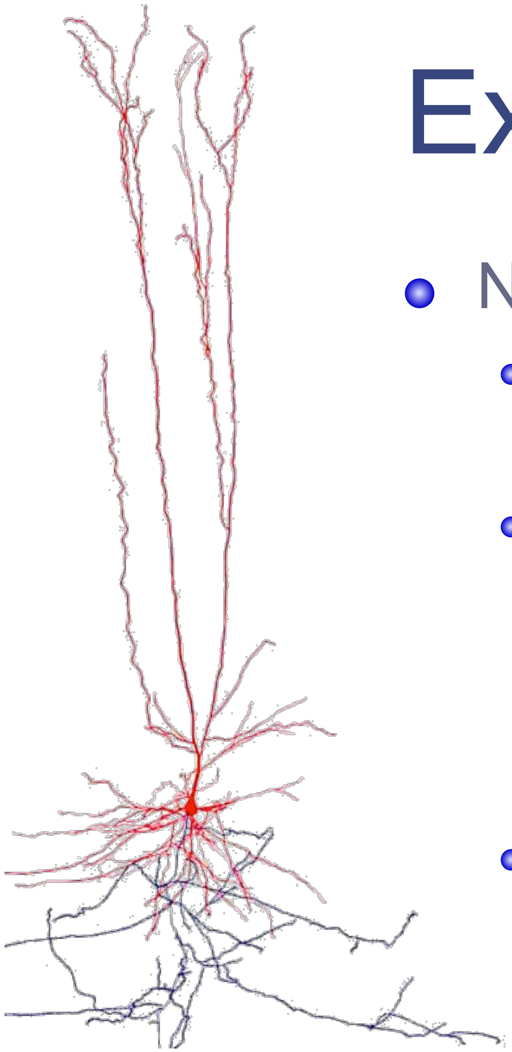
- The junctions where axons meet dendrites and signals are transmitted from the former to the latter are called *synapses*
- Synapses are not direct electrical connections. Rather, there is a tiny gap between the axon and the dendrite in which a complex electrochemical process takes place that allows a signal to be transmitted



Synapses 2

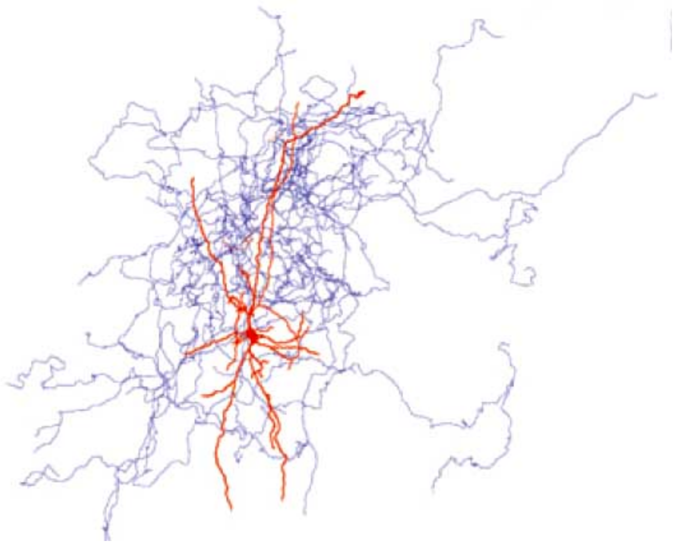
- This process of synaptic transmission is fundamental to the operation of the brain
  - There is a whole soup of electrically significant chemicals in the synaptic cleft. These are called *neurotransmitters*, and include serotonin, dopamine, and adrenaline
  - Many antidepressant drugs work by modifying serotonin uptake
  - Adrenaline influences behaviour in “fight or flight” situations
  - Dopamine is involved in the brain’s reward system
- However, in this course we *will* treat synapses as simple weighted connections, because our focus is dynamics on a larger scale. But it’s important to recognise the limitations of this simplification

Excitation and Inhibition



Pyramidal cell (excitatory)

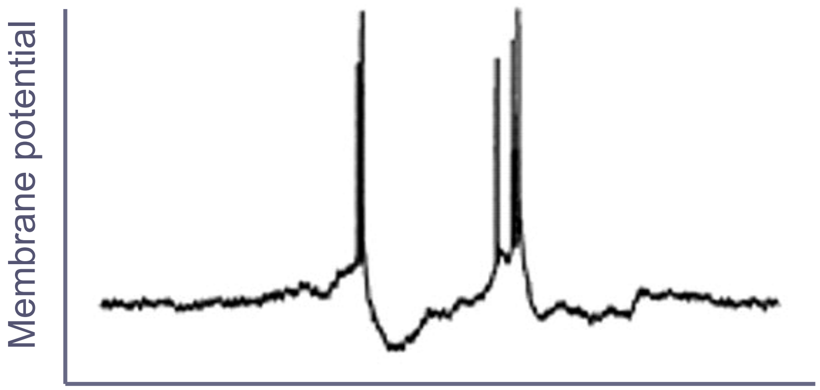
- Neurons fall into two major sub-classes
  - *Excitatory* neurons increase the activity of the neurons they are connected to
  - *Inhibitory* neurons decrease the activity of neurons they are connected to
  - Neurons are either excitatory or inhibitory, but not both



Inhibitory interneuron

Basic Neuron Behaviour

- Neurons receive and transmit electrical pulses, or *spikes*
- Incoming spikes travel along a neuron's dendrites, and cause charge to build up in the body of the neuron. When this charge reaches a threshold, the neuron fires, and sends a spike along its axon

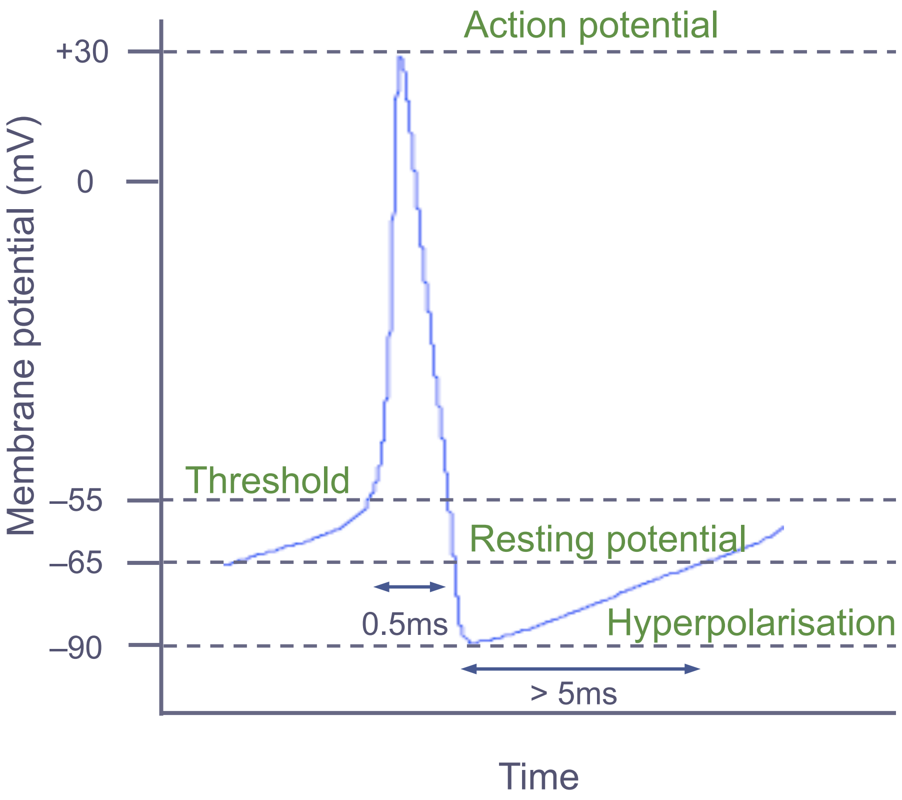


From Hirsch, *et al*. (2002). J. Physiol 540:335-350

- This plot shows the spiking behaviour of a single neuron recorded in the visual cortex of a cat
- Axons meet dendrites at synapses. The transmission of a signal across a synapse involves a complex electrochemical process which we shan't go into

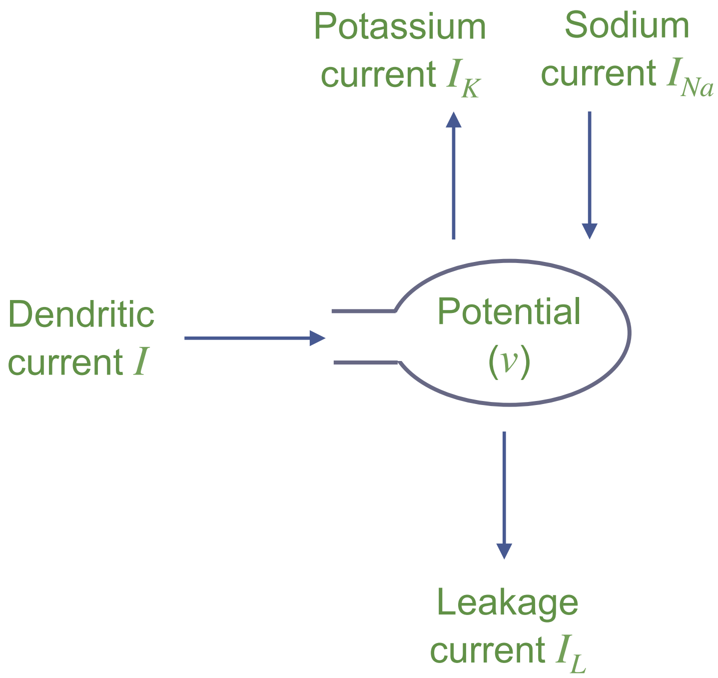
Detailed Neuron Behaviour

- Current flowing into a neuron along its dendrites, causes its *membrane potential* to increase
- Eventually the membrane potential reaches a *threshold* and the neuron rapidly *depolarises*, emitting a spike along its axon
- It then *repolarises*, typically undershooting its resting potential
- This undershoot gives rise to a *refractory period*, during which the neuron cannot fire again
- When unperturbed, the neuron tends towards a stable *resting potential*



Towards a Computer Model

- To see how this behaviour can modeled mathematically, and then simulated on a computer, we need to understand a bit more about the underlying physical processes
- The neuron's potential (v) exhibits its characteristic spiky profile thanks to the interplay of three currents that flow across the neuron's membrane, in addition to the incoming current from its dendrites (I)
  - The potassium current I_K
  - The sodium current I_{Na}
  - The leakage current I_L



The Hodgkin-Huxley Model 1

- More formally, according to the Hodgkin-Huxley model, we have

$$C\frac{dv}{dt} = -\sum_k I_k + I$$

where C is the capacitance of the neuron (set to 1), and

$$\sum_k I_k = g_{Na} m^3 h(v - E_{Na}) + g_K n^4 (v - E_K) + g_L (v - E_L)$$

Sodium current I_{Na}

Potassium current I_K

Leakage current I_L

The Hodgkin-Huxley Model 2

- The gs and Es are parameters of the model, determined empirically. The following values are the ones reported by Hodgkin and Huxley in their 1952 paper

$g_{Na} = 120$	$E_{Na} = 115$
$g_K = 36$	$E_K = -12$
$g_L = 0.3$	$E_L = 10.6$

- Three further differential equations govern the evolution of m, n, and h

The Hodgkin-Huxley Model 3

- The potassium and sodium currents behave as if *gates* open and close, allowing strong but brief flows of current, first in (sodium) then out (potassium)

$$\frac{dm}{dt} = \alpha_m(v)(1-m) - \beta_m(v)m$$

$$\alpha_m = (2.5 - 0.1v)/(e^{(2.5-0.1v)} - 1)$$

$$\beta_m = 4e^{-v/18}$$

$$\frac{dn}{dt} = \alpha_n(v)(1-n) - \beta_n(v)n$$

where

$$\alpha_n = (0.1 - 0.01v)/(e^{(1-0.1v)} - 1)$$

$$\beta_n = 0.125e^{-v/80}$$

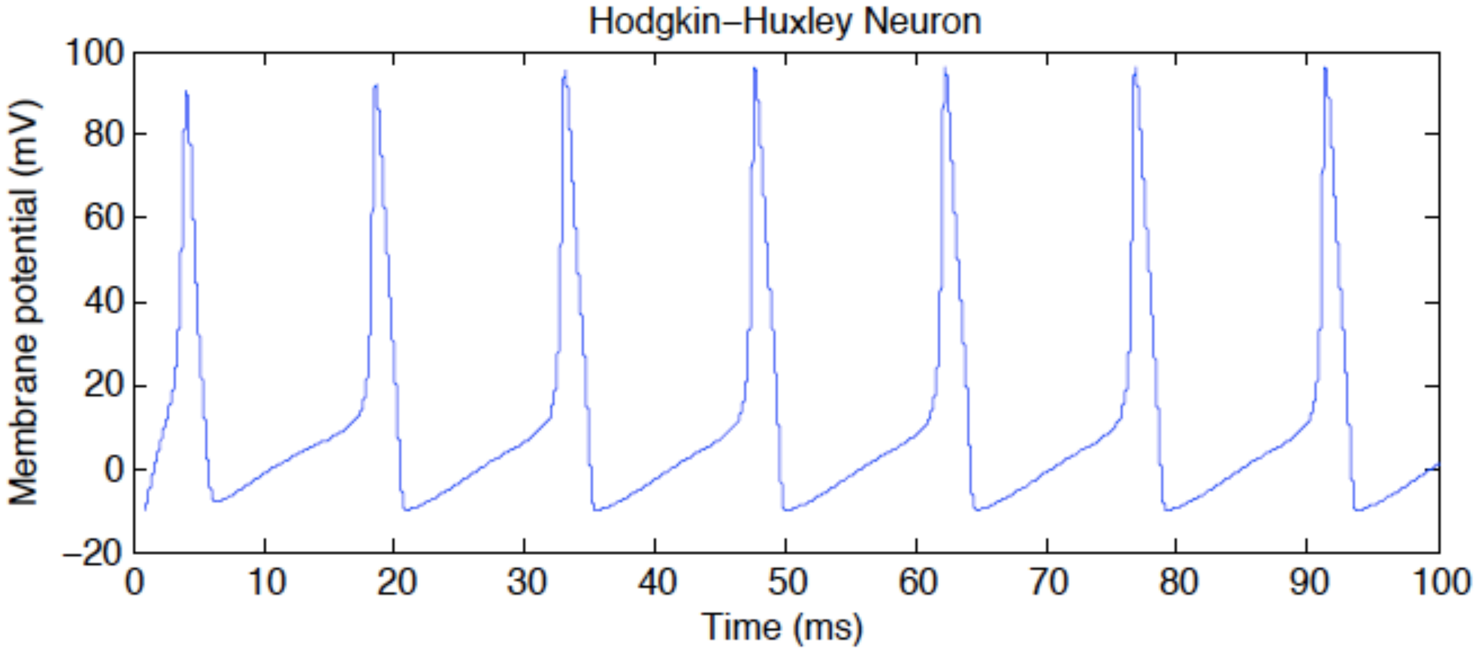
$$\frac{dh}{dt} = \alpha_h(v)(1-h) - \beta_h(v)h$$

$$\alpha_h = 0.07e^{-v/20}$$

$$\beta_h = 1/(e^{(3-0.1v)} + 1)$$

The Hodgkin-Huxley Model 4

- The resulting model accurately reproduces the signalling properties of neurons, and is still the standard mathematical model used today



Related Reading

Trappenberg, T.P. (2010). *Fundamentals of Computational Neuroscience*. Oxford University Press.