Part IV Brains

Chapter 11 From Soap to Volts

Chapter 12 Hodgkin-Huxley Model

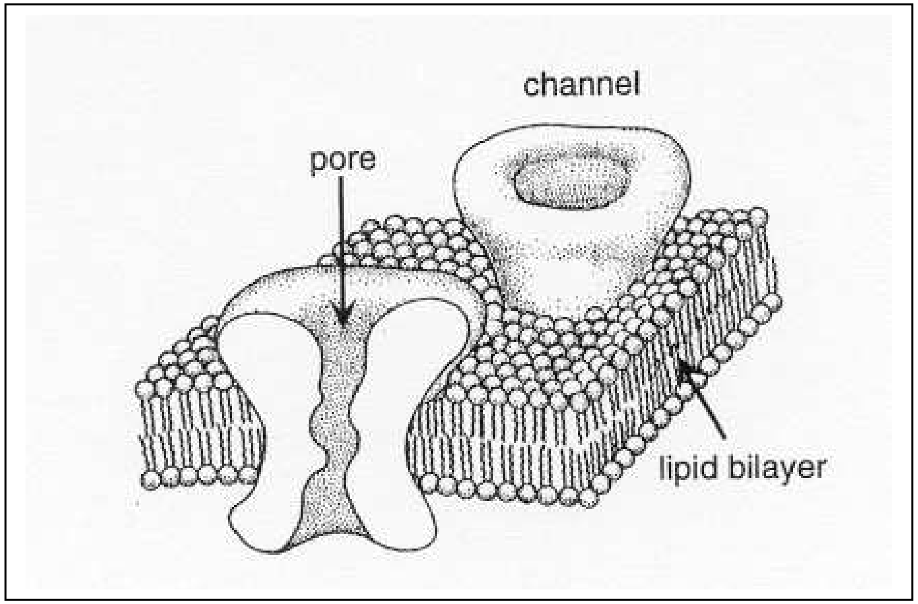
Chapter 13 Compartment Modelling

Chapter 14 From Artificial Neural Network to Realistic Network

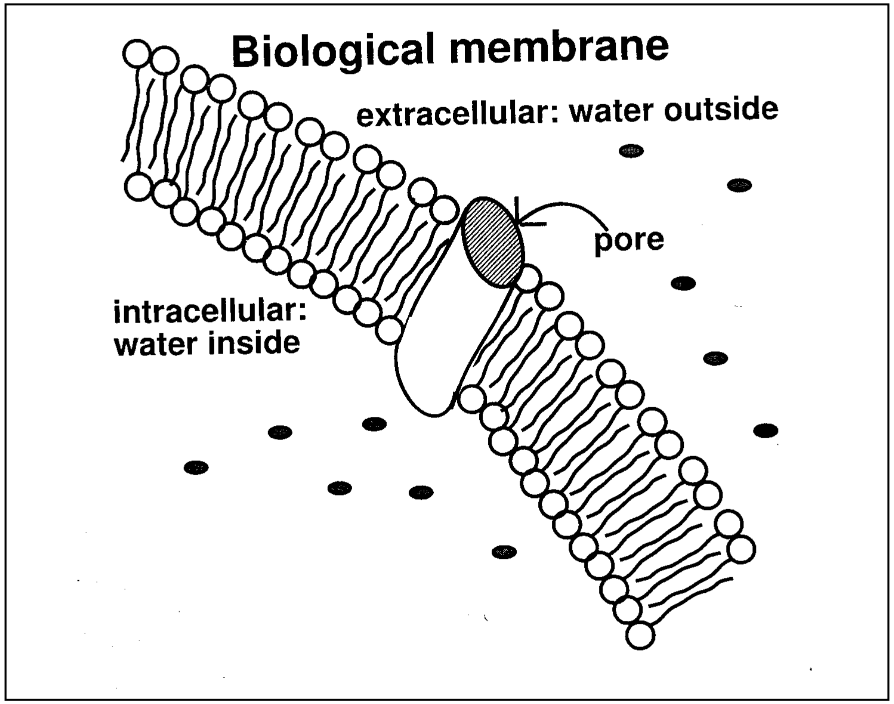
Chapter 15 Neural Circuits

This is a bottom up approach, starting with a more detailed model of the neuron and ending with some notes on organizational characteristics in different parts of the brain.

Chapter 11 From Soap to Volts, The Neuron's Membrane



From Dayan and Abbott



From Lytton

The lipid bilayer is a strong barrier to any movement of charged ions through the membrane.
The channel, or pore, will let ions through, but not without resistance.
There are many types of channels, so far we only study a generic channel.

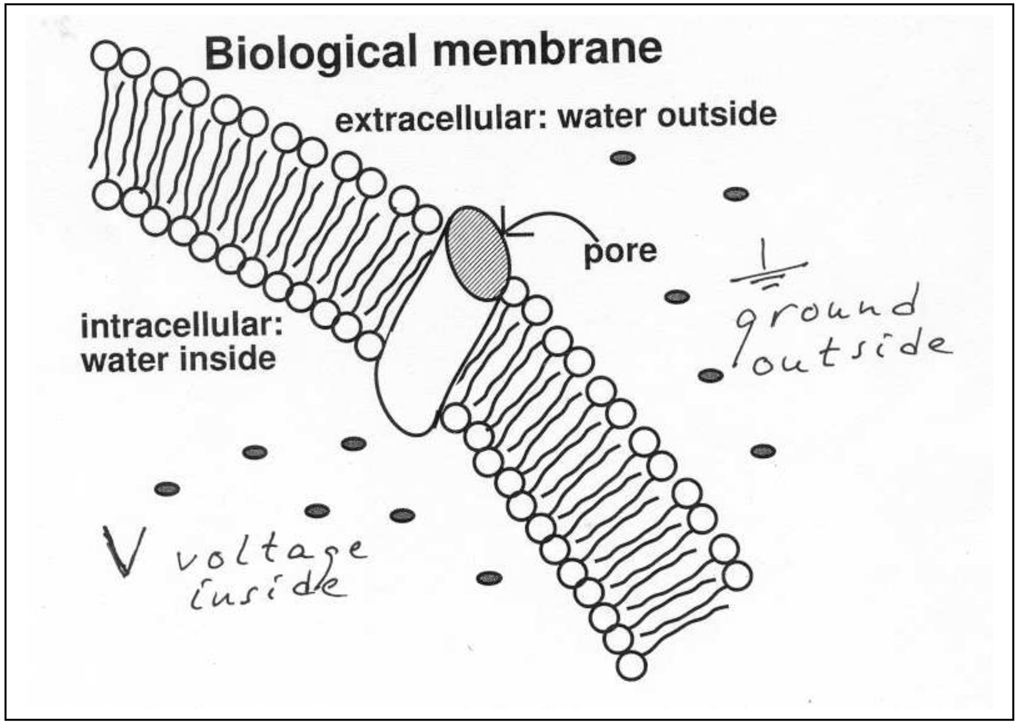
Chapter 11 From Soap to Volts

It is arguably in the varying voltages across neurons' membranes where information resides and is processed (the chemical processes in the synaptic cleft also play an important role). It is therefore important to study the electrical properties of the membrane.

In this chapter we give a first, very simplified version of an electrical model of the neuron's membrane.

Chapter 11 From Soap to Volts, Voltage across membrane

By convention we let the potential on the outside of the membrane, in the extracellular liquid, be 0. The voltage on the inside of the membrane, in the intracellular liquid, is then *V*.



V can be, and indeed normally is, negative. The resting membrane potential RMP, is on the order of –70 mV.

Chapter 11 From Soap to Volts, Capacitance of membrane

We have a barrier the charges cannot move across. The charges are free to move (in the liquid, intracellular and extracellular) on both sides of the barrier.

From an electrical point of view that barrier is a capacitor and has capacitance C or capacitance per unit area c.

The SI unit is F and F/m^2 respectively but values are often given in units such as μF and μF/cm^2 respectively.

If we have a charge $+Q$ on one side of the barrier and $-Q$ on the other, then we will have a voltage, or potential difference, V across the barrier. Assuming the relation between Q and V is linear we can express the relation by $Q = CV$. The same relation can be given between charge q per unit area, and voltage, $q = cV$.

The unit for charge is Coulomb (abbreviated C but not the same C as for capacitance) and for voltage Volt (abbreviated V) or milliVolt (mV).

Chapter 11 From Soap to Volts, Capacitance of membrane

Moving charges constitute current. A charge ΔQ that moves across a given surface in time Δt constitutes a current $I = \Delta Q / \Delta t$ across that surface. Current is measured in Amperes (A) or µA.

Likewise a charge Δq that moves across a surface of unit area in time Δt constitutes a current density $i = \Delta q / \Delta t$. Current density is often measure in µA/ cm^2.

Assuming that the capacitor is constant we also have the relations $\Delta Q = C\Delta V$ and $\Delta q = c\Delta V$.

During build-up of voltage across a capacitor, charge must flow to its "plates" (i.e. to the two sides of the neuron's membrane in our case). This constitutes a current $I = \Delta Q / \Delta t = C\Delta V / \Delta t$ directed to the plate with charge $+Q$. Or, in density terms, $i = \Delta q / \Delta t = \mathrm{c}\Delta V / \Delta t$.

If we let Δt become infinitesimally small we can write these relations as $I = CdV / dt$ or $i = \mathrm{c}dV / dt$.

These relations are called constitutive relations for the capacitor.

Chapter 11 From Soap to Volts, Resistance and conductance of membrane

There are many channels in the membrane. These let charge pass through but not without resistance. Summing up their action we get a resistor, or conductor which is two ways of expressing the same thing.

We now make the assumption that the resistor is linear, i.e. that we can use Ohm's "law"
$V = RI$ or, conversely, $I = GV$.

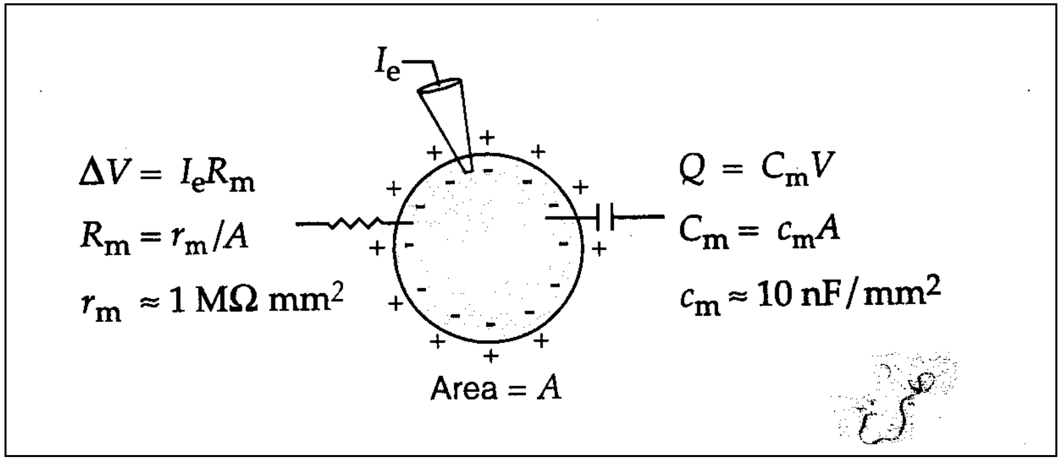
R is the resistance measured in Ohm (Ω), G is the conductance measured in Siemens (S). Often kΩ or mS is used instead.

In density terms we often use $k\Omega/cm^2$ or mS/cm^2.

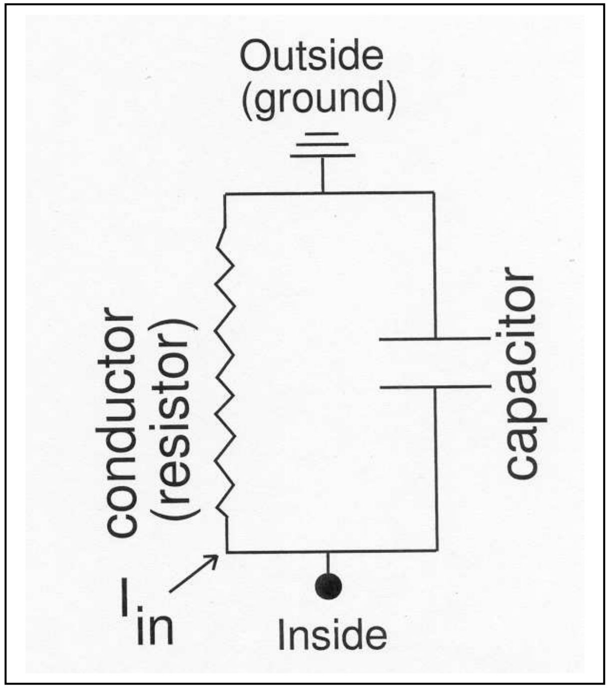
$V = RI$ is called the constitutive relation for a linear resistor.

Chapter 11 From Soap to Volts

An electrical model of the neuron's membrane: a first, very simplified version. I_e and I_{in} below will be dealt with later.



From Dayan and Abbott



From Lytton

Chapter 11 From Soap to Volts

The voltage across membrane constitutes a dynamic process

A word of caution: this chapter doesn't come close to tell the truth or the whole truth. Let us say that the goal is to study something much simpler than the real neuron's membrane with the intention of complementing the model afterwards.

Chapter 11 From Soap to Volts

Voltage across membrane: a dynamic process

Kirchhoff's current law: The sum of all currents from a node is zero.

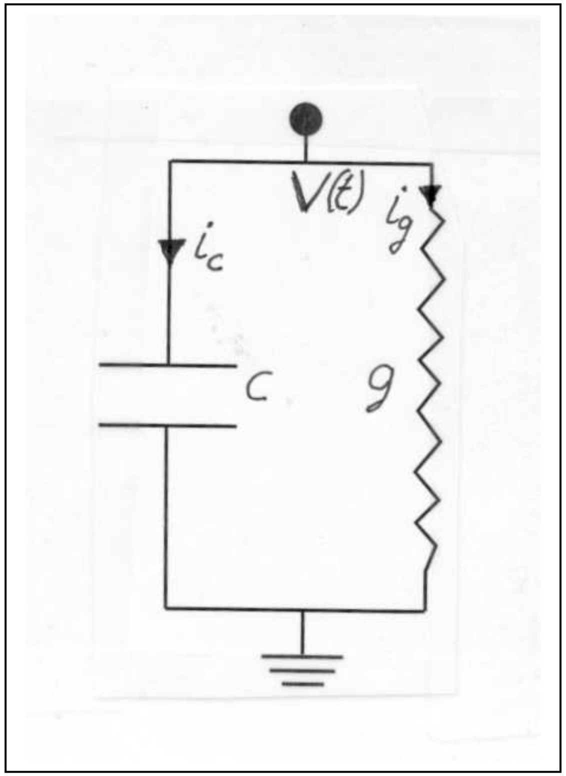
In our case the outside of the neuron's membrane is a node and so is the inside.

Now let us combine the capacitance and conductance densities in one electric circuit model of the membrane and apply Kirchhoff's current law.

$$i_c + i_g = 0$$

$$c dV/dt + gV(t) = 0$$

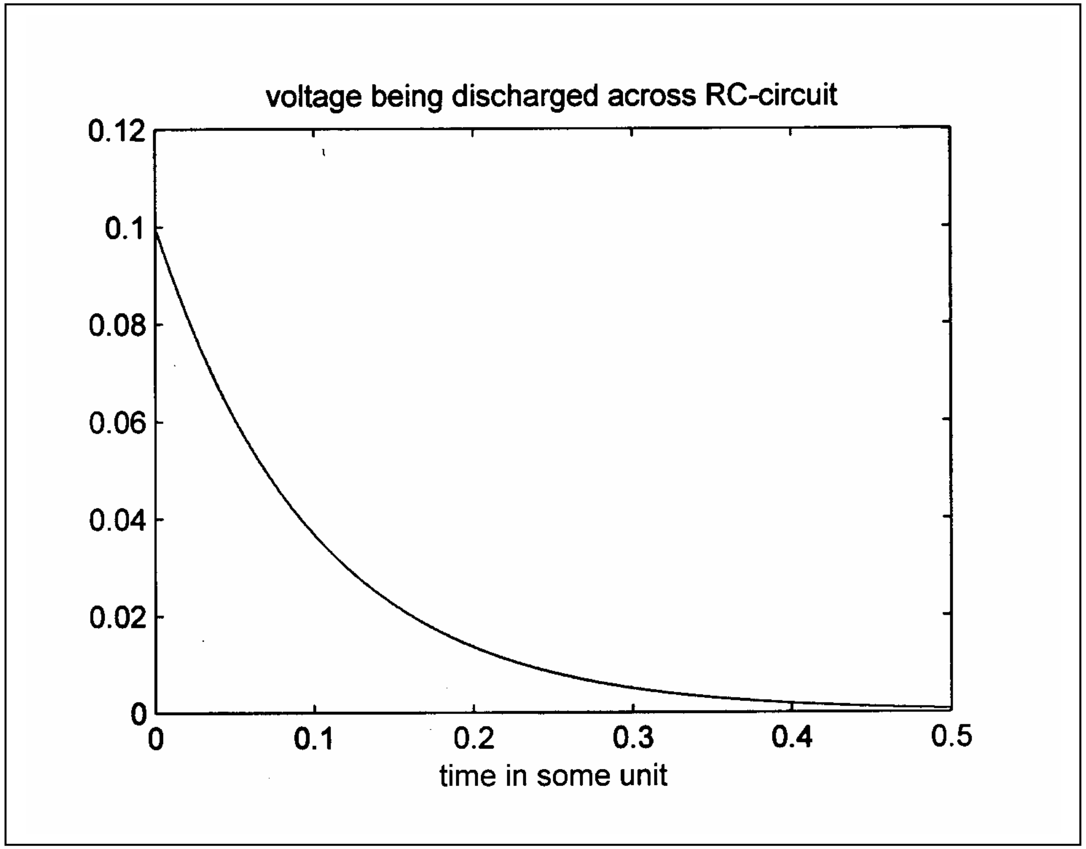
$$dV/dt + (g/c)V(t) = 0$$



Chapter 11 From Soap to Volts

Voltage across membrane: a dynamic process

$dV/dt + (g/c)V(t) = 0$ is a homogenous first order differential equation. Its solution for time t > 0 depends on the value of $V(0)$ and is $V(t) = V(0)e^{-(g/c)t}$ (here $V(0) = 0.1$, $g = 0.1$, $c = 0.01$)



Chapter 11 From Soap to Volts

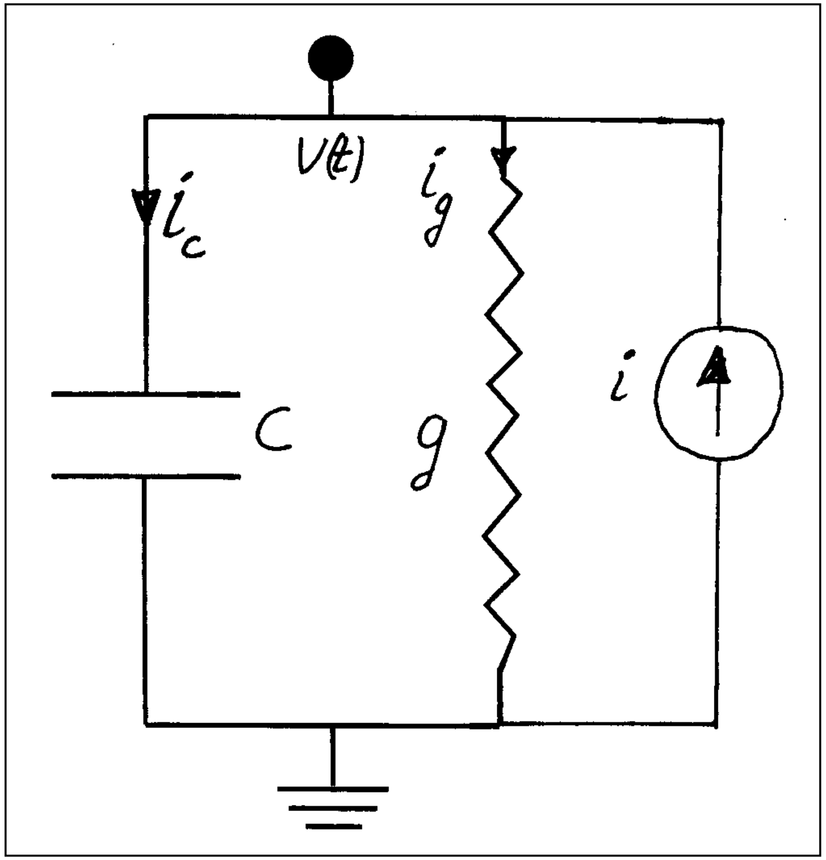
Injection of a current into neuron through neuron's membrane

We study densities, so we use a current density i

$$-i + i_c + i_g = 0$$

$$c\,dV/dt + gV(t) = i$$

$$dV/dt + (g/c)V(t) = i/c$$



Chapter 11 From Soap to Volts

Injection of current into neuron through neuron's membrane

$dV/dt + (g/c)V(t) = i/c$ is an inhomogenous first order differential equation. Its solution for time t > 0 depends on the value of $V(0)$, which we set as 0 in order to study the same case as Lytton, and the injected current i.

Lytton injects a current pulse, and so do we. We need two parameters, the height i_0 of the pulse and the duration T of the pulse.

$$V(t) = (i_0/g)(1- e^{-(g/c)t})\sigma(t) - (i_0/g)(1- e^{-(g/c)(t-T)})\sigma(t-T)$$

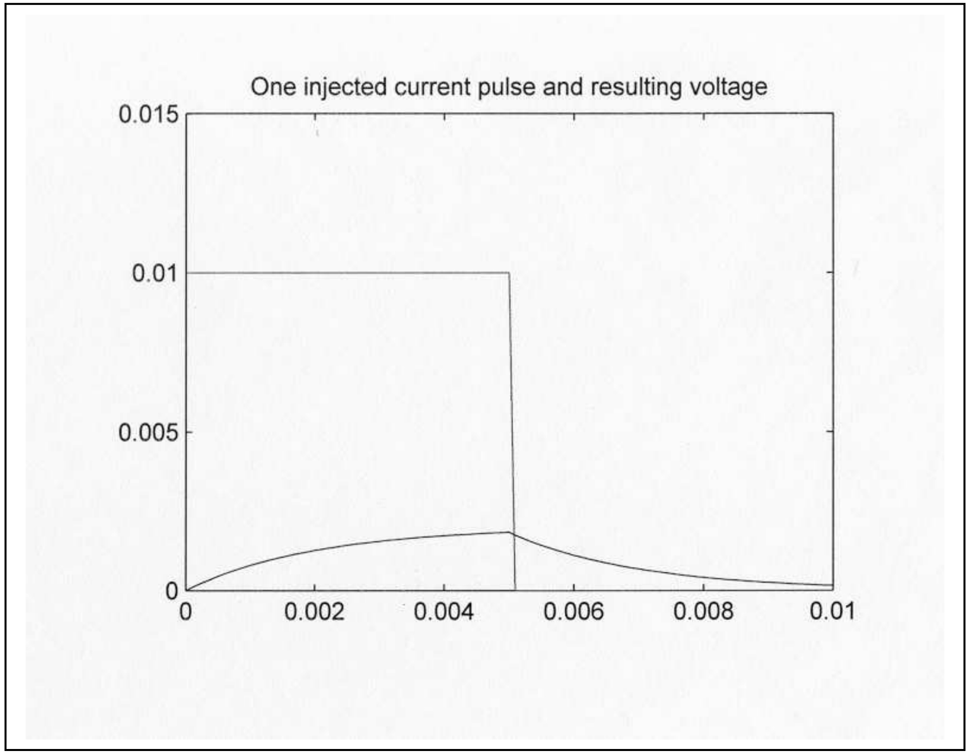
where $\sigma(t)$ is a step function, 0 for $t < 0$ and 1 for $t > 0$.

When we have more complicated shapes of the injected current it is easier to solve the differential equation numerically and present the solution as a graph.

A graph is always instructive so let us give one for our *V(t) as well.*

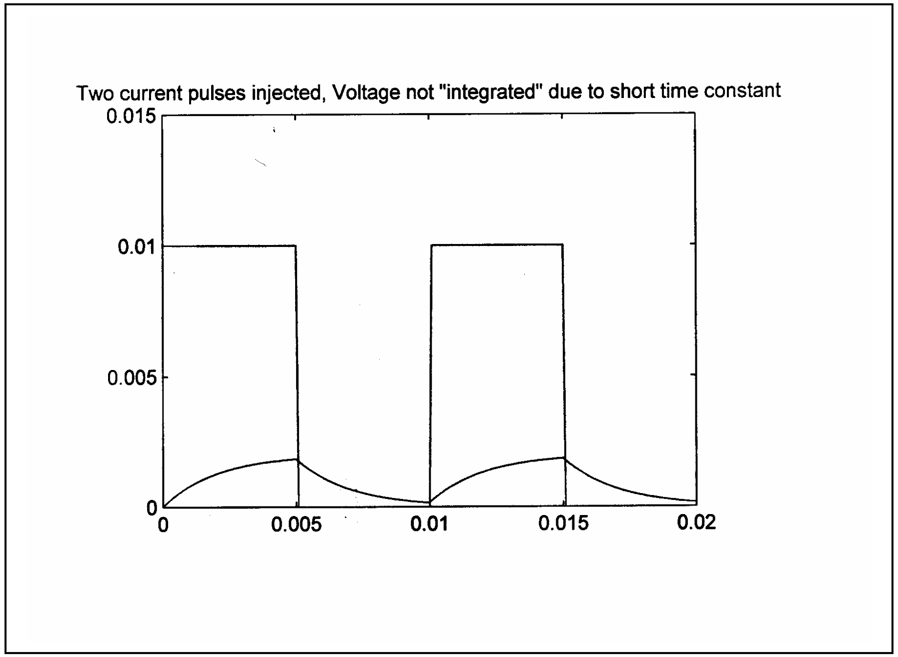
Chapter 11 From Soap to Volts

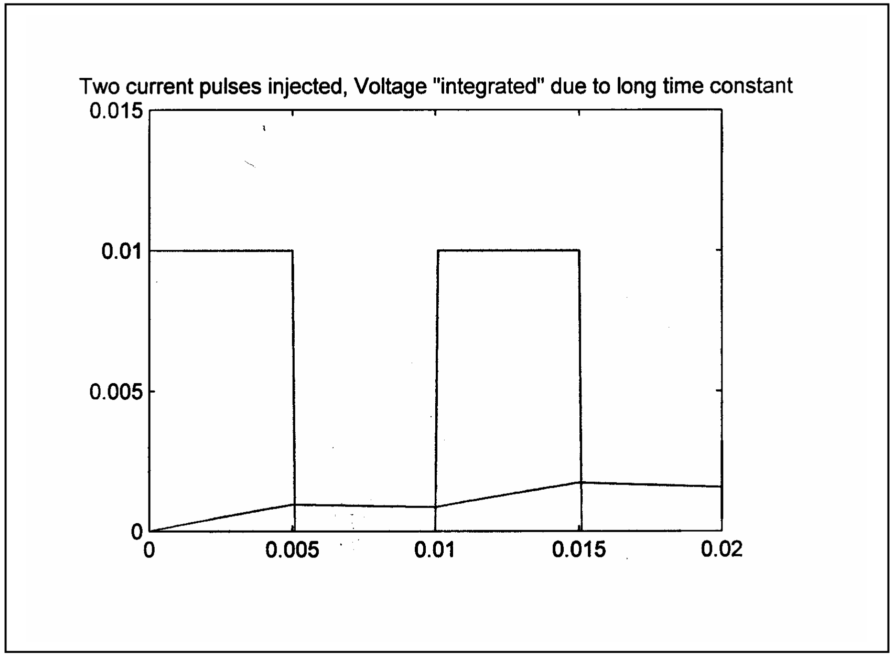
Injection of one current pulse into neuron through neuron's membrane



Chapter 11 From Soap to Volts

Injection of two current pulse into neuron through neuron’s membrane





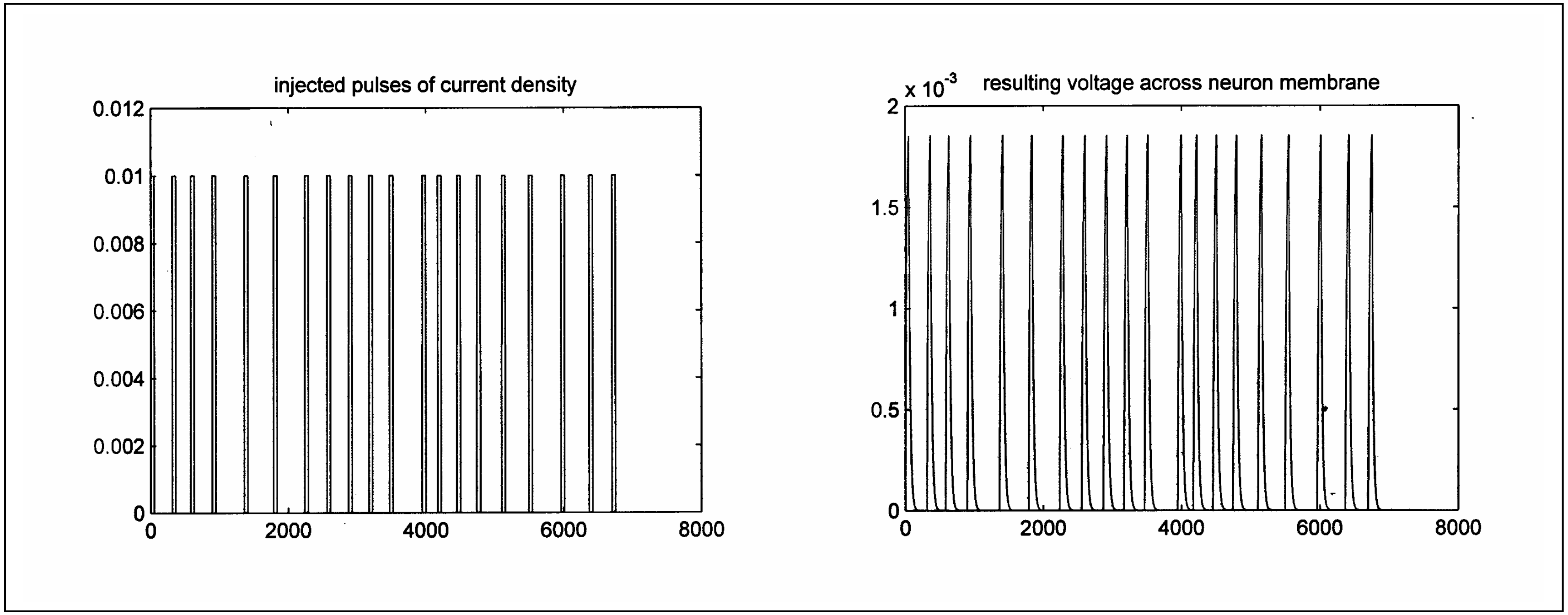
No integration

Integration!

Chapter 11 From Soap to Volts

Injection of many current pulses into neuron through neuron's membrane

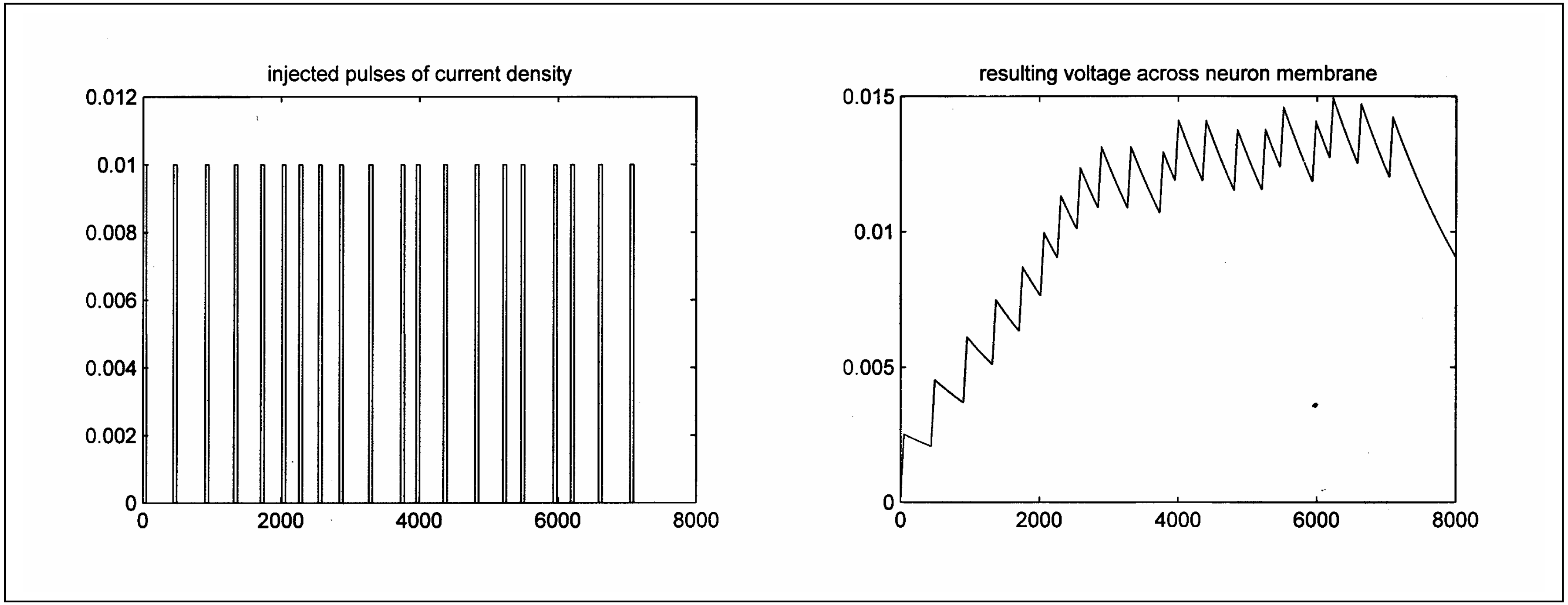
Below 20 current pulses have been injected. The time intervals between pulses vary a little. Nothing interesting happens. The voltage resembles the current pulses in this case. The membrane is too quick to respond.



Chapter 11 From Soap to Volts

Injection of many current pulses into neuron through neuron’s membrane

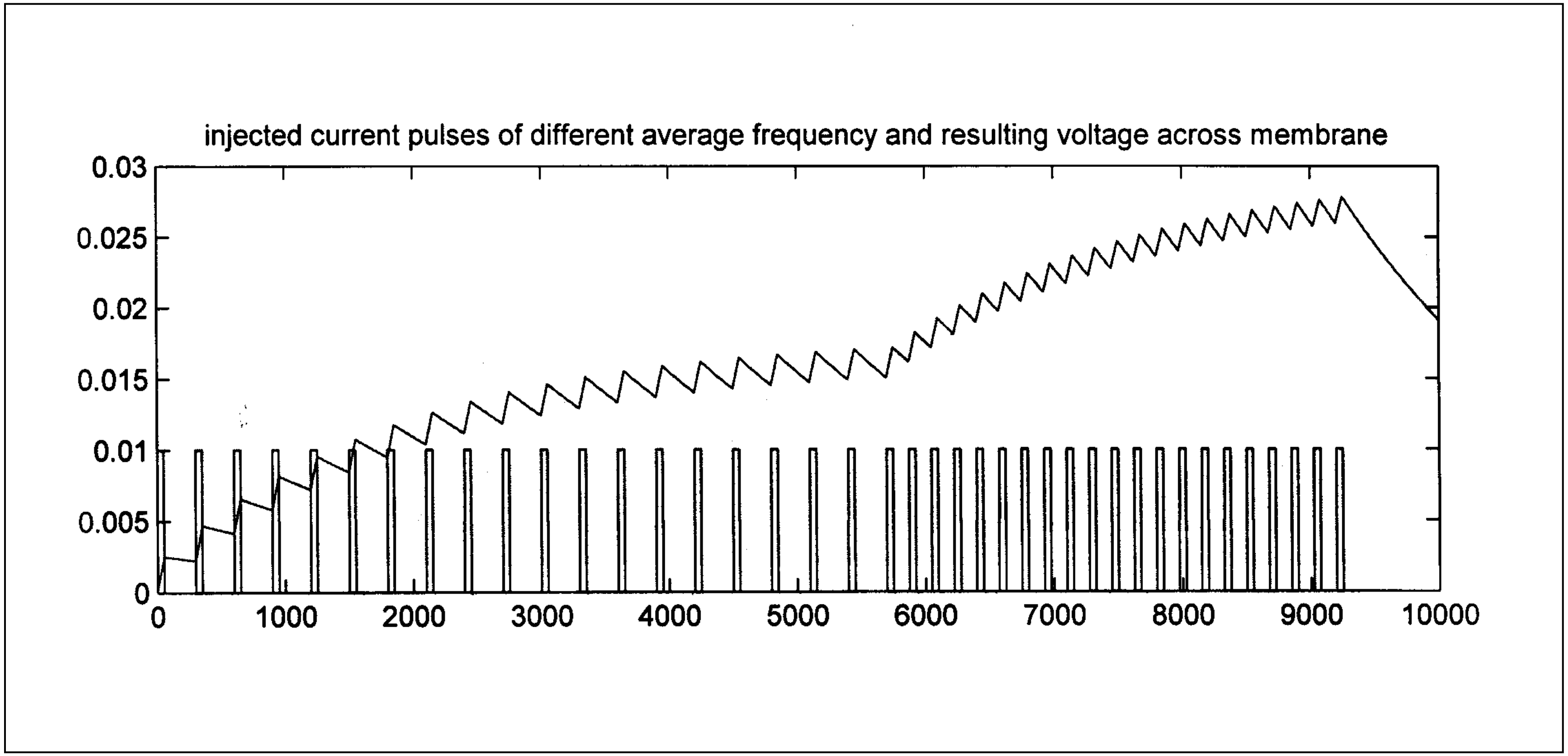
Below 20 current pulses have been injected. The time intervals between pulses vary a little. Here the membrane reacts slower to the pulses – the voltages caused by each current pulse are “stretched out” in time and therefore add up. **This is temporal integration**.



`Chapter 11 From Soap to Volts

Injection of many current pulses into neuron through neuron's membrane

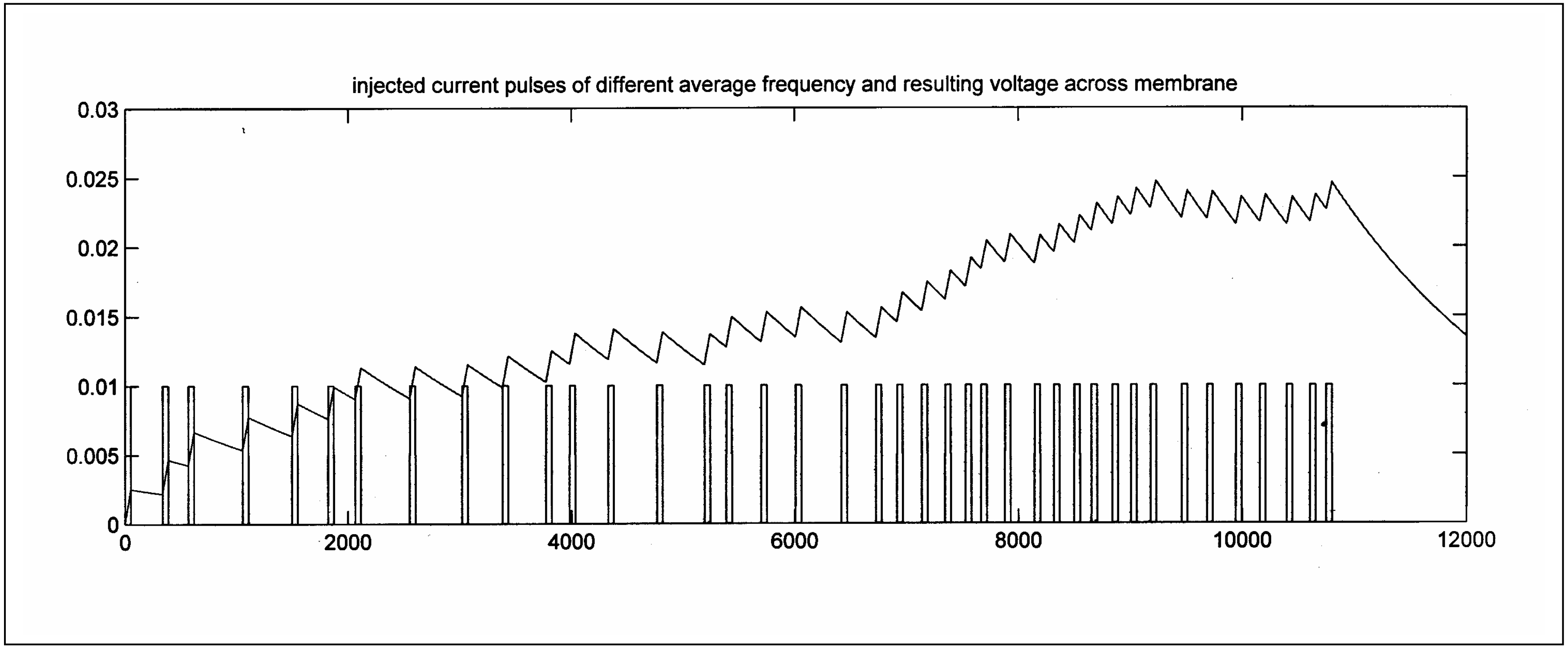
Below the pulses have been generated to have a low frequency initially and a high frequency towards the end of the pulse train you can clearly see when the frequency changes, but the resulting voltage doesn't quite settle down within the time for the high frequency pulses.



Chapter 11 From Soap to Volts

Injection of many current pulses into neuron through neuron's membrane

Below the pulses have been generated to have a low frequency initially and a high frequency towards the end of the pulse train. There is, in addition, also some randomness in the times between the pulses (does the voltage settle down to its "right" value?)



Chapter 11 From Soap to Volts – A Dilemma

We often make compromises between two goals that cannot be fulfilled at the same time. This chapter treats one such dilemma, and what's more, Lytton leaves us without a solution to the dilemma.

We assume that the pulse rate carries information and we also assume that short-time variations of this pulse rate constitute noise, i.e. that they don't carry information. So we want to find averages, through temporal integration, that indicate the pulse rate variations which carry information and suppress the pulse rate variations which are just noise.

If the pulse rate variations that carry information vary very slowly and the noisy short time variations are brief the task of separating the two is easy – we just choose our temporal integration to average over long times. But, as Lytton points out, we want to be able to carry information that changes quickly, and then we have a dilemma – then temporal integration must average over short times and it will not suppress the noisy short time variations.

We can find an optimal solution to this dilemma, but an optimal solution is just the best possible solution, it might not be a good solution.

Chapter 11 From Soap to Volts – A Dilemma Illustrated by Lytton

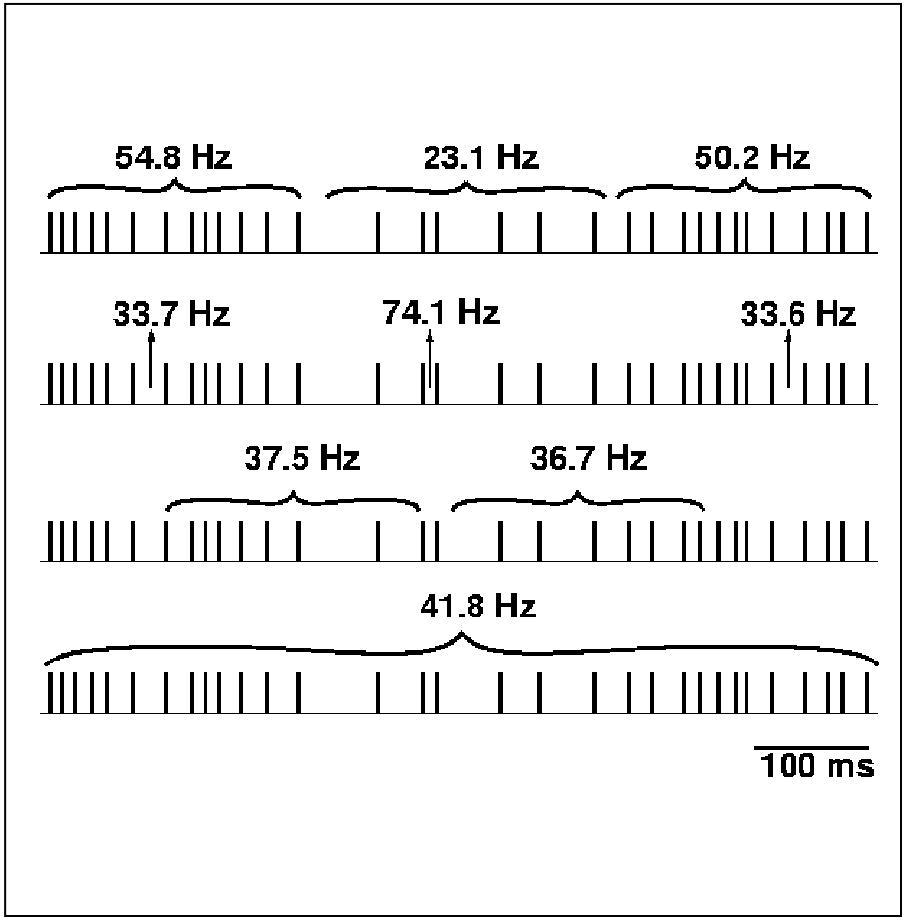
Data is generated in three packages with three average frequencies, as shown on the first row.

The second row is an interpretation over too short time intervals.

The third row is an interpretation over reasonable time intervals but with poorly chosen start and stop.

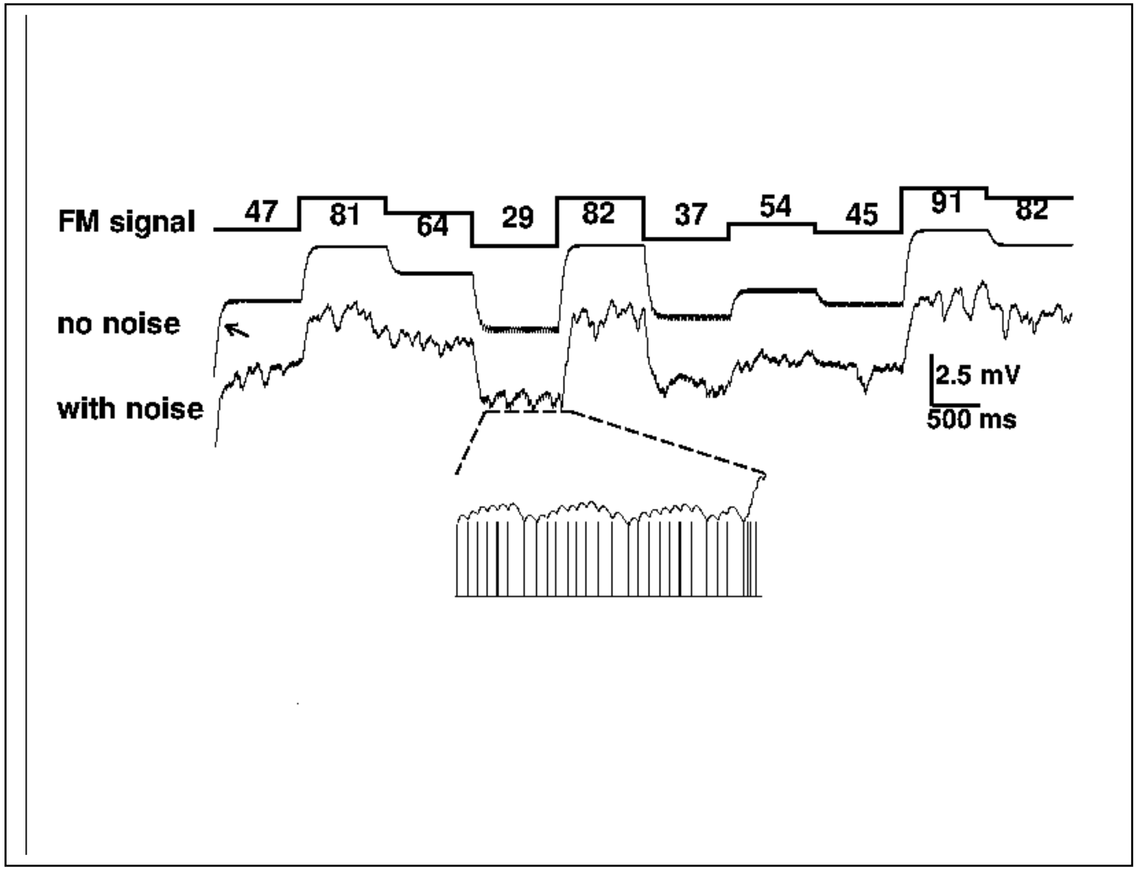
The fourth row is an interpretation over a time interval that is too long.

Note that these interpretations are slightly different from the temporal integration!



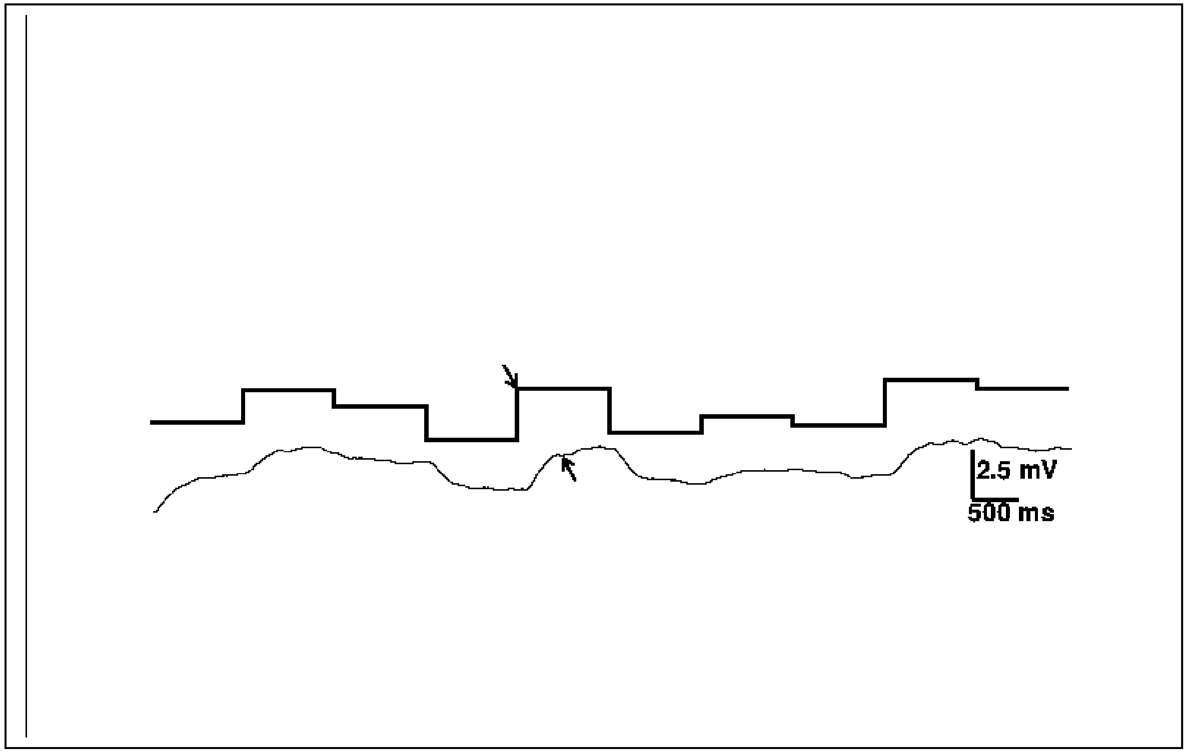
Chapter 11 From Soap to Volts

Fast temporal integration quickly finds changes in information carrying pulse rates, but with noise introduced becomes hard to interpret. (From Lytton)



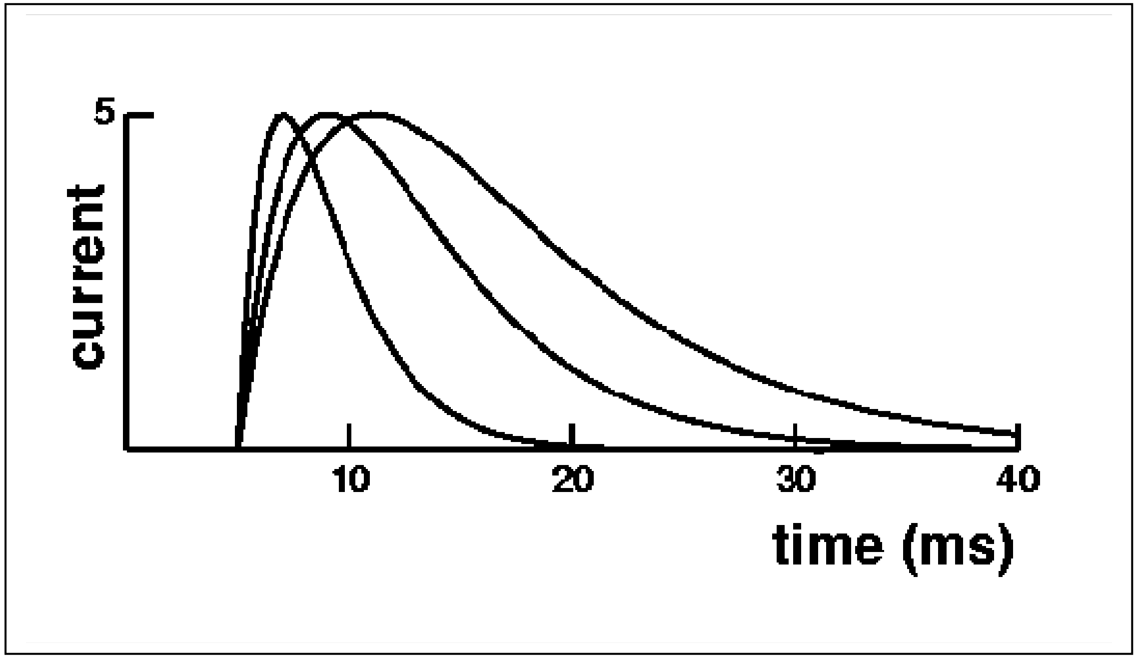
Chapter 11 From Soap to Volts

Slow temporal integration takes a long time to find changes in information carrying pulse rates, but even with noise introduced becomes straightforward to interpret, after some time i.e.. (From Lytton)



Chapter 11 From Soap to Volts

The alpha function describes a more realistic current injection than the rectangular pulses used above. It is based on the functioning of real synapses. It changes the computations but not the essential results and it doesn't solve the dilemma. Lytton gives an expression of the function and the figure below is also from Lytton.



Chapter 11 From Soap to Volts

Electrical model, first version

There is liquid on both sides of the membrane, extracellular liquid and intracellular liquid.

There are charged particles in the liquid on both sides of the membrane.

Outside (in the extracellular liquid) there are more Na^+ (sodium) ions than inside.

Inside there are more K^+ (potassium) ions than outside.

There are more kinds of ions, but these will do for now.

There are ion pumps that see to it, at great energy expenditure, that these concentration differences are upheld, most of the time.

Chapter 11 From Soap to Volts

Electrical model, first version

Differences in concentration of charge