2. Building a Passive Neuron

2.1. Batteries, Resistors, and Capacitors

The signals in the brain arise from the motion of charged particles - typically ions of sodium, Na^+, chloride, Cl^-, potassium, K^+, and calcium, Ca^{++}.

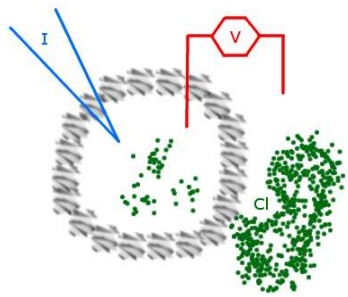


Figure 2.1. The typical neuron pumps chloride out of the cell to the degree that its intracellular concentration is one tenth of its extracellular concentration. This imbalance establishes a nonzero rest potential, V_{Cl}. We impale the cell with an electrode that delivers current I and measures the resulting potential, V.

The energy required to move charge is called **voltage** while the rate at which charge moves is called **current**.

A **battery** is a source of constant voltage, e.g., V_{Cl}.

A **resistor** is a device that resists (or diminishes) current. Voltage, current and resistance come together in the circuit model, see Figure 2.1, that biologists use of the cell's chloride channel. In this case we denote the resistance of the channel by R_{Cl} and place it line (or in series) with the chloride battery, V_{Cl}. We then denote by I_{Cl} the current traveling through the resistor. We connect these quantities to the **transmembrane potential**,

$$V \equiv V_{in} - V_{out} \tag{2.1}$$

via

> **Ohm's Law:** The current through a resistor equals the voltage drop across the resistor divided by its resistance.

To put this into practice, with reference to Figure 2.1, we find

$$I_{Cl} = (V_{mid} - V_{out})/R. \tag{2.2}$$

As voltages in series add we find

$$V_{mid} + V_{Cl} = V_{in}. \tag{2.3}$$

On combining (2.1)–(2.3) we arrive at the final mathematical model of the chloride channel,

$$I_{Cl} = (V - V_{Cl})/R_{Cl}. \tag{2.4}$$

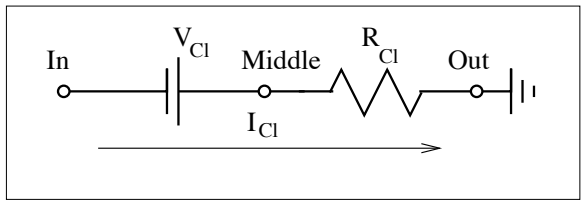


Figure 2.2 We model the cell membrane as a battery of size V_{Cl} in series with a resistance R_{Cl}.

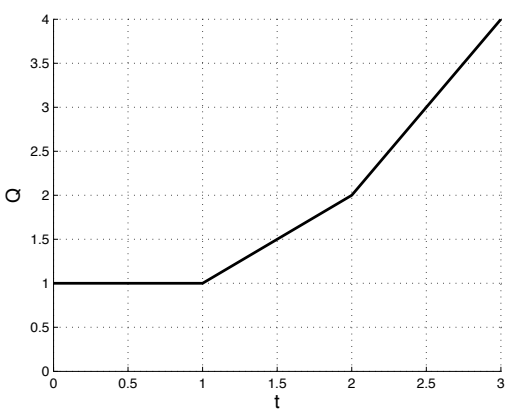
A **capacitor** is a device that stores charges in proportion to the voltage V across it. In particular, the charge Q stored by a capacitor of capacitance C will be

$$Q = C \cdot V. \tag{2.5}$$

When we say that current is the velocity of the charge we mean that current is the slope of the charge graph. That is

$$I(t) = \frac{\text{change in charge}}{\text{change in time}} = \frac{Q(t+dt) - Q(t)}{dt} \tag{2.6}$$

for some small time step, dt. For example, consider



t	Q(t)	Q(t+dt)	I(t)
0			
0.5			
1			
1.5			
2			
2.5			

Figure 2.3. For small dt, please confirm that if we substitute this Q into (2.6) we find $I(t) = 0$ when $0 < t < 1$, $I(t) = 1$ when $1 < t < 2$ and $I(t) = 2$ when $2 < t < 3$.

If we now combine equations (2.5) and (2.6) we arrive at a current–voltage relationship for capacitors,

$$I_C(t) = C \cdot \frac{V(t+dt) - V(t)}{dt} \tag{2.7}$$

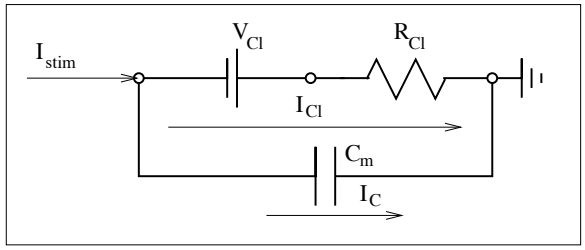


Figure 2.4. We add to the model above a parallel current that mimics the membrane's ability to store charge.

The fundamental circuit law is a simple balance law that requires current in to balance current out. In our case this reads

$$\begin{aligned} I_{stim}(t) &= I_{Cl}(t) + I_C(t) \\ &= (V(t) - V_{Cl})/R_{Cl} + C \cdot \frac{V(t+dt) - V(t)}{dt}, \end{aligned} \tag{2.8}$$

and it is very important to make sure that we are balancing consistent quantities. The conventional unit of current in the brain is one millionenth of an Ampere, written "micro–ampere," or μA for short.

1. The neuron's chloride resistance, R_{Cl}, is the ratio of its membrane resistivity, $\rho_{Cl} \approx 10/3\ k\Omega \cdot cm^2$, to the cell's surface area, $S \approx 10^{-5}\, cm^2$.

2. A typical chloride reversal potential, V_{Cl}, is $70\, mV$, i.e., 70 millivolts.

3. A neuron's capacitance, C, is the product of its membrane capacity $C_m \approx 1\, \mu F/cm^2$, i.e, 1 micro–farad per square centimeter, and its surface area, S.

The convential units for brain voltage and time are mV (milli-volts) and ms (milli-seconds) respectively. Please confirm that (2.8) is indeed equating μA to μA.

We typically rearrange (2.8) to express "the future in terms of the present," i.e., we solve for $V(t+dt)$ in terms of quantities at t,

$$V(t+dt) = (1 - dt/\tau)V(t) + (dt/\tau)V_{Cl} + (dt/C)I_{stim}(t), \tag{2.9}$$

where $\tau = R_{Cl}C$ is called the membrane time constant. This allows us to deduce $V(dt)$ from the known $V(0)$, and from there to step from $V(dt)$ to $V(2dt)$ and so on. Let us carry this out, with the parameter set above, along with

$$dt = 0.1\ ms \quad \text{and} \quad I_{stim}(t) = 10^{-5} \cdot (t >= 0.5) \cdot (t <= 1.5)\ \mu A.$$

The latter is using the Octave notation for truth functions to build a a 1 ms pulse of current of amplitude $10^{-5}\ \mu A$. The pulse turns on when $t = 0.5$ and off when $t = 1.5$. Please confirm that (2.9) takes the concrete form

$$V(t + 0.1) = 0.97 \cdot V(t) - 2.1 + 0.1 \cdot (t >= 0.5) \cdot (t <= 1.5), \tag{2.10}$$

and so, commencing from $V(0) = V_{Cl} = -70$ we find, while $t < 0.5$, i.e., prior tothe stimulus,

$$V(0.1) = V(0.2) = V(0.3) = V(0.4) = V(0.5) = -70,$$

while

$$\begin{aligned}
V(0.6) &= 0.97 \cdot (-70) - 2.1 + 0.1 = -69.9 \\
V(0.7) &= 0.97 \cdot (-69.9) - 2.1 + 0.1 = -69.803 \\
V(0.8) &= 0.97 \cdot (-69.803) - 2.1 + 0.1 = -69.709 \\
V(0.9) &= 0.97 \cdot (-69.709) - 2.1 + 0.1 = -69.618 \\
V(1.0) &= 0.97 \cdot (-69.618) - 2.1 + 0.1 = -69.529 \\
V(1.1) &= 0.97 \cdot (-69.529) - 2.1 + 0.1 = -69.443 \\
V(1.2) &= 0.97 \cdot (-69.443) - 2.1 + 0.1 = -69.360 \\
V(1.3) &= 0.97 \cdot (-69.360) - 2.1 + 0.1 = -69.279 \\
V(1.4) &= 0.97 \cdot (-69.279) - 2.1 + 0.1 = -69.201 \\
V(1.5) &= 0.97 \cdot (-69.201) - 2.1 + 0.1 = -69.125 \\
V(1.6) &= 0.97 \cdot (-69.125) - 2.1 + 0.1 = -69.051 \\
V(1.7) &= 0.97 \cdot (-69.051) - 2.1 = -69.079 \\
V(1.8) &= 0.97 \cdot (-69.079) - 2.1 = -69.107 \\
V(1.9) &= 0.97 \cdot (-69.107) - 2.1 = -69.134 \\
V(2.0) &= 0.97 \cdot (-69.134) - 2.1 = -69.160 \\
V(2.1) &= 0.97 \cdot (-69.160) - 2.1 = -69.185
\end{aligned}$$

We see the voltage rise during the pulse and then fall back after the pulse. The substitutions into (2.10) are however tedious and error–prone. For such things computers are very useful.

2.2. Building the Neuron in Software

Lets see how to code (2.10) in Octave. We will accumulate time and voltage in two **vectors** of the form

$$t = (0,\ 0.1,\ 0.2,\ 0.3,\ 0.4,\ 0.5,\ 0.6,\ \ldots)$$
$$V = (-70,\ -70,\ -70,\ -70,\ -70,\ -70,\ -69.9,\ \ldots)$$

and then plot V *vs.* t. In the computer it is natural to use whole numbers to index the elements of vectors. For example, the first element of t is $t(1)$ and the third element of V is $V(3)$. In our Octave implementation of (2.10) we use n and our growing index, and in order to grow it we place (2.10) inside of a **for loop**. Please enter and run this program in Octave.

```
t(1) = 0;
V(1) = -70;
for n=1:150,
   t(n+1) = n*0.1;
   V(n+1) = 0.97*V(n) - 2.1 + 0.1*(t(n)>=0.5)*(t(n)<=1.5);
end
plot(t,V,'x')
grid on
xlabel('t (ms)','fontsize',14)
ylabel('V (mV)','fontsize',14)
```

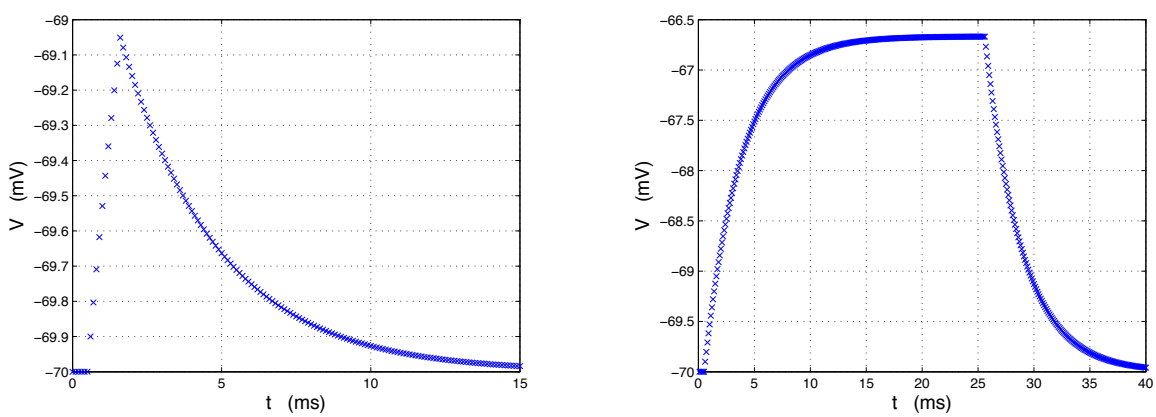


Figure 2.5. (Left) The result of the simulation coded above. (Right) The result of using a longer pulse. What did we change in the program?

How would we change the program to deliver a sinusoidal current rather than a single pulse? How could we instead deliver a train of pulses? Experiment with

vectors, for loops and plotting before proceeding.

Lets take a careful look at sinusoidal input, of frequency f and amplitude 10^{-4} μA, i.e.,

$$I_{stim}(t) = 10^{-4}\sin(2\pi f t).$$

In this case our marching rule takes the form

$$V(t+dt) = (1 - dt/\tau) * V(t) + (dt/\tau)V_{Cl} + \sin(2\pi f t).$$

With the parameter set as above, beginning from $V(0) = -70$ we find $V(0.1) = -70$ then

$$\begin{aligned}
V(0.2) &= -70 + \sin(2\pi f/10) \\
V(0.3) &= -70 + 0.97 * \sin(2\pi f/10) + \sin(4\pi f/10) \\
V(0.4) &= -70 + (0.97)^2 * \sin(2\pi f/10) + 0.97 * \sin(4\pi f/10) + \sin(6\pi f/10)
\end{aligned}$$

and we observe the pattern

$$V((n+2)/10) = -70 + a^{-n}\sum_{j=1}^{n} a^j \sin(jb), \qquad a = 1/0.97,\ b = 2\pi f/10.$$

This sum

$$S_n \equiv \sum_{j=1}^{n} a^j \sin(jb) \tag{2.11}$$

is a fairly imposing object. Our objective is to demystify it by showing how it can be summed by hand using no more than few trigonometry identities, each of which we will derive from scratch.

The small n are easy

$$S_1 = a\sin(b) \quad \text{and} \quad S_2 = a\sin(b) + a^2\sin(2b) = a\sin(b) + 2a^2\cos(b)\sin(b).$$

Where we have used the lovely double angle formula $\sin(2b) = 2\sin(b)\cos(b)$. Let us begin with a derivation of the more general addition formula

$$\boxed{\sin(a+b) = \sin(a)\cos(b) + \sin(b)\cos(a)} \tag{2.12}$$

To "see" this formula we look to the left panel in Figure 2.5, where we have rotated the unit segment AB first through angle a to AC then through b to AD. Please note that

$$\sin(a+b) = DE.$$

In the subsequent panel we drop a line from D that meets AC at a right angle at F. From F we drop a vertical to G and horizontal to H.

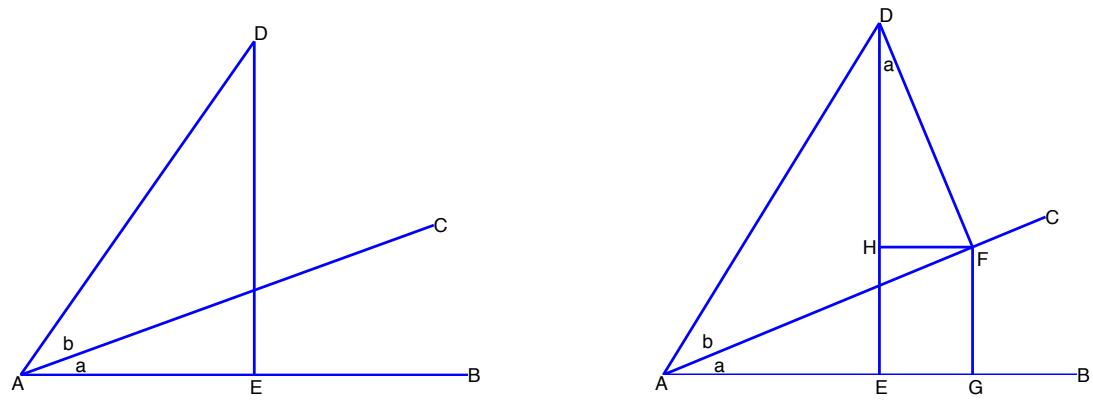


Figure 2.6. Initial (left) and final (right) constructions in the derivation of (2.12).

From the right panel in Figure 2.6 you should be able to confirm

1. $AF = \cos(b)$.
2. $a = \angle FDH$.
3. $\sin(a) = (FG)/(AF)$.
4. $FG = \sin(a)\cos(b)$.
5. $DF = \sin(b)$.
6. $\cos(a) = (DH)/(DF)$.
7. $DH = \cos(a)\sin(b)$.

Finally, deduce (2.12) from $\sin(a+b) = DH + FG$.

We note that the very same construction permits us to establish the addition formula for cosine, namely,

$$\boxed{\cos(a+b) = \cos(a)\cos(b) - \sin(a)\sin(b).} \tag{2.13}$$

Recall that our goal is to sum the S_n in (2.11). Our next step is to use the angle sum formula, (2.12), to deduce the lovely recurrence relation

$$\boxed{\sin(jb) = 2\cos(b)\sin((j-1)b) - \sin((j-2)b)} \tag{2.14}$$

valid for arbitrary b and integer j. To establish (2.14) we expand

$$\sin((j-1)b) = \sin(jb)\cos(b) - \cos(jb)\sin(b) \tag{2.15}$$

and

$$\begin{aligned}\sin((j-2)b) &= \sin(jb)\cos(2b) - \cos(jb)\sin(2b) \\ &= \sin(jb)(2\cos^2(b)-1) - 2\cos(jb)\sin(b)\cos(b).\end{aligned} \tag{2.16}$$

On multiplying (2.15) by $2\cos(b)$ and subtracting (2.16) we arrive at (2.14).

On substituting (2.14) into the definition of S_n, i.e., (2.11) we find

$$\begin{aligned}S_n &= 2\cos(b)\sum_{j=1}^{n} a^j \sin((j-1)b) - \sum_{j=1}^{n} a^j \sin((j-2)b) \\ &= 2\cos(b)\sum_{j=2}^{n} a^j \sin((j-1)b) + a\sin(b) - \sum_{j=3}^{n} a^j \sin((j-2)b) \\ &= a\sin(b) + 2a\cos(b)\sum_{j=1}^{n-1} a^j \sin(jb) - a^2\sum_{j=1}^{n-2} a^j \sin(jb) \\ &= a\sin(b) + 2a\cos(b)S_{n-1} - a^2 S_{n-2}.\end{aligned}$$

We pause to note that this gives us a relation between our sums at neighboring values of n. More precisely, the S_n obey the **difference equation**

$$\boxed{S_n = a\sin(b) + 2a\cos(b)S_{n-1} - a^2 S_{n-2}.} \tag{2.17}$$

We first examine its steady state solution by supposing that $S_n \to S_\infty$ as $n \to \infty$, in which case (2.17) takes the form

$$S_\infty = a\sin(b) + 2a\cos(b)S_\infty - a^2 S_\infty.$$

This we dispatch at once, with

$$S_\infty = \frac{a\sin(b)}{a^2 - 2a\cos(b) + 1}. \tag{2.18}$$

With this term out of the way, we note the

$$X_n \equiv S_n - S_\infty$$

obey the simpler difference equation

$$X_{n+2} = 2a\cos(b)X_{n+1} - a^2 X_n. \tag{2.19}$$

If we make the hopeful guess that $X_n = x^n$ then (2.19) reduces to the simple quadratic equation

$$x^2 = 2a\cos(b)x - a^2. \tag{2.20}$$

The quadratic formula identifies the **complex** roots

$$x_\pm = \frac{2a\cos(b) \pm \sqrt{4a^2\cos^2(b) - 4a^2}}{2} = a(\cos(b) \pm i\sin(b)),$$

where $i \equiv \sqrt{-1}$ is the **imaginary unit**. We have illustrated these roots below

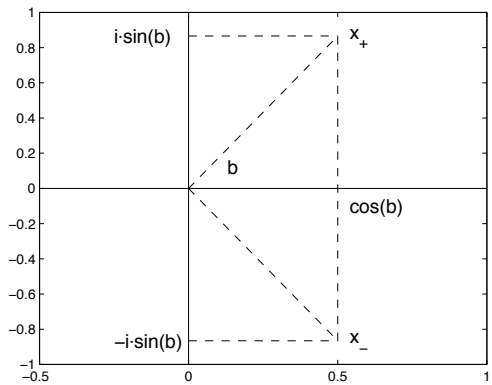


Figure 2.7 The roots of (2.20) plotted in the complex plane.

We combine these roots, with complex weights, $c_\pm$, to produce the general solution

$$X_n = c_+ x_+^n + c_- x_-^n.$$

The $x_\pm^n$ are extremely well behaved, for notice that

$$\begin{aligned} x_+^2 &= (\cos(b) + i\sin(b))(\cos(b) + i\sin(b)) \\ &= \cos^2(b) - \sin^2(b) + i2\sin(b)\cos(b) \\ &= \cos(2b) + i\sin(2b) \end{aligned}$$

where the last step uses only (2.12) and (2.13). Continuing in this fashion we find the lovely identities

$$x_\pm^n = ((\cos(b) \pm i\sin(b))^n = \cos(nb) \pm i\sin(nb). \tag{2.21}$$

As $x_\pm^n$ are complex conjugates of one another (i.e., reflections of one another across the real axis) and X_n is real it follows (can you prove it) that $c_\pm$ must also be complex conjugates of one another. Writing $c_+ = \alpha + i\beta$ it follows that

$$X_n = 2a^n(\alpha\cos(nb) - \beta\sin(nb)). \tag{2.22}$$

The real α and β are then determined by the two real equations

$$X_1 = S_1 - S_\infty \quad \text{and} \quad X_2 = S_2 - S_\infty$$

i.e., by

$$\begin{aligned}\alpha\cos(b)-\beta\sin(b) &= \frac{\sin(b)(a^2-2a\cos(b))}{2(a^2-2a\cos(b)+1)}\\ \alpha\cos(2b)-\beta\sin(2b) &= \frac{a\sin(b)+2\cos(b)\sin(b)(a^2-2a\cos(b))}{2(a^2-2a\cos(b)+1)}.\end{aligned} \tag{2.23}$$

On multiplying the first equation by $\cos(2b)$ and the second by $-\cos(b)$ and adding we find

$$\beta = \frac{a\cos(b)-a^2}{2(a^2-2a\cos(b)+1)}.$$

Conversely, on multiplying the first equation in (2.23) by $\sin(2b)$ and the second by $-\sin(b)$ and adding we find

$$\alpha = \frac{-a\sin(b)}{2(a^2-2a\cos(b)+1)}$$

On substitution back into (2.22) we find

$$X_n = \frac{a^n(a^2-a\cos(b))\sin(nb)-a^{n+1}\sin(b)\cos(nb)}{a^2-2a\cos(b)+1}$$

and so

$$S_n = X_n + S_\infty = \frac{a\sin(b)+a^n(a^2-a\cos(b))\sin(nb)-a^{n+1}\sin(b)\cos(nb)}{a^2-2a\cos(b)+1}$$

and so

$$V((n+2)/10) = -70 + \frac{a^{1-n}\sin(b)+(a^2-a\cos(b))\sin(nb)-a\sin(b)\cos(nb)}{a^2-2a\cos(b)+1}.$$

Although explicit it is not an easy manner to "see" the weighted difference of $\sin(nb)$ and $\cos(nb)$. To finish the story we need one more identity

$$\boxed{c_1\sin(\theta)+c_2\cos(\theta) = A\sin(\theta+\phi), \quad A=\sqrt{c_1^2+c_2^2}, \quad \tan\phi = c_1/c_2.} \tag{2.24}$$

To derive this simply expand $\sin(\theta+\phi)$ via our angle sum formula, (2.12). Finally, we arrive the exact representation

$$V((n+2)/10) = -70+\frac{a^{1-n}\sin(b)}{a^2-2a\cos(b)+1}+\frac{a}{\sqrt{a^2-2a\cos(b)+1}}\sin(nb+\phi), \tag{2.25}$$

where

$$\phi = \tan^{-1}((\cos(b)-a)/\sin(b)).$$

The first term is simply rest, the second is "evanescent" in the sense that it vanishes for large n. The last term simply oscillates with amplitude captured by the gain function

$$G(f) = \frac{a}{\sqrt{a^2 - 2a\cos(2\pi f dt) + 1}}. \tag{2.26}$$

We illustrate V and G below.

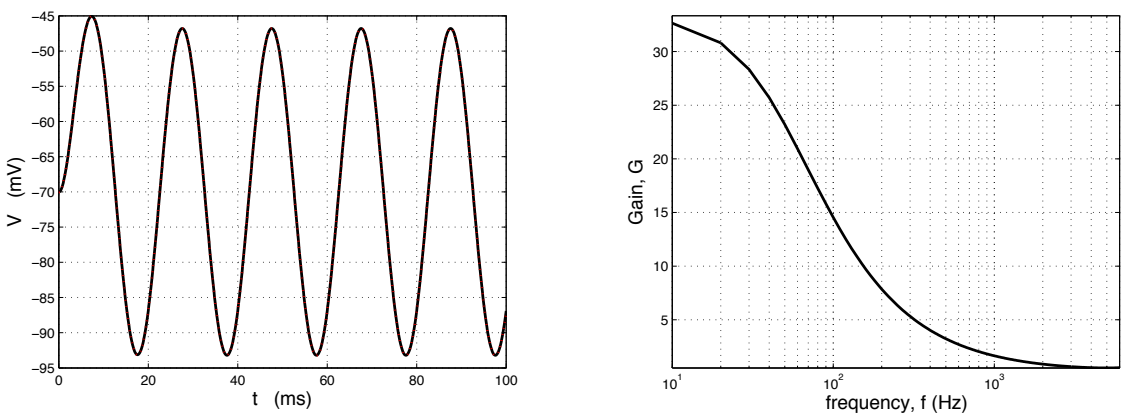
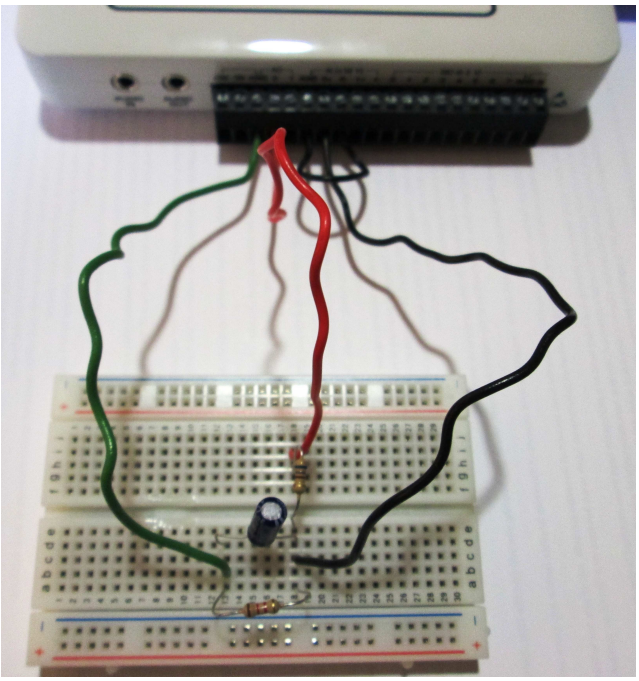


Figure 2.8. (left) The response, (2.25), to a 50 HZ sine wave. (right) The Gain function, (2.26), demonstrates that the circuit damps or attenuates high frequency input.

2.3. Building the Neuron in Hardware

It is not a simple matter to deliver a prescribed current, I_{stim}. We rather drive a known, 672 Ω, resistor with the NI myDAQ Function Generator, and record its response with the associated Oscilloscope.



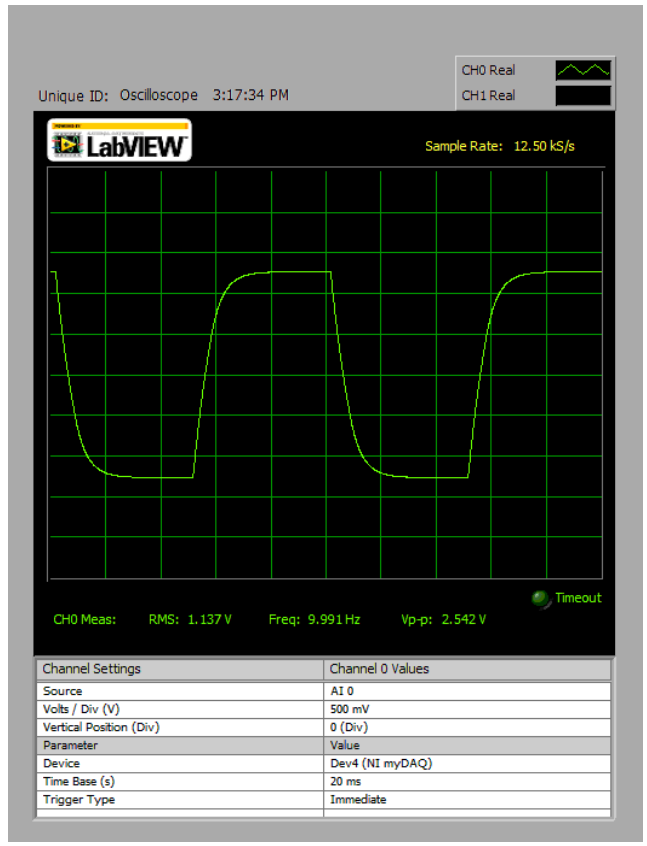


Figure 2.9 The red wire connects the Function Generator (pin AO 0) to the (vertical) 672 Ω resistance. This serves as I_{stim} into the membrane RC circuit, $R = 1.17\,k\Omega$ and $C = 9.87\,\mu F$. On selected a 10 Hertz, 4 Volt peak-to-peak square wave from the Function Generator, the Oscilloscope (black wire to pin AI 0+) captures the charge, plateau and discharge that we expect from our numerical simulation. The green wire is to ground, and the small black jumper connects pin AI 0- to ground.

We next switch from square to sine waves and note that peak-to-peak response diminishes as we increase frequency. Please record, on a sheet of paper, the response Vpp for frequencies $10^0, 10^1, 10^2, 10^3$ and 10^4, and graph your results in Octave, like that below. We define **gain** to be the ratio of the Vpp of the response to the Vpp of the stimulus.

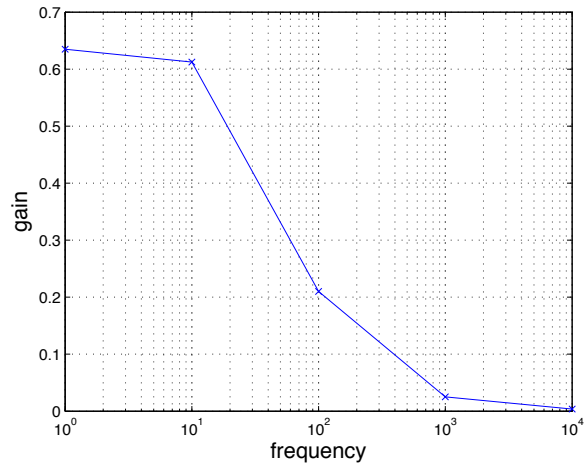


Figure 2.10 The membrane circuit behaves like a low–pass filter. Compare to Figure 2.8.

2.4. The Limiting Cell Equation and its Gain Function

Please check that if we define,

$$v(t) = V(t) - V_{Cl}$$

then (2.8) takes the simpler form

$$RI_{stim}(t) = v(t) + \tau \frac{v(t+dt) - v(t)}{dt}.$$

For those that have been exposed to calculus you might recognize that the difference quotient

$$\frac{v(t+dt) - v(t)}{dt} \quad \text{approaches the derivative} \quad v'(t)$$

as dt approaches 0. The limiting passive neuron equation is then

$$RI_{stim}(t) = v(t) + \tau v'(t). \tag{2.27}$$

There are many ways to analyze such a "differential equation." To begin we will demonstrate that if a sinusoid goes in then a sinusoid comes out. More precisely, we suppose that

$$I_{stim}(t) = I_0(f)\exp(2\pi i f t) \quad \text{and} \quad v(t) = V_0(f)\exp(2\pi i f t)$$

where f denotes frequency. (An Octave digression/appendix on $\exp(2\pi i f t)$ would be nice, simply typing `help plot3` gets you very far). On substituting these into (2.27) we find

$$RI_0(f)\exp(2\pi i f t) = V_0(f)\exp(2\pi i f t) + (2\pi i f \tau)V_0(f)\exp(2\pi i f t)$$

On canceling the common exponential we find

$$RI_0(f) = (1 + 2\pi i f \tau)V_0(f),$$

and rearrange slightly to arrive at the analytical Gain Function

$$G(f) \equiv \frac{|V_0(f)|}{|I_0(f)|} = \frac{1}{R\sqrt{1 + (2\pi f \tau)^2}}.$$

As this function decreases as f increases we speak of the passive neuron as a "Low Pass Filter."