

Control of Virtual Impedances in a Parallel RLC Circuit

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In a hair cell, deflection of the hair bundle causes current to flow into the bundle, depolarizing the cell below. The electrical properties of the hair cell can be considered to be a combination of three circuits [Fisher et al., 2011]. An apical resistance and capacitance describe the voltage drop at the level of the hair bundle for a given current injection. A shunt resistance and capacitance describe a shunt pathway through supporting cells and the extracellular space. Finally, a basolateral resistance, inductance, and capacitance describe the voltage drop at the basolateral surface of the hair-cell soma. We can simply this circuit to include only the basolateral circuit, excluding the details of hair-bundle conductance and the shunt pathway.

A parallel RLC circuit has a total current I equal to

$$I = I_R + I_L + I_C,$$

in which the three currents correspond to the currents passing through a resistor with resistance R , an inductor with inductance L , and a capacitor with capacitance C . Inserting the voltages corresponding to each current, we obtain

$$\begin{aligned} I - \frac{V}{R} - \frac{1}{L} \int V dt - C \frac{dV}{dt} &= 0, \\ I - V'' - \frac{1}{RC} V' + \frac{1}{LC} V &= 0. \end{aligned}$$

The corresponding impedance, Z , is equal to

$$Z = \frac{V}{I} = \frac{1}{\sqrt{\frac{1}{R^2} + (\frac{1}{\omega L} - \frac{1}{\omega C})^2}} = \frac{1}{\sqrt{\frac{1}{R^2} + (\frac{1}{\omega L} - \omega C)^2}},$$

in which ω is the angular frequency.

In a voltage clamp, the output voltage (V_o) is calculated by taking the difference between a command voltage (V_c) and the membrane voltage (V_m) and subsequently multiplying it by a proportional gain

$$V_o = G(V_c - V_m).$$

For a given current I and access resistance R_a , noting that the output voltage is divided between the access resistance and the membrane resistance,

$$V_o = V_m + R_a I,$$

which becomes

$$V_m = V_c \frac{1}{1+G} - \frac{R_a I}{1+G}$$

after combining the two previous equations. As the gain G becomes large, the membrane voltage approaches the command voltage, and the effects of the access resistance are reduced.

We can combine the equation for a parallel RLC circuit with the hair bundle to include a virtual capacitance, resistance and inductance, along with some additional current, yielding

$$I_{HB} - \frac{1}{RC} V'_m - \frac{1}{LC} V_m = I - \frac{1}{R_V C_V} V'_m - \frac{1}{L_V C_V} V_m.$$

Note that the second derivative of the voltage is not included in this equation. Substituting the equation for membrane voltage in a voltage clamp and assuming that the effect of the access resistance is small with high gain, this becomes

$$(I - I_{HB}) - \left(\frac{1}{R_V C_V} - \frac{1}{RC}\right) \frac{G}{1+G} V'_c - \left(\frac{1}{L_V C_V} - \frac{1}{LC}\right) \frac{G}{1+G} V_c = 0.$$

The first derivative of the command voltage can be calculated by taking the difference between each value of command voltage and dividing by a time step dt , yielding

$$\begin{aligned} & (I_n - I_{HB,n}) - \left(\frac{1}{R_V C_V} - \frac{1}{RC}\right) \frac{G}{1+G} \frac{V_{c,n} - V_{c,n-1}}{\delta t} - \left(\frac{1}{L_V C_V} - \frac{1}{LC}\right) \frac{G}{1+G} V_{c,n} = 0, \\ & \delta t (I_n - I_{HB,n}) - \left(\frac{1}{R_V C_V} - \frac{1}{RC}\right) \frac{G}{1+G} V_{c,n} + \left(\frac{1}{R_V C_V} - \frac{1}{RC}\right) \frac{G}{1+G} V_{c,n-1} - \\ & \delta t \left(\frac{1}{L_V C_V} - \frac{1}{LC}\right) \frac{G}{1+G} V_{c,n} = 0, \\ & \left[\left(\frac{1}{R_V C_V} - \frac{1}{RC}\right) \frac{G}{1+G} + \delta t \left(\frac{1}{L_V C_V} - \frac{1}{LC}\right) \frac{G}{1+G} \right] V_{c,n} = \delta t (I_n - I_{HB,n}) + \\ & \left(\frac{1}{R_V C_V} - \frac{1}{RC}\right) \frac{G}{1+G} V_{c,n-1}, \\ & \left[\left(\frac{1}{R_V C_V} - \frac{1}{RC}\right) + \delta t \left(\frac{1}{L_V C_V} - \frac{1}{LC}\right) \right] V_{c,n} = \frac{\delta t (I_n - I_{HB,n})(1+G)}{G} + \left(\frac{1}{R_V C_V} - \frac{1}{RC}\right) V_{c,n-1}, \\ & V_{c,n} = \frac{\delta t (I_n - I_{HB,n})(1+G)}{G \left[\left(\frac{1}{R_V C_V} - \frac{1}{RC}\right) + \delta t \left(\frac{1}{L_V C_V} - \frac{1}{LC}\right) \right]} + \frac{\left(\frac{1}{R_V C_V} - \frac{1}{RC}\right) V_{c,n-1}}{\left(\frac{1}{R_V C_V} - \frac{1}{RC}\right) + \delta t \left(\frac{1}{L_V C_V} - \frac{1}{LC}\right)}, \\ & \text{and } V_{c,n} = \frac{\delta t (I_n - I_{HB,n})(1+G)}{G \left[\left(\frac{1}{R_V C_V} - \frac{1}{RC}\right) + \delta t \left(\frac{1}{L_V C_V} - \frac{1}{LC}\right) \right]} + \frac{\left(\frac{1}{R_V C_V} - \frac{1}{RC}\right) V_{c,n-1}}{\left(\frac{1}{R_V C_V} - \frac{1}{RC}\right) + \delta t \left(\frac{1}{L_V C_V} - \frac{1}{LC}\right)}. \end{aligned}$$

This equation modifies the hair bundle current and membrane impedances by virtual parameters to yield modified electrical properties of the hair cell. If one were to ignore the properties of the hair cell or set these values to zero, the above equation becomes

$$V_{c,n} = \frac{\delta t I_n (1+G)}{\frac{G}{R_V C_V} + G \delta t \frac{1}{L_V C_V}} + \frac{V_{c,n-1}}{1 + \delta t \frac{R_V C_V}{L_V C_V}}.$$

This equation allows one to define a virtual resistance, virtual capacitance, virtual inductance, and an arbitrary current waveform on a point-by-point basis. If the current waveform is set to zero, the equation simplifies to

$$V_{c,n} = \frac{V_{c,n-1}}{1 + \delta t \frac{R_V C_V}{L_V C_V}}.$$

This formula for a command voltage in a voltage-clamp system provides a feed-forward protocol to adjust different control parameters in a voltage-clamp feedback setup. Note that the resonant frequency in a parallel RLC circuit is

$$f_0 = \frac{1}{2\pi\sqrt{LC}}.$$

Changing either the inductance or the capacitance in the circuit will change the natural frequency of electrical resonance in a hair cell. Prior work has shown that a simple circuit with the same components plus parameter-dependent and time-dependent calcium and potassium conductance allows the hair cell to cross a supercritical Hopf bifurcation [Ospeck et al., 2008]. It may be possible to do the same by adjusting these parameters in an active hair cell. Additionally, the feedback between the mechanical activity of a hair bundle and the electrical activity of a hair cell can be dissected by implementing mechanical-load and electrical-impedance clamps.

References

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