A model for understanding membrane potential using springs

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Cardozo, David L. A model for understanding membrane potential using springs. Adv Physiol Educ 29: 204–207, 2005; doi:10.1152/advan.00067.2004.—In this report, I present a simple model using springs to conceptualize the relationship between ionic conductances across a cellular membrane and their effect on membrane potential. The equation describing the relationships linking membrane potential, ionic equilibrium potential, and ionic conductance is of similar form to that describing the force generated by a spring as a function of its displacement. The spring analogy is especially useful in helping students to conceptualize the effects of multiple conductances on membrane potential.

WHEN STUDENTS ARE FIRST INTRODUCED to the concept of a cell’s membrane potential ($V_m$), they often find it difficult to intuitively understand how changes in ionic conductances produce changes in the cell’s $V_m$. In particular, they have difficulty in conceptualizing how multiple conductances interact to arrive at a particular value for $V_m$. For instance, how do variations in potassium conductance ($G_K$) and sodium conductance ($G_{Na}$) (Fig. 1) determine $V_m$? I introduced a model using springs to help students gain an intuition for the relationship between ionic conductances and potential across the membrane. The essence of the idea is that influence or “pull” of an ionic conductance on $V_m$ can be conceptualized as the pull of a spring on a pointer. For students to understand the model, they need to recall Hooke’s law, which is usually presented in a standard high school physics curriculum. The law is completely intuitive, because it simply states that a spring will exert a restorative force ($F$) proportional to its stiffness ($K$) and to the length of stretch ($x$), as follows: $F = -Kx$ (2). This is the only classical physics necessary for appreciating the analogy between springs and ionic conductances. Even students with a limited background in physics should be able to draw upon their everyday experiences with springs to understand the concept. Students lacking in an understanding of these physical ideas can be given springs of differing stiffness to manipulate so that they can discover these principles for themselves.

The ionic basis for the resting potential is explained by establishing the idea that a $K^+$ concentration gradient across the cell membrane ($K^+$ high inside) results in a greater number of random collisions of the ion against the intracellular surface, establishing the diffusional force driving the ions out of the cell through $K^+$-selective channels. The exiting $K^+$, unaccompanied by counterbalancing negative ions, creates an electric potential across the membrane that drives positive ions back into the cell, opposing the force of diffusion. Equilibrium is established when the potential across the membrane provides an electromotive force that is equal and opposite to the force of diffusion.

Once the concept of the equilibrium (or reversal) potential is established, it is stressed that each conductance tends to move the $V_m$ toward the equilibrium potential for the particular ion species and that there is no net flow of current at the equilibrium potential. The influence of an ion on $V_m$ can be modeled as a simple electrical circuit, as shown in Fig. 2 for $K^+$. The equilibrium potential for $K^+$ ($E_K$) acts as a battery that generates a $K^+$ current ($I_K$) across the membrane through $G_K$.

With the use of the ohmic model for membrane currents:

$$V = IR \text{ or } I = VG$$

where $V$ is voltage, $I$ is current, and conductance ($G$) = 1/resistance ($R$).

For instance, when considering the current carried by a particular ion, the equation for the ion-dependent conductance is produced based on the relationships among ion current ($I_{ion}$), ion conductance ($G_{ion}$), and displacement from the ion’s equilibrium potential ($E_{ion}$) (1). $I_{ion}$ is the product of the displacement of $V_m$ from $E_{ion}$ and $G_{ion}$, which reflects the number and properties of the channels through which a particular ion species travels:

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Fig. 1. Cell with sodium ($G_{Na}$) and potassium conductances ($G_K$).

Fig. 2. Flow of potassium ions modeled as an electrical circuit. $E_K$, equilibrium potential for potassium; $I_K$, $K^+$ current.
Hooke’s law describes the force generated by a spring

\[ F_{\text{spring}} = G_{\text{spring}}(X - P_{\text{spring}}) \]

where \( X \) is the position to which the spring is displaced. Figure 3 shows how a spring models a single conductance. In this case, the spring models \( G_K \) (which represents the spring’s intrinsic stiffness) and \( E_K \) is represented by the resting position of the pointer (when no tension is applied).

Any displacement to the right (in the positive direction) produces a tension on the spring that will produce a counteracting force whose magnitude is dependent on the distance from \( E_K \) and the stiffness of the spring \( G_K \). The further the pointer is shifted away from \( E_K \), the greater the restorative tendency, as shown in Fig. 4.

The relationships between the terms used to describe \( V_m \) and \( F_{\text{spring}} \) are listed in Table 1.

Similarly, \( G_{Na} \) can be modeled by a spring with a pointer whose rest position (when the spring is under no tension) is the equilibrium potential for sodium (\( E_{Na} \)), as shown in Fig. 5. When presenting the model, it is important to explain to students that the spring model applies for either side of the reversal potential. The theoretical spring will oppose movement of the pointer in either direction from the equilibrium position. Students have to flip the spring over in their minds.

The spring model is especially useful in understanding how \( V_m \) is determined when multiple conductances are involved. In the classical approach, the contributions of multiple conductances to the resting potential are resolved by solving simultaneous equations for the steady state in which there is zero net current flowing across the membrane (2). The equivalent electrical circuit is shown in Fig. 6.

At steady state, the net inward and outward currents will be equal so that the net current is zero. If we take the example of just two currents, one inward Na\(^+\) current (\( I_{Na} \)) and one outward \( I_K \),

\[ I_{Na} + I_K = 0 \]

Consequently,

\[ G_K(V_m - E_K) + G_{Na}(V_m - E_{Na}) = 0 \]

and this rearranges to the familiar equation

\[ V_m = E_{Na}[G_K/(G_K + G_{Na})] + E_{Na}[G_{Na}/(G_K + G_{Na})] \]

The general expression for multiple conductances is

\[ V_m = \sum E_{\text{ion}}(G_{\text{ion}}/G_{\text{total}}) \]

where \( G_{\text{total}} \) is total conductance. Therefore, \( V_m \) reflects two parameters: 1) \( E_{\text{ion}} \) and 2) \( G_{\text{ion}} \) relative to \( G_{\text{total}} \). \( V_m \) results from summing the individual equilibrium potentials for each of the ion species after each has been adjusted for its relative contribution to overall conductance.

The most useful aspect of the spring model is that it provides an intuitive way of visualizing the effects of multiple conductances. As is shown in Fig. 7, the resting position (\( X \)) of a

Fig. 3. Influence of K\(^+\) on membrane conductance. \( E_K \) is the position of the pointer when there is no tension on the spring (\( G_K \)). \( V_m \), membrane potential.

Fig. 4. Model for the restorative tendency of K\(^+\).

Table 1. Relationship between the terms used to describe springs and \( V_m \)

<table>
<thead>
<tr>
<th>Term</th>
<th>Spring</th>
<th>Physiology</th>
</tr>
</thead>
<tbody>
<tr>
<td>( G )</td>
<td>Stiffness (or force constant)</td>
<td>Ionic conductance</td>
</tr>
<tr>
<td>( I )</td>
<td>Force exerted</td>
<td>Ionic current</td>
</tr>
<tr>
<td>( E_{\text{ion}} )</td>
<td>Rest position (no tension on spring)</td>
<td>Equilibrium potential for the ion</td>
</tr>
<tr>
<td>( V_m )</td>
<td>Position of the pointer</td>
<td>Membrane potential</td>
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pointer influenced by two springs (spring1 and spring2) will be the position at which the sum of the forces generated by the opposing springs is zero. That is, the forces will be equal and opposite. Therefore,

\[
\frac{X_{\text{or } V_m}}{H} = G_{\text{spring1}} \times \frac{G_{\text{spring1}} + G_{\text{spring2}}}{(G_{\text{spring1}} + G_{\text{spring2}})} + \frac{P_{\text{spring2}}}{G_{\text{spring2}}}(G_{\text{spring1}} + G_{\text{spring2}})
\]

This is the same expression as that for the two ionic conductances, and so resting \( V_m \) can be conceptualized as resulting from the resolution of multiple springs attached to a pointer (Fig. 7). The parameters are the relative strength of the springs and each spring’s displacement from its “rest” position.

The activation of additional ion channels by voltage or other means can be modeled by either changing the strength of springs or by adding springs in parallel, as shown in Fig. 8A. Voltage-activated conductances can be modeled by adding “catches” to the springs so that they act on the pointer only once it attains a particular value on the \( V_m \) axis.

For instance, a voltage-dependent \( I_{K_v} \), with voltage-sensitive \( G_K \) \([G_{K_{\text{voltage}}}]\), is modeled in Fig. 8b. For \( G_{K_{\text{voltage}}} \) to influence the pointer, \( G_{\text{Na}} \) has to pull the pointer sufficiently to the right to engage the second spring. When this happens, there are two springs opposing further displacement in the positive direction.

**DISCUSSION**

The spring model is adaptable to any number of conductances and can incorporate such properties as ligand-gated and voltage-dependent conductances. In addition, the spring is an effective way to conceptualize the buffering or restorative quality of an ionic conductance, which is to say, its tendency to oppose movement away from its equilibrium potential. I have used this model for the past 5 years while teaching neuronal physiology to second-year medical students. I have found that it is a successful way to help students gain an intuition for the relationship between conductances and \( V_m \). I haven’t conducted a formal survey of students’ assessment of the model’s utility. I have, however, noted that many students employ the model when reasoning...
through membrane physiology problems both in small group exercises and on examination papers.

At the medical and graduate school level, it hasn’t seemed necessary to demonstrate the concepts using actual springs. Working with a pointer attached to real springs of different tensions would not be expensive and might constitute a worthwhile activity for undergraduate or high school education.

REFERENCES