Stability analysis based on nullcline topology

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We're going to analyze the stability of fixed points in two dimensions. This would be easy if we had the equations, but let's assume that all we have are the nullclines and the direction of the derivatives. This is illustrated for a simplified Hodgkin-Huxley model in Fig. 1A.

We want to determine whether or not the equilibrium circled in green in Fig. 1A is stable. For this we use linear analysis, which means we get to assume that the nullclines are locally linear, as in Fig. 1B. Given this figure, we can write down a differential equation for δV and δh, {lin1}

$$\frac{d\delta V}{dt} = a\delta V + b\delta h \tag{1a}$$

$$\frac{d\delta h}{dt} = -d\delta h - c\delta V \tag{1b}$$

where a, b, c and d are all positive. To determine the sign of these parameters, we used the following reasoning, based on the blue and red arrows in Fig. 1B: starting at the origin in Fig. 1B, moving to the right increases $d\delta V/dt$ (so a is positive) and moving up also increases $d\delta V/dt$ (so b is positive); similarly, again starting at the origin in Fig. 1B, moving up decreases $d\delta h/dt$ (so d is positive) and moving to the right decreases $d\delta h/dt$ (so c is positive).

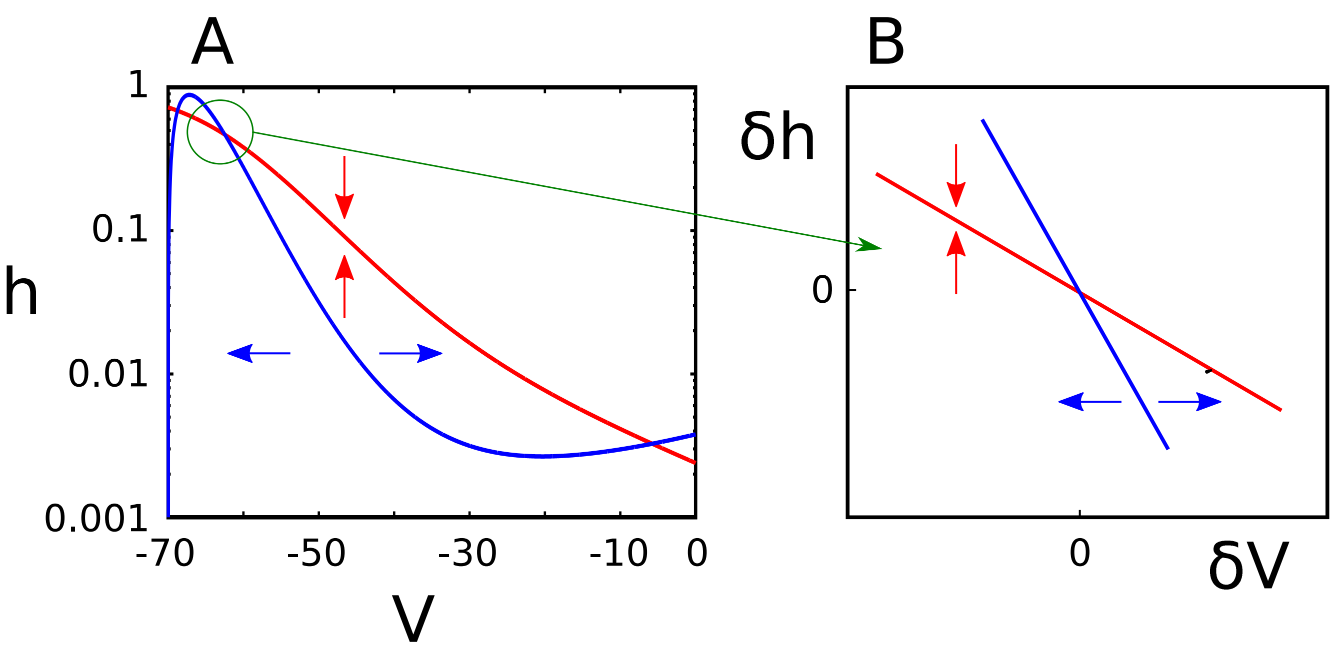

Figure 1: Nullclines. **A.** Nullclines for a reduced Hodgkin-Huxley model in which $m \to m_\infty(V)$ and $n \to 0$. Blue is the V-nucllcline and red is the h-nullcline. Blue arrows indicate the sign of dV/dt at fixed h; red arrows indicate the sign of dh/dt at fixed V. **B.** Blowup of the nullclines, in a sufficiently small range that the nullclines are linear. Origin is at $(0, 0)$.

To analyze these equations, it's useful to write them as

$$\frac{d}{dt}\begin{pmatrix} \delta V \\ \delta h \end{pmatrix} = \begin{pmatrix} a & b \\ -c & -d \end{pmatrix}\begin{pmatrix} \delta V \\ \delta h \end{pmatrix}. \tag{2}$$ {lin2}

This has the solution

$$\begin{pmatrix} \delta V \\ \delta h \end{pmatrix} = \begin{pmatrix} \delta V_0 \\ \delta h_0 \end{pmatrix} e^{\lambda t}. \tag{3}$$

Substitution this into Eq. (2) and rearranging terms gives us

$$\begin{pmatrix} a-\lambda & b \\ -c & -d-\lambda \end{pmatrix}\begin{pmatrix} \delta V_0 \\ \delta h_0 \end{pmatrix} = 0. \tag{4}$$

This has a nontrivial solution if the determinant vanishes, which implies that λ can take two values,

$$\lambda_{\pm} = \frac{T \pm \sqrt{T^2 - 4D}}{2} \tag{5}$$ {eigen}

where T and D are the trace and determinant, respectively,

$$T = a - d \tag{6a}$$
$$D = bc - ad. \tag{6b}$$

The fixed point is stable if $T < 0$ and $D > 0$. For $T < 0$ we need $d > a$; that is, we need trajectories to be attracted more strongly to the h-nullcline than the V-nullcline. Which makes sense. What about the determinant? It turns out that we can determine whether the condition on the determinant is satisfied from the slopes of the nullclines. Points on the h-nullcline corresponds to $d\delta h/dt = 0$ and points on the V-nullcline to $d\delta V/dt = 0$. Examining Eq. (1), we see that

$$\left.\frac{d\delta h}{dt}\right|_{V\text{-nullcline}} = -\frac{a}{b} \tag{7a}$$
$$\left.\frac{d\delta h}{dt}\right|_{h\text{-nullcline}} = -\frac{c}{d} \tag{7b}$$

As can be seen in Fig. 1B, the h-nullcline has steeper slope. This means $c/d > a/b$, or

$$bc > ad. \tag{8}$$

This condition implies that $D > 0$. Consequently, because the h-nullcline is steeper than the V-nullcline, the only condition for stability id $d > a$.

Finally, assume that initially $d > a$, but there is some change in parameters that causes d to eventually become less than a. Along the way, we must have $d = a$. When that happens, the pair of eigenvalues, $\lambda_{\pm}$, is purely imaginary (see Eq. (5)). This is a Hopf bifurcation, and it's always accompanied by a purely oscillatory mode. At least locally.

This technique can, of course, be applied to any arrangement of nullclines.