FitzHugh-Nagumo model

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The **FitzHugh-Nagumo model**

$$\begin{aligned} \dot{V} &= V - V^3/3 - W + I \\ \dot{W} &= 0.08(V + 0.7 - 0.8W) \end{aligned}$$

is a two-dimensional simplification of the Hodgkin-Huxley model of spike generation in squid giant axons. Here,

- V is the membrane potential,
- W is a recovery variable,
- I is the magnitude of stimulus current.

This system was suggested by FitzHugh (1961), who called it "Bonhoeffer-van der Pol model", and the equivalent circuit by Nagumo et al. (1962; see Figure 1).

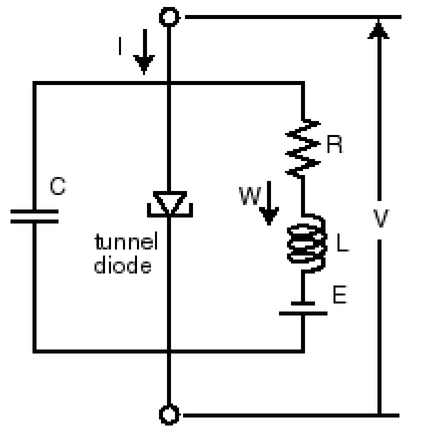

Figure 1: Circuit diagram of the tunnel-diode nerve model of Nagumo et al. (1962).

Contents

Principal assumptions

The motivation for the FitzHugh-Nagumo model was to isolate conceptually the essentially mathematical properties of excitation and propagation from the electrochemical properties of sodium and potassium ion flow. The model consists of

- a *voltage-like variable* having cubic nonlinearity that allows regenerative self-excitation via a positive feedback, and
- a *recovery variable* having a linear dynamics that provides a slower negative feedback.

The model is sometimes written in the abstract form

$$\begin{aligned}\dot{V} &= f(V) - W + I \\ \dot{W} &= a(bV - cW)\end{aligned}$$

where $f(V)$ is a polynomial of third degree, and a, b, and c are constant parameters (notice that a constant term in the second equation can be removed by a linear shift of V or W; also one of the constants, b or c could be assumed to be 1).

FitzHugh modified the van der Pol model to explain the basic properties of excitability as exhibited by the more complex HH equations. The nullclines of the van der Pol equation are a vertical line and a cubic that intersect in a single rest point which is always unstable. In order to resemble a real nerve, this new model should also have only one restpoint, now basically stable, and display a threshold phenomenon for a parameter change that preferably should look like 'current stimulation'. He realized that the slope of a rotated version of the linear isocline figures in the stability condition of the restpoint (FitzHugh (1961), eqs 9 and 10). That enables the construction of a model with a stable restpoint by the addition of a linear term cW to the second equation of the van der Pol model. FitzHugh restricted that slope b/c to the set of cases with only one intersection with the cubic, staying out of the complexities of a more general case.

Adding a constant term to the second equation allowed him to shift the restpoint along the cubic. That restpoint is now always stable on the ascending parts but with the parameters involved in the stability properties on the descending middle limb. One may verify that adding a(nother) constant term to the first equation instead of adding one to the second has the same effect. Formally, this would be a minimal and sufficient parametrization to display all the properties explained below. However, to make the model a bit more palatable for physiologists, both equations got a constant term

$$I$$

in the fast equation, mimicking the experimental injection of external current into the membrane; the second equation got another, mathematically redundant, constant c. It ensures that the restpoint for $I = 0$ (no stimulation) lies on the right ascending branch and is stable.

Explained phenomena

While the Hodgkin-Huxley Model is more realistic and biophysically sound, only projections of its four-dimensional phase trajectories can be observed. The simplicity of the FitzHugh-Nagumo model permits the entire solution to be viewed at once. This allows a geometrical explanation of important biological phenomena related to neuronal excitability and spike-generating mechanism.

The phase portrait of the FitzHugh-Nagumo model in the figure depicts

- V-nullcline, which is the N-shaped curve obtained from the condition $\dot{V} = 0$, where the sign of $\dot{V}$ passes through zero,
- W-nullcline, which is a straight line obtained from the condition $\dot{W} = 0$, where the sign of $\dot{W}$ passes through zero, and
- some typical trajectories starting with various initial conditions.

The intersection of nullclines is an equilibrium (because $\dot{V} = \dot{W} = 0$), which may be unstable if it is on the middle branch of the V-nullcline, i.e., when I is strong enough. In this case, the model exhibits periodic (tonic spiking) activity.

Most of the labels in the figure are explained in the text. The "no man's land" region of the phase space is highly unstable, containing trajectories starting very close to the quasi-threshold.

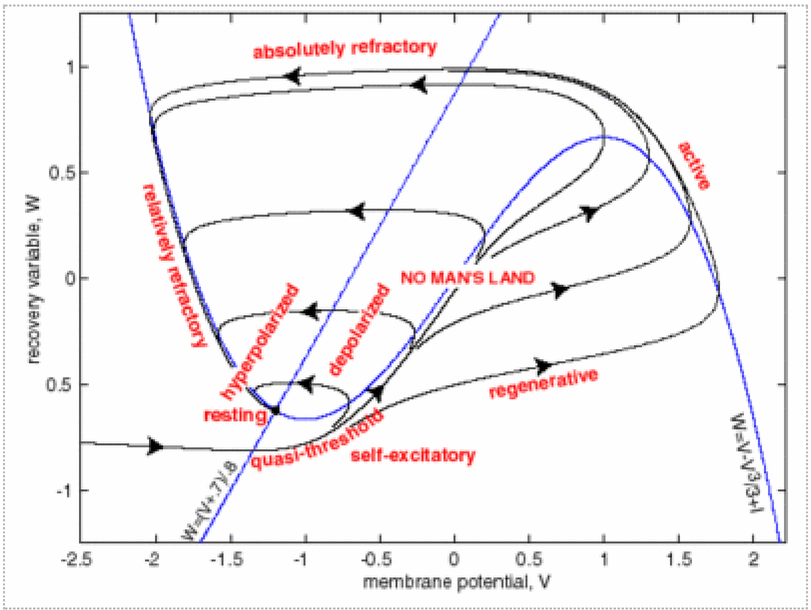

Figure 2: Phase portrait and physiological state diagram of FitzHugh-Nagumo model (modified from FitzHugh 1961).

Absence of all-or-none spikes

The FitzHugh-Nagumo model explained the absence of all-or-none spikes in the HH model in response to stimuli, i.e., pulses of the injected current I. Weak stimuli (small pulses of I) result in small-amplitude trajectories that correspond to subthreshold responses; stronger stimuli result in intermediate-amplitude trajectories that correspond to partial-amplitude spikes; and strong stimuli result in large-amplitude trajectories that correspond to suprathreshold response -- firing a spike.

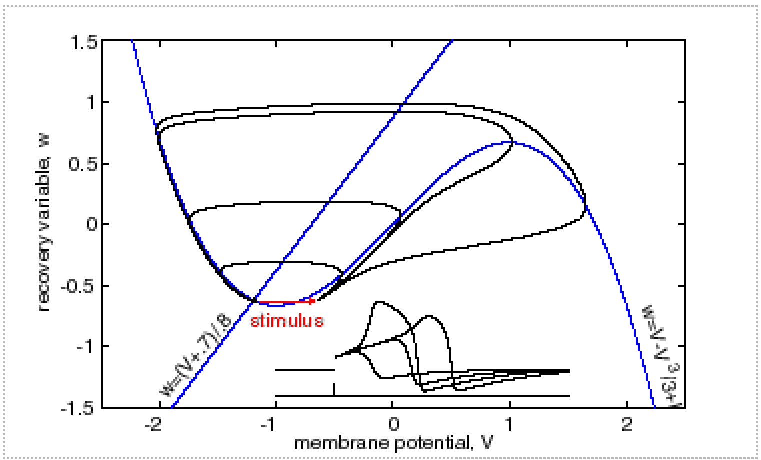

Figure 3: Absence of all-or-none spikes in the FitzHugh-Nagumo model.

Absence of threshold

Similarly to the HH model, FitzHugh-Nagumo model does not have a well-defined firing threshold. This feature is the consequence of the absence of all-or-none responses, and it is related, from the mathematical point of view, to the absence of a saddle equilibrium (FitzHugh 1955). The apparent illusion of threshold dynamics and all-or-none responses in both models is due to the existence of the ‘’quasi-threshold’’, which is a canard trajectory that follows the unstable (middle) branch of the N-shaped V-nullcline. Nearby trajectories diverge sharply away from the canard trajectory to the left or right, producing an apparently "all-or-none" response and threshold-like behavior. (A point moving along a canard trajectory is like a tightrope walker walking slowly along a rope; if he loses his balance, he quickly falls away from the rope to one side or the other.)

Excitation block

The FitzHugh-Nagumo model explains the *excitation block* phenomenon, i.e., the cessation of repetitive spiking as the amplitude of the stimulus current increases. When I is weak or zero, the equilibrium (intersection of nullclines) is on the left (stable) branch of V-nullcline, and the model is resting. Increasing I shifts the nullcline upward and the equilibrium slides onto the middle (unstable) branch of the nullcline. The model exhibits periodic spiking activity in this case. Increasing the stimulus further shifts the equilibrium to the right (stable) branch of the N-shaped nullcline, and the oscillations are blocked (by excitation!). The precise mathematical mechanism involves appearance and disappearance of a limit cycle attractor, and it is reviewed in detail by Izhikevich (2007).

Anodal break excitation

The FitzHugh-Nagumo model explained the phenomenon of post-inhibitory (rebound) spikes, called *anodal break excitation* at that time. As the stimulus I becomes negative (hyperpolarization), the resting state shifts to the left. As the system is released from hyperpolarization (anodal break), the trajectory starts from a point far below the resting state (outside the quasi-threshold, see the first figure), makes a large-amplitude excursion, i.e., fires a transient spike, and then returns to the resting state.

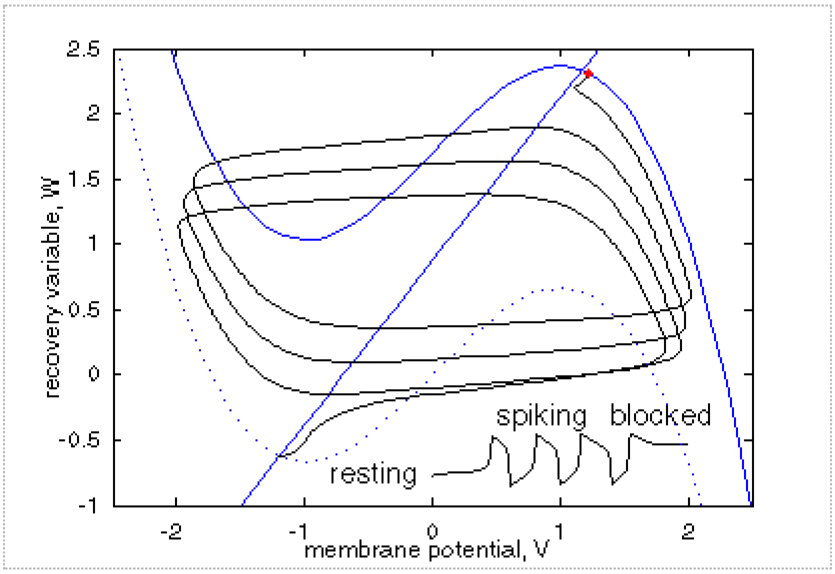

Figure 4: Excitation block in the FitzHugh-Nagumo model.

Spike accommodation

The FitzHugh-Nagumo model explained the dynamical mechanism of *spike accommodation* in HH-type models. When stimulation strength I increases slowly, the neuron remains quiescent. The resting equilibrium of the FitzHugh-Nagumo model shifts slowly to the right, and the state of the system follows it smoothly without firing spikes. In contrast, when the stimulation is increased abruptly, even by a smaller amount, the trajectory could not go directly to the new resting state, but fires a transient spike; see figure. Geometrically, this phenomenon is similar to the post-inhibitory (rebound) response.

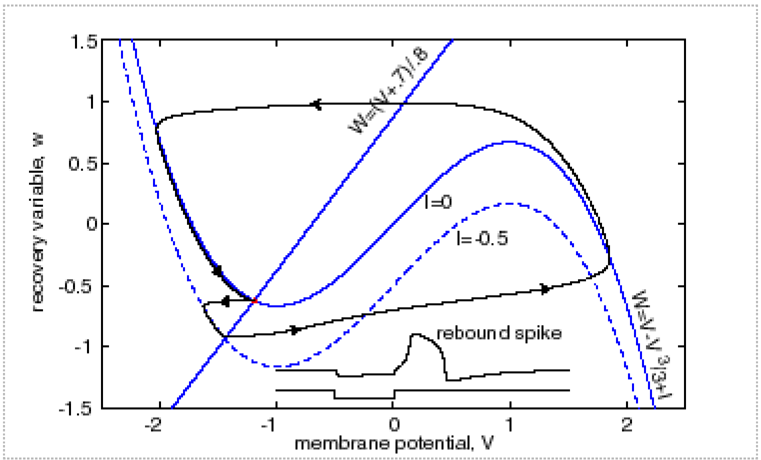

Figure 5: Anodal break excitation (post-inhibitory rebound spike) in the FitzHugh-Nagumo model.

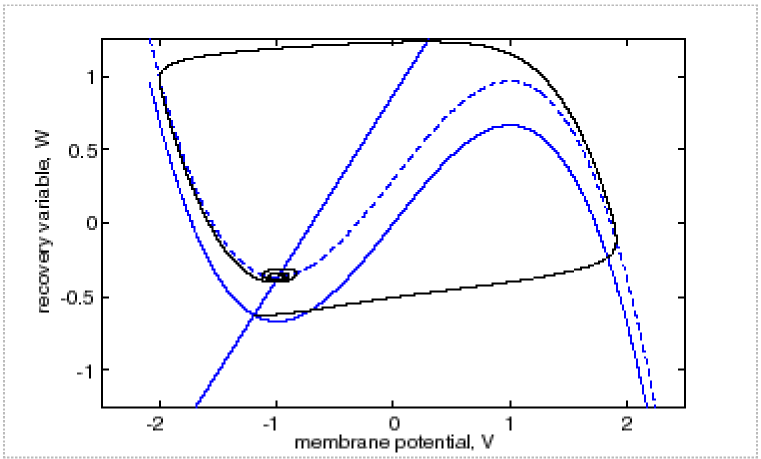

Figure 6: Spike accommodation to slowly increasing stimulus in the FitzHugh-Nagumo model.

Traveling waves

The FitzHugh-Nagumo equations became a favorite model for reaction-diffusion systems

$$\begin{aligned} \dot{V} &= f(V) - W + I + V_{xx} \\ \dot{W} &= a(bV - cW) \end{aligned}$$

which simulate propagation of waves in excitable media, such as heart tissue or nerve fiber. Here, the diffusion term V_{xx} is the second derivative with respect to spatial variable x. Its success is mostly due to the fact that the model is analytically tractable, and hence it allows derivation of many important properties of traveling pulses without resort to computer simulations.

FitzHugh has prepared a motion picture (a movie) of nerve impulse propagation using computer animation techniques available around 1960 (FitzHugh 1968). The movie can be downloaded here

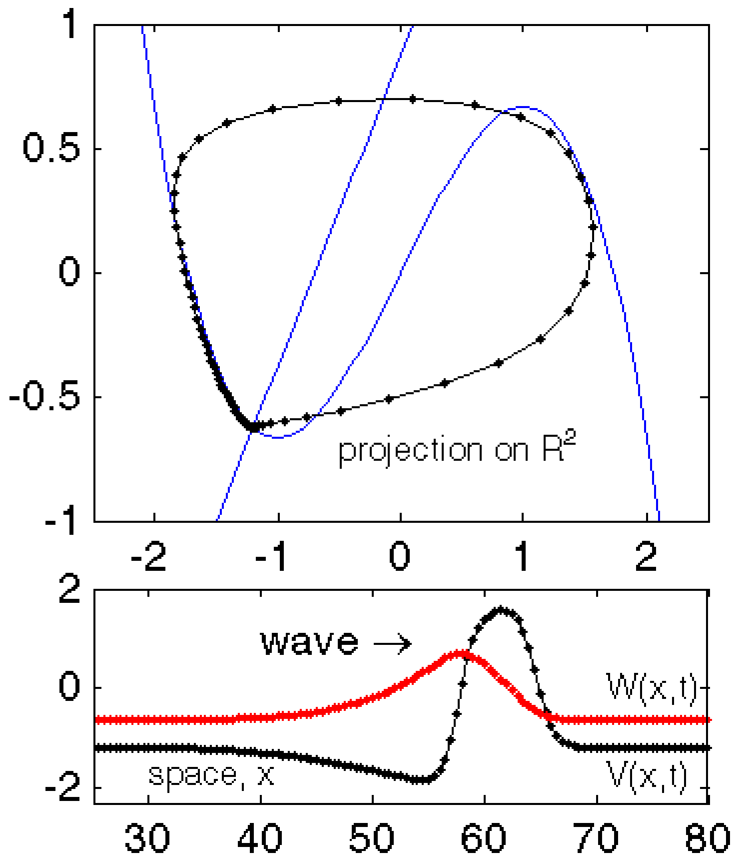

Figure 7: Traveling pulse the FitzHugh-Nagumo reaction-diffusion model. All spatial points are projected onto their V and W coordinates, so that the traveling pulse looks like a circle on the phase plane (notice that because of the diffusion term, the points do not exhibit relaxation oscillations).

(http://www.scholarpedia.org/wiki/images/ftp/FitzHugh_movie.mov) and it is fun to watch.

History

Shortly after the publication of Hodgkin and Huxley's equations for the squid giant axon, Richard FitzHugh was working at the Biophysics Laboratory of the National Institutes of Health (NIH) in Bethesda, Maryland. He undertook an analysis of the mathematical properties of their equations. He used the new techniques of nonlinear mechanics which had been developed by Russian mathematicians led by A. A. Andronov. This was before digital computers became easily accessible. John Moore and FitzHugh started by planning how to program an analog computer which could be used to solve the Hodgkin-Huxley equations. The equipment needed included operational amplifiers, function generators, multipliers, and an ink pen plotter. The laboratory purchased the computer, which occupied four floor-to-ceiling relay racks, full of vacuum tubes. These were continually failing, and FitzHugh had to find and replace several tubes a week, requiring some detective work. The heat from all these tubes sometimes overloaded the air conditioning, so that on hot summer days he had to take off his shirt and wear shorts to be comfortable.

With this computer he plotted solutions of the HH equations. The operation of the analog computer required the skill of an electronic engineer as well as those of a mathematician.

In this analog computer, the variables in the HH equations, V, m, h, n, are represented by voltages. Each variable was transformed into a voltage with a separate scale factor. These voltage signals were passed from one unit to another.

One of the basic units of the computer was the operational amplifier (Op Amp). Each one occupied a metal box about six inches long with six vacuum tubes on top. (Today one can buy a tiny solid-state chip with several Op Amps in it.) To these Op Amps one could connect highly accurate resistors and capacitors to perform the mathematical operations of addition, subtraction and also integration of the signals representing first derivatives with respect to time. Another type of unit was the function generator. There were six of these, for the alpha and beta functions in the HH equations. The voltage value of each function was set into the unit at the evenly spaced points, at intervals of ten volts, between which the function was approximated by straight line segments. This was not accurate enough for the computation. To provide smoothing of the function curve, a high frequency zigzag signal of ten volts peak-to-peak amplitude from a signal generator was added to the input. This was of too high a frequency to appear in the slowly changing voltage passed to the plotter. The effect was to average the function locally, to produce a smooth curve, which however no longer exactly fitted accurately at the set points. Finally, after readjusting the output to accurately fit the function curve at the original set points, an accurate fit to all the function was obtained.

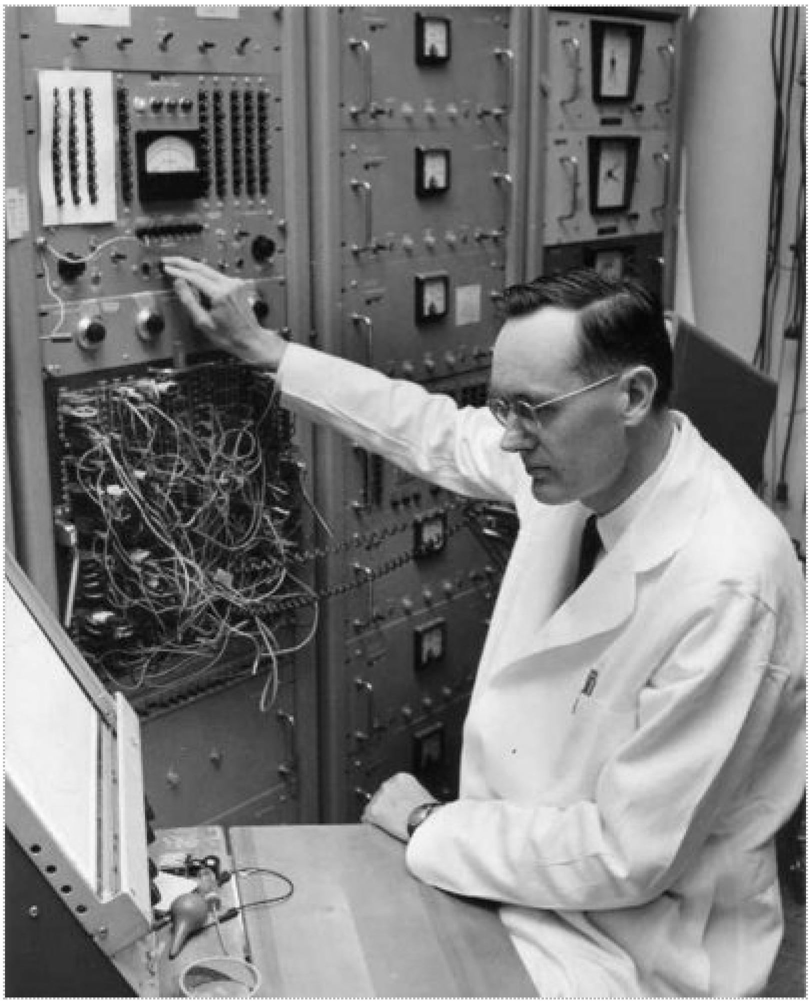

Figure 8: Richard FitzHugh with analog computer at NIH, ca. 1960.

All the units were connected by the maze of wires shown in the photo of FitzHugh operating the computer. The wires protrude from an insulated board, underneath which they made contact with terminals connected to the various units. To change the connections on the board, for a different problem, it was disengaged from its position, exposing the terminals behind. The computer power supply delivered voltages from -100 volts to +100 volts, and if one of the terminals was accidentally touched, one might receive a nasty shock.

The first thing to do in the morning was to turn on the computer and let it warm up until the voltages from the power supply stabilized. Then computation could begin.

In order to distinguish between the physical basis of the HH equations, in terms of the flow through the axon membrane of sodium and potassium ions, on the one hand, and the phenomena of excitation above a threshold value of stimulus, and propagation along the axon, on the other, it seemed that it would be useful to simplify their equations in order to isolate these properties from each other. At the suggestion of his lab chief, Dr. Kenneth S. (Kacy) Cole, FitzHugh modified the van der Pol equations for the nonlinear relaxation oscillator. The result had a stable resting state, from which it could be excited by a sufficiently large electrical stimulus to produce an impulse. A large enough constant current stimulus produced a train of impulses (FitzHugh 1961,1969).

Figure 9: Richard FitzHugh during the preparation of the movie on impulse propagation (circa 1968).

These equations were similar to those describing the electronic circuit called a monostable multivibrator. At about the same time, an electronic circuit was built by the Japanese engineer Jin-Ichi Nagumo, using tunnel (Esaki) diodes; see Figure 1. These diodes have a current-voltage curve similar to the cubic shape used in FitzHugh's equations. These equations have since become known as the FitzHugh-Nagumo equations, though they were originally called "Bonhoeffer-van der Pol model" by FitzHugh. Reprogramming the analog computer for the FitzHugh-Nagumo equations was much simpler. Only two multipliers and no function generators were needed.

Figure 10: The original Nagumo circuit is held as a trust in the laboratory of Dr. K. Aihara in University of Tokyo. Photo provided by H. Suetani and K. Aihara with permissions.

A note on the corresponding electronic circuits may be helpful. Some textbooks (e g Hirsch, Smale and Devaney, Strogatz) use a circle of a capacitor, inductor and nonlinear element in series to 'derive' the van der Pol and BVP models. The nonlinear element then has its voltage as cubic function of the current across it. The fast variable in such a circuit is the current and the thing is really fast when the capacitor is big compared to the inductor. In the original circuits of van der Pol and Nagumo, like in the excitable membrane, the three elements are in parallel. Now the nonlinear element has a current that depends cubically upon the voltage across it, the fast variable is the voltage and the capacitor is relatively small. Again, neglecting the tricks that are needed in practice to get the cubic into the desired quadrant, both circuits lead to the same abstract set of equations.

Aside from mathematicians in the computer division and in John Rinzel's mathematical biology section, there were few people at NIH who were interested in the application of mathematics to biological problems. Most did experiments only. FitzHugh fulfilled his obligations in such work by going each summer to the Marine Biological Laboratory at Woods Hole Massachusetts, where he assisted Cole and Moore in their experiments, using Cole's voltage clamp technique on the squid which were caught at sea there. Otherwise, at NIH there was not much interest in mathematical models.

Within 30-40 years of this first forage by FitzHugh and co-workers into mathematical neuroscience whole communities of mathematicians, physicists, and engineers studying nonlinear dynamics of biological systems have started and matured. Over that time the Fitzhugh-Nagumo model has remained the prototypical example of an excitable system and new discoveries with this system are still being made.

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Further reading

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See also

Hodgkin-Huxley model, Relaxation oscillator, Canards, Periodic orbit, Reaction-diffusion systems, Traveling wave, van der Pol oscillator

External links

- Interactive FitzHugh-Nagumo. (http://thevirtualheart.org/FHNindex.html) Java applet, includes phase space and parameters can be changed at any time.
- Interactive FitzHugh-Nagumo in 1D. (http://thevirtualheart.org/FHN1dindex.html) Java applet to simulate 1D waves propagating in a ring. Parameters can also be changed at any time.
- Interactive FitzHugh-Nagumo in 2D. (http://thevirtualheart.org/FHN2dindex.html) Java applet to simulate 2D waves including spiral waves. Parameters can also be changed at any time.

- Interactive FitzHugh-Nagumo in 3D. (http://thevirtualheart.org/GPU/WebGL_GPU_spiral_waves_heart.html) WebGL to simulate 3D waves including scroll wave instabilities. Parameters can also be changed at any time.

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