

Single neuron models

Reduced models and phase-plane analysis of their dynamics: 3

Kevin Gurney

Adaptive Behaviour Research Group

2008

Outline

- 1 Capturing neural dynamics in the abstract

Outline

- 1 Capturing neural dynamics in the abstract
- 2 The Fitzhugh-Nagumo model

Outline

- 1 Capturing neural dynamics in the abstract
- 2 The Fitzhugh-Nagumo model
- 3 The simple model of Izhikevich

Outline

- 1 Capturing neural dynamics in the abstract
- 2 The Fitzhugh-Nagumo model
- 3 The simple model of Izhikevich

Capturing the essentials of spiking dynamics

- We know the essence of the dynamic behaviour is captured by the nullclines - their functional forms and their intersection at equilibria

Capturing the essentials of spiking dynamics

- We know the essence of the dynamic behaviour is captured by the nullclines - their functional forms and their intersection at equilibria
- The nullclines act as 'guidelines' that lend structure to the vector field which, in turn determines trajectories

Capturing the essentials of spiking dynamics

- We know the essence of the dynamic behaviour is captured by the nullclines - their functional forms and their intersection at equilibria
- The nullclines act as 'guidelines' that lend structure to the vector field which, in turn determines trajectories
- Hitherto, these functional forms have arisen from physiologically plausible models and the Hodgkin-Huxley formalism

Capturing the essentials of spiking dynamics

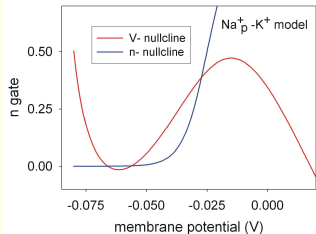
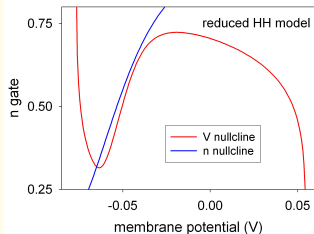
- We know the essence of the dynamic behaviour is captured by the nullclines - their functional forms and their intersection at equilibria
- The nullclines act as 'guidelines' that lend structure to the vector field which, in turn determines trajectories
- Hitherto, these functional forms have arisen from physiologically plausible models and the Hodgkin-Huxley formalism
- A new strategy is to establish models, independent of any physiological framework, whose dynamics are equivalent to their biologically grounded counterparts

Capturing the essentials of spiking dynamics

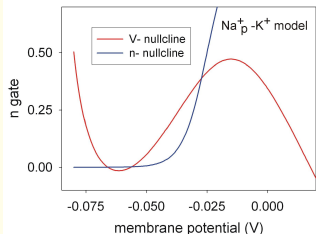
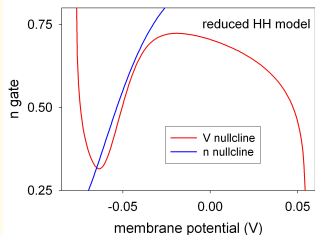
- We know the essence of the dynamic behaviour is captured by the nullclines - their functional forms and their intersection at equilibria
- The nullclines act as 'guidelines' that lend structure to the vector field which, in turn determines trajectories
- Hitherto, these functional forms have arisen from physiologically plausible models and the Hodgkin-Huxley formalism
- A new strategy is to establish models, independent of any physiological framework, whose dynamics are equivalent to their biologically grounded counterparts
- This programme requires we describe, as simply as possible, the nullclines of typical neural models

The V-nullcline

- The V-nullcline of both models we have studied consists of an inverted 'N'-shape



The V-nullcline



- The V-nullcline of both models we have studied consists of an inverted 'N'-shape
- The simplest function of V which has such a form is

$$y(V) = V - AV^3 + B \quad (1)$$

i.e. a simple 'cubic' with parameters A, B

The V -nullcline

- If the recovery variable in our model is w , then a membrane equation of the form

$$\frac{dV}{dt} = V - AV^3 - w + I \quad (2)$$

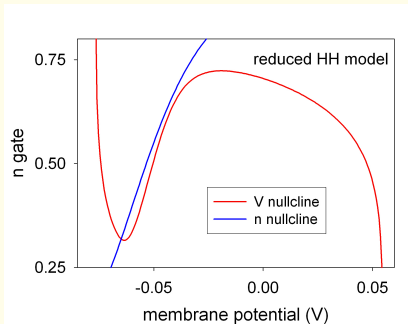
gives rise to a nullcline of the form in (1), for putting $dV/dt = 0$ gives

$$w = V - AV^3 + I \quad (3)$$

where $I \leftrightarrow B$ in (1)

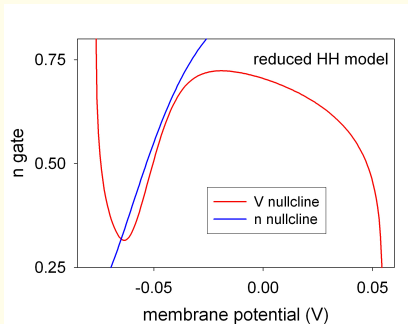
calling the recovery variable w , helps remind us it is an abstract variable and not related to the HH-formalism like n

The w -nullcline



- In the reduced-HH model, the nullcline for the recovery variable is roughly linear over the relevant part of phase space

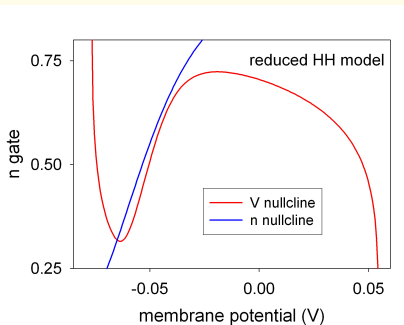
The w -nullcline



- In the reduced-HH model, the nullcline for the recovery variable is roughly linear over the relevant part of phase space
- if we aim to capture HH model-like dynamics, then we may therefore approximate the nullcline by a linear function

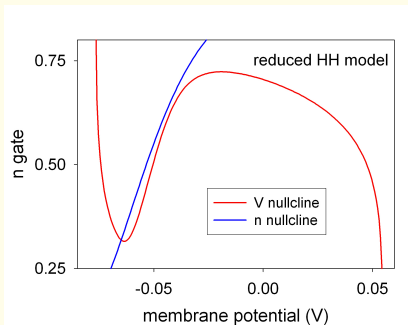
$$w = CV + D \quad (4)$$

The w -nullcline



- In fact, a linear w -nullcline is sufficient to enable many variations of the dynamics

The w -nullcline



- In fact, a linear w -nullcline is sufficient to enable many variations of the dynamics
- The number, and location, of intersections with the V -nullcline is determined by the slope of the w -nullcline, and these are key to the dynamics

The w -nullcline

- A recovery variable equation of the form

$$\frac{dw}{dt} = CV + D - w \quad (5)$$

gives rise to a w -nullcline of the form in (4) (put $dw/dt = 0$)

The w -nullcline

- A recovery variable equation of the form

$$\frac{dw}{dt} = CV + D - w \quad (5)$$

gives rise to a w -nullcline of the form in (4) (put $dw/dt = 0$)

- (5) may be written

$$\frac{dw}{dt} = C(V + E - Fw) \quad (6)$$

where the new constants E, F are given in terms of the old ones by $E = D/C, F = 1/C$

Outline

- 1 Capturing neural dynamics in the abstract
- 2 The Fitzhugh-Nagumo model
- 3 The simple model of Izhikevich

The Fitzhugh-Nagumo model

- Equations (2) and (6) constitute the model developed by Fitzhugh (1961)

The Fitzhugh-Nagumo model

- Equations (2) and (6) constitute the model developed by Fitzhugh (1961)
- In particular, one parametrisation which gives dynamics characteristic of an HH-like model is

An HH-like model

$$\begin{aligned}\frac{dV}{dt} &= V - \frac{V^3}{3} - w + I \\ \frac{dw}{dt} &= 0.8(V + 0.7 - 0.8w)\end{aligned}\tag{7}$$

The Fitzhugh-Nagumo model

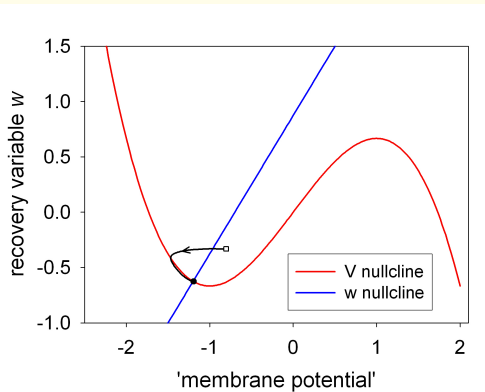
- Equations (2) and (6) constitute the model developed by Fitzhugh (1961)
- In particular, one parametrisation which gives dynamics characteristic of an HH-like model is

An HH-like model

$$\begin{aligned}\frac{dV}{dt} &= V - \frac{V^3}{3} - w + I \\ \frac{dw}{dt} &= 0.8(V + 0.7 - 0.8w)\end{aligned}\tag{7}$$

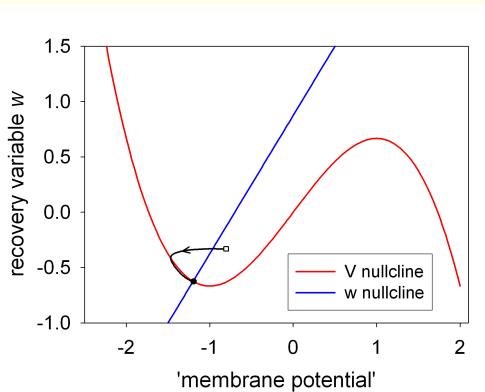
- An implementation of a similar model in electronic hardware by Nagumo in 1962 leads to the joint naming *Fitzhugh-Nagumo* for this model

Phase diagram and resting state



- The nullclines with $I = 0$ are exactly as we expect (they were constructed to be so!)

Phase diagram and resting state



- The nullclines with $I = 0$ are exactly as we expect (they were constructed to be so!)
- A typical trajectory terminating on a stable focus is shown

Status of variables and constants

- The variables V and w are supposed to correspond to the membrane potential and recovery variable respectively

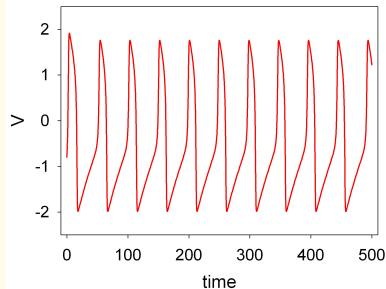
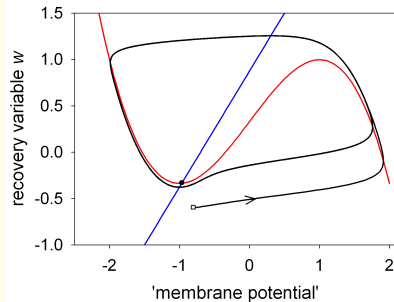
Status of variables and constants

- The variables V and w are supposed to correspond to the membrane potential and recovery variable respectively
- However, the model pays no heed to dimensions, so a value of 1.5, say, for V should not be interpreted as 2mV or 2V

Status of variables and constants

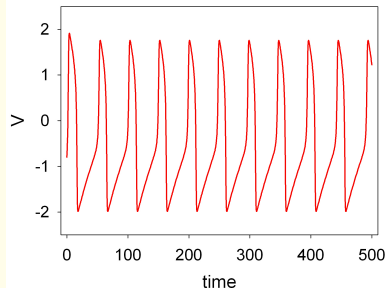
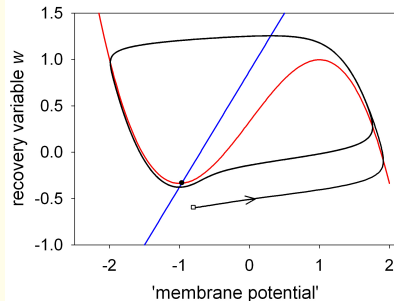
- The variables V and w are supposed to correspond to the membrane potential and recovery variable respectively
- However, the model pays no heed to dimensions, so a value of 1.5, say, for V should not be interpreted as 2mV or 2V
- Physiologically plausible units could be imposed by rescaling all the constants

Limit cycles and spikes



- With a 'current' of 0.33, regular spiking is observed associated with a limit cycle

Limit cycles and spikes



- With a 'current' of 0.33, regular spiking is observed associated with a limit cycle
- The model displays the same bifurcations as the reduced HH model and thereby captures the essentials of its dynamics

Equivalent forms

- Suppose we chose to use the variable $\hat{V} = V - V_{rest}$

Equivalent forms

- Suppose we chose to use the variable $\hat{V} = V - V_{rest}$
- Substituting $V = \hat{V} + V_{rest}$ into (7) would give a new set of equations in the new membrane potential variable \hat{V}

Equivalent forms

- Suppose we chose to use the variable $\hat{V} = V - V_{rest}$
- Substituting $V = \hat{V} + V_{rest}$ into (7) would give a new set of equations in the new membrane potential variable \hat{V}
- However, the membrane equation would still be a cubic in \hat{V} (albeit with quadratic terms too), and the recovery variable equation would still be affine in \hat{V}

Equivalent forms

- Suppose we chose to use the variable $\hat{V} = V - V_{rest}$
- Substituting $V = \hat{V} + V_{rest}$ into (7) would give a new set of equations in the new membrane potential variable \hat{V}
- However, the membrane equation would still be a cubic in \hat{V} (albeit with quadratic terms too), and the recovery variable equation would still be affine in \hat{V}
- Variable substitutions lead to equivalent forms for the model which involve cubics in the membrane equation and linear (or affine) expressions in the recovery equation

Equivalent forms

- Suppose we chose to use the variable $\hat{V} = V - V_{rest}$
- Substituting $V = \hat{V} + V_{rest}$ into (7) would give a new set of equations in the new membrane potential variable \hat{V}
- However, the membrane equation would still be a cubic in \hat{V} (albeit with quadratic terms too), and the recovery variable equation would still be affine in \hat{V}
- Variable substitutions lead to equivalent forms for the model which involve cubics in the membrane equation and linear (or affine) expressions in the recovery equation
- These would all be classified as Fitzhugh-Nagumo models

Outline

- 1 Capturing neural dynamics in the abstract
- 2 The Fitzhugh-Nagumo model
- 3 The simple model of Izhikevich

Further simplification

- The Fitzhugh-Nagumo model is a considerable computational simplification compared to the physiological models
 - The latter require expensive computations such as sigmoid functions for gating variables

Further simplification

- The Fitzhugh-Nagumo model is a considerable computational simplification compared to the physiological models
 - The latter require expensive computations such as sigmoid functions for gating variables
- Is it possible to simplify further?

Further simplification

- The Fitzhugh-Nagumo model is a considerable computational simplification compared to the physiological models
 - The latter require expensive computations such as sigmoid functions for gating variables
- Is it possible to simplify further?
- Computation is most intensive when a system is changing most rapidly - time must be partitioned very finely to ensure the correct dynamics are computed

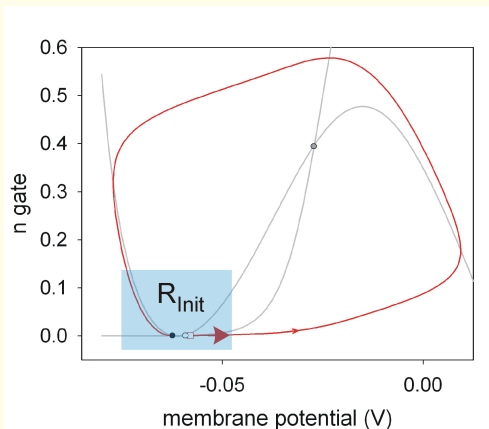
Further simplification

- The Fitzhugh-Nagumo model is a considerable computational simplification compared to the physiological models
 - The latter require expensive computations such as sigmoid functions for gating variables
- Is it possible to simplify further?
- Computation is most intensive when a system is changing most rapidly - time must be partitioned very finely to ensure the correct dynamics are computed
- For neuron models, this corresponds to computing the behaviour during a spike

Further simplification

- The Fitzhugh-Nagumo model is a considerable computational simplification compared to the physiological models
 - The latter require expensive computations such as sigmoid functions for gating variables
- Is it possible to simplify further?
- Computation is most intensive when a system is changing most rapidly - time must be partitioned very finely to ensure the correct dynamics are computed
- For neuron models, this corresponds to computing the behaviour during a spike
- Izhikevich has recently proposed a simple 2D model of neural behaviour which circumvents spike computation but which is rich enough to model a wide variety of spiking behaviours

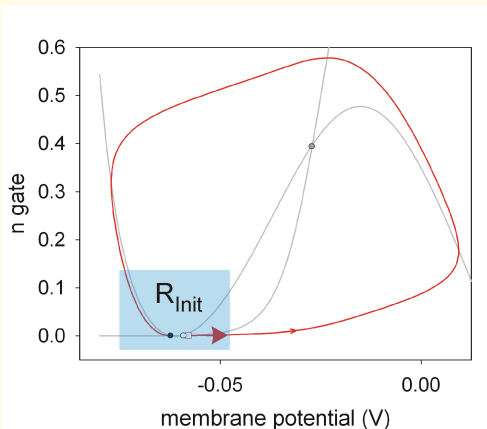
Spike initiation is localised in phase space



- In all the reduced 2D models we have seen, the overall spiking behaviour is controlled in a fairly limited part of phase space (R_{init}) around the 'dip' in the V -nullcline

spike initiation in the $\text{Na}_p^+ - \text{K}^+$ model

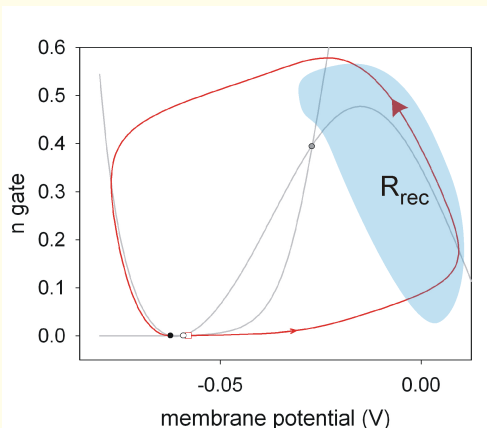
Spike initiation is localised in phase space



- In all the reduced 2D models we have seen, the overall spiking behaviour is controlled in a fairly limited part of phase space (R_{init}) around the 'dip' in the V -nullcline
- The vector field here determines if a spike will be initiated, or if the trajectory returns to a stable equilibrium

spike initiation in the $\text{Na}_p^+ - \text{K}^+$ model

Spike recovery is localised in phase space



- Similarly, the recovery phase (or 'downstroke') of the spike is controlled by the rightmost portions (R_{rec}) of the V -nullcline

spike recovery in the $\text{Na}_p^+ - \text{K}^+$ model

Bypassing spike simulation *per se*

- Izhikevich suggested that we could bypass the computationally intensive process of spike simulation as follows

Bypassing spike simulation *per se*

- Izhikevich suggested that we could bypass the computationally intensive process of spike simulation as follows

- 1 Simulate the subthreshold behaviour of the model in limited phase space like that in R_{init}

Bypassing spike simulation *per se*

- Izhikevich suggested that we could bypass the computationally intensive process of spike simulation as follows

- 1 Simulate the subthreshold behaviour of the model in limited phase space like that in R_{init}
- 2 Watch for spike initiation by noting if V reaches some value V_{peak}

Bypassing spike simulation *per se*

- Izhikevich suggested that we could bypass the computationally intensive process of spike simulation as follows

- 1 Simulate the subthreshold behaviour of the model in limited phase space like that in R_{init}
- 2 Watch for spike initiation by noting if V reaches some value V_{peak}
- 3 If a spike is detected, then reset the membrane and recovery variables to values back in R_{init}

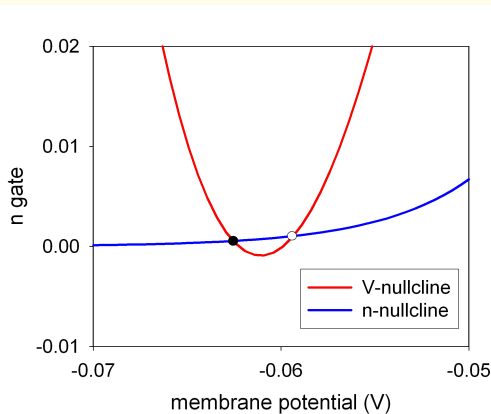
Bypassing spike simulation *per se*

- Izhikevich suggested that we could bypass the computationally intensive process of spike simulation as follows

- 1 Simulate the subthreshold behaviour of the model in limited phase space like that in R_{init}
- 2 Watch for spike initiation by noting if V reaches some value V_{peak}
- 3 If a spike is detected, then reset the membrane and recovery variables to values back in R_{init}

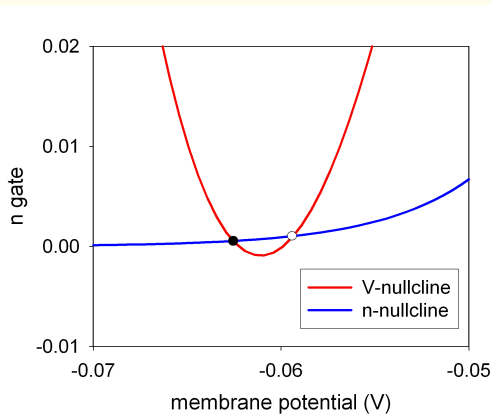
- We now quantify this scheme

Describing nullclines in R_{init}



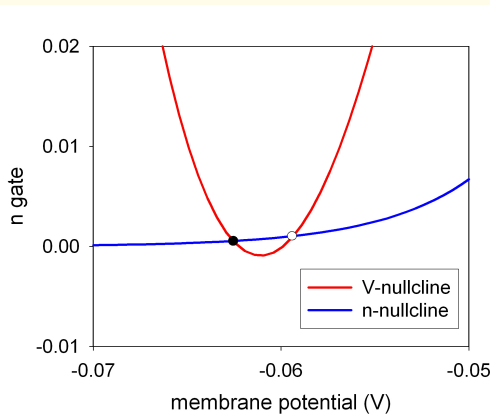
- The V-nullcline in a region like R_{init} appears to be roughly quadratic

Describing nullclines in R_{init}



- The V-nullcline in a region like R_{init} appears to be roughly quadratic
- The recovery variable nullcline appears to be roughly linear

Describing nullclines in R_{init}



- The V-nullcline in a region like R_{init} appears to be roughly quadratic
- The recovery variable nullcline appears to be roughly linear
- We use these descriptions to define the simple model

The Izhikevich simple model

The simple model: membrane potential V , recovery variable u

$$\frac{dV}{dt} = \frac{1}{C} [k(V - V_r)(V - V_t) - u + I] \quad (8)$$

Here, C behaves like the membrane capacitance, V_r is the resting potential, I the injection current. Other quantities are illustrated in the next two slides

The Izhikevich simple model

The simple model: membrane potential V , recovery variable u

$$\frac{dV}{dt} = \frac{1}{C} [k(V - V_r)(V - V_t) - u + I] \quad (8)$$

$$\frac{du}{dt} = a[b(V - V_r) - u] \quad (9)$$

Here, C behaves like the membrane capacitance, V_r is the resting potential, I the injection current. Other quantities are illustrated in the next two slides

The Izhikevich simple model

The simple model: membrane potential V , recovery variable u

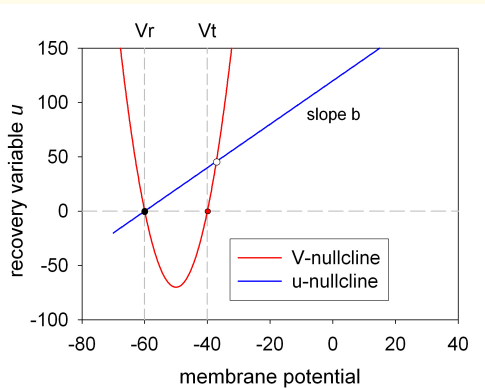
$$\frac{dV}{dt} = \frac{1}{C} [k(V - V_r)(V - V_t) - u + I] \quad (8)$$

$$\frac{du}{dt} = a[b(V - V_r) - u] \quad (9)$$

$$\text{if } V \geq V_{peak} \text{ then } V \leftarrow c, u \leftarrow u + d \quad (10)$$

Here, C behaves like the membrane capacitance, V_r is the resting potential, I the injection current. Other quantities are illustrated in the next two slides

Dynamics with no input

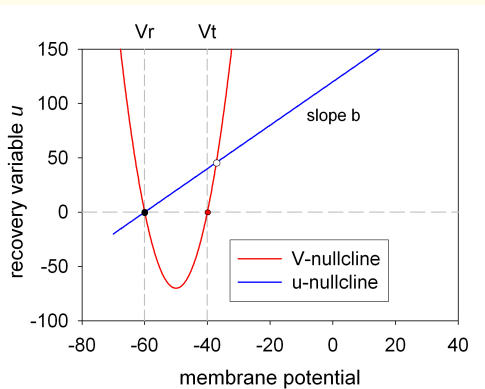


Some features with $I = 0$ are:

- In the resting state, $u = 0$

Nullclines and key features of Izhikevich simple model with $I = 0$

Dynamics with no input

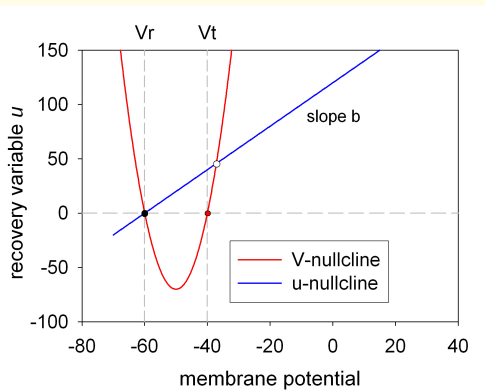


Some features with $I = 0$ are:

- In the resting state, $u = 0$
- V_t, V_r are the values of V when $u = 0$

Nullclines and key features of Izhikevich simple model with $I = 0$

Dynamics with no input

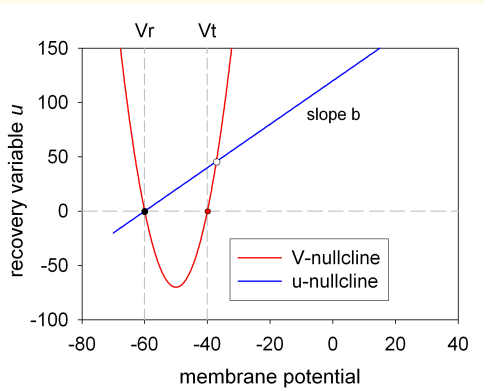


Some features with $I = 0$ are:

- In the resting state, $u = 0$
- V_t, V_r are the values of V when $u = 0$
- The slope of the n -nullcline is the constant b in (8)

Nullclines and key features of Izhikevich simple model with $I = 0$

Dynamics with no input

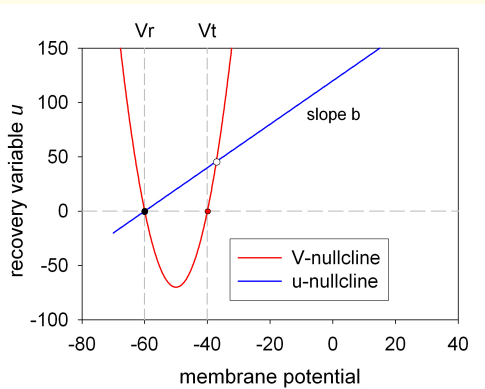


Nullclines and key features of Izhikevich simple model with $I = 0$

Some features with $I = 0$ are:

- In the resting state, $u = 0$
- V_t, V_r are the values of V when $u = 0$
- The slope of the n -nullcline is the constant b in (8)
- With the parameters chosen here, there is a stable node equilibrium at V_r and a saddle node equilibrium at $V_s > V_t$

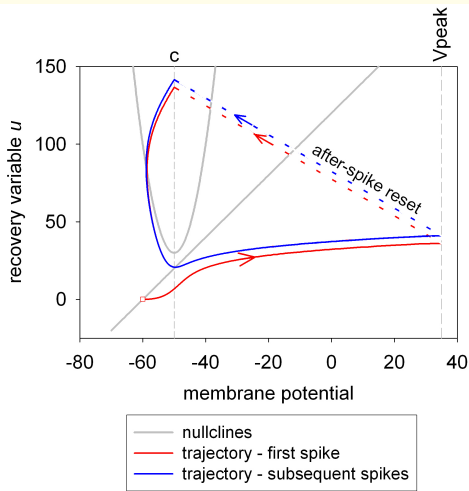
Dynamics with no input



- Note that the parameters have been chosen so that the membrane potential may be plausibly interpreted in mV

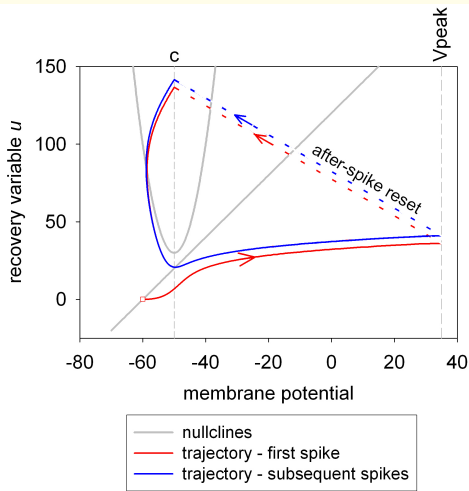
Nullclines and key features of Izhikevich simple model with $I = 0$

Appearance of spikes



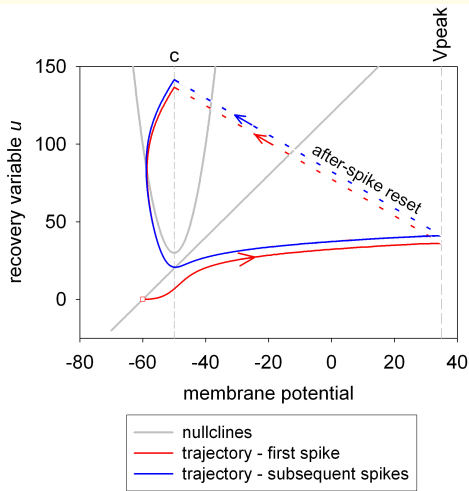
- There are no equilibria at $I = 100$ and so spiking is a necessity

Appearance of spikes



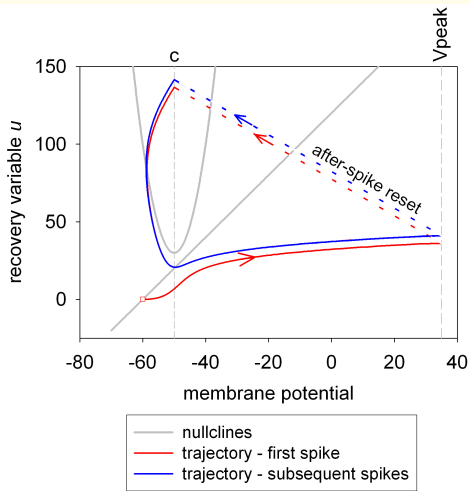
- There are no equilibria at $I = 100$ and so spiking is a necessity
- The trajectory rapidly gives rise to the up-phase of a spike (shown in red)

Appearance of spikes



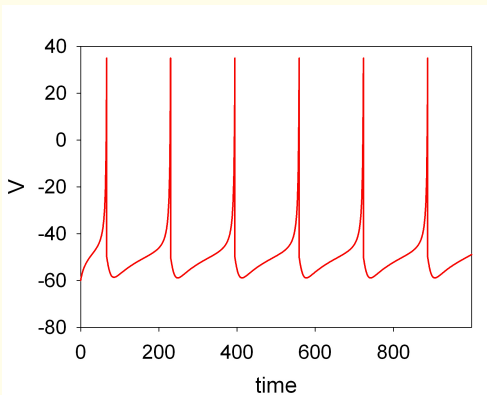
- There are no equilibria at $I = 100$ and so spiking is a necessity
- The trajectory rapidly gives rise to the up-phase of a spike (shown in red)
- This would carry on to indefinitely large values of V unless reset at V_{peak}

Appearance of spikes



- While the reset potential is always c , the reset value of u is $u + d$, which may vary (the initial spike has a smaller value of u at reset)
 - The value of c is at the minimum of the V -nullcline here - this is purely incidental

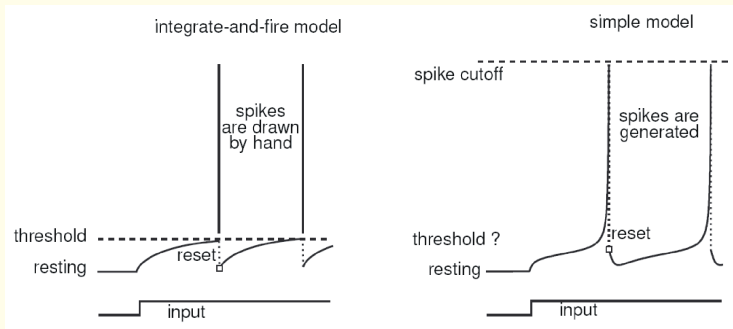
Appearance of spikes



- In the time domain, it is clear that there is repetitive spiking

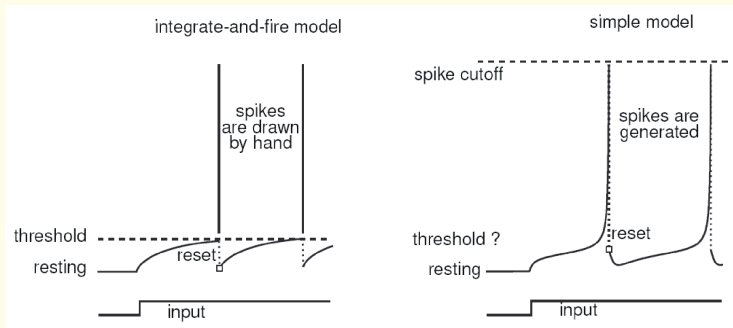
Izhikevich simple model with $I = 100$

LIF and simple model compared



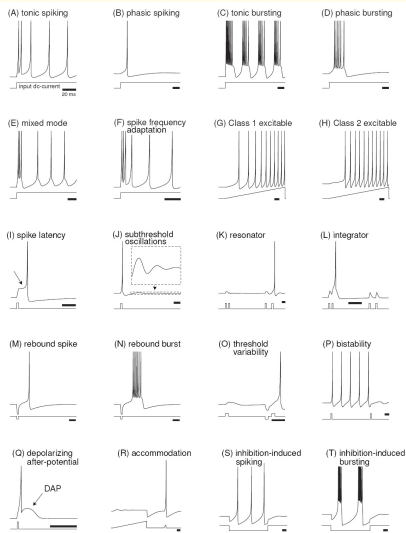
- In the LIF model, spikes are *initiated* at a threshold

LIF and simple model compared



- In the LIF model, spikes are *initiated* at a threshold
- In the simple model they are initiated by the dynamics of the system (as in the more complex reduced models) and *terminated* at a peak value

The simple model is a powerful one



- The simple model is capable of a very wide diversity of firing behaviour using different parameterisations [figure from ch 8 of (Izhikevich, 2007)]

Summary

- It is possible to abstract the essential dynamics of a spiking neuron by establishing equations that give neural-like phase plane structures (nullclines and vector fields)

Summary

- It is possible to abstract the essential dynamics of a spiking neuron by establishing equations that give neural-like phase plane structures (nullclines and vector fields)
- These models have, however, abandoned direct links with any physiological basis

Summary

- It is possible to abstract the essential dynamics of a spiking neuron by establishing equations that give neural-like phase plane structures (nullclines and vector fields)
- These models have, however, abandoned direct links with any physiological basis
- This strategy gives the Fitzhugh-Nagumo model and the simple models of Izhikevich

Summary

- It is possible to abstract the essential dynamics of a spiking neuron by establishing equations that give neural-like phase plane structures (nullclines and vector fields)
- These models have, however, abandoned direct links with any physiological basis
- This strategy gives the Fitzhugh-Nagumo model and the simple models of Izhikevich
- In sum, the analysis of 2D, reduced models is a very powerful approach giving insights into a range of phenomena including, excitability classification, rebound inhibition etc.

Further reading

- Izhikevich and Fitzhugh (2006) have an article on the Fitzhugh-Nagumo model in Scholarpedia which has a nice historical note
- Ch 8 of the book by Izhikevich (2007) deals with the Simple Model
- Matlab code is available on MOLE

References

- Izhikevich, E. (2007). *Dynamical systems in neuroscience: The geometry of excitability and bursting*. MIT Press.
- Izhikevich, E., & Fitzhugh, R. (2006). Fitzhugh-nagumo model. In *Scholarpedia* (p. 5642). online material. (http://www.scholarpedia.org/wiki/index.php?title=FitzHugh-Nagumo_Model&&oldid=7128)