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## Resonate-and-fire neurons

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### Abstract

We suggest a simple spiking model—resonate-and-fire neuron, which is similar to the integrate-and-fire neuron except that the state variable is complex. The model provides geometric illustrations to many interesting phenomena occurring in biological neurons having subthreshold damped oscillations of membrane potential. For example, such neurons prefer a certain resonant frequency of the input that is nearly equal to their eigenfrequency, they can be excited or inhibited by a doublet (two pulses) depending on its interspike interval, and they can fire in response to an inhibitory input. All these properties could be observed in Hodgkin–Huxley-type models. We use the resonate-and-fire model to illustrate possible sensitivity of biological neurons to the fine temporal structure of the input spike train. Being an analogue of the integrate-and-fire model, the resonate-and-fire model is computationally efficient and suitable for simulations of large networks of spiking neurons. © 2001 Elsevier Science Ltd. All rights reserved.

*Keywords:* Pulse-coupled neurons; Spikes; Resonance; FM interactions; Andronov–Hopf bifurcation

### 1. Introduction

Damped or sustained fast subthreshold oscillations of membrane potential (see Fig. 1) have been observed in many biological neurons (see e.g. Hutcheon, Miura, & Puil, 1996a; Llinas, 1988; Llinas, Grace, & Yarom, 1991; Pedroarena & Llinas, 1997, and references therein) and in almost all biophysically detailed Hodgkin–Huxley-type neural models (see e.g. FitzHugh, 1969; Hodgkin & Huxley, 1952; Hutcheon & Yarom, 2000; Hutcheon, Miura, & Puil 1996b; Manor, Rinzel, Segev, & Yarom, 1997; Morris & Lecar, 1981; Pike, Goddard, Suckling, Ganter, Kasthuri, & Paulsen, 2000).

This dynamic property makes neurons sensitive to the timing of a stimulus. Indeed, during the oscillation the distance between the membrane potential and the threshold changes. A strong stimulus may or may not elicit a spike depending on its timing relative to the phase of oscillation, as we illustrate in Fig. 2b. This leads to many interesting nonlinear phenomena, such as oscillation of spiking probability, sensitivity to the interspike period of incoming doublets, triplets and bursts, selective communication, resonance, FM interactions, etc. All these phenomena are relatively simple, but they are obscured by the complexity of the Hodgkin–Huxley-type models. As a result, they may be difficult to understand and simulate, especially in a network of many neurons. Moreover, some scientists believe that such phenomena are peculiar only to the Hodgkin–

Huxley-like models and cannot be seen in simple spiking neurons (Luk & Aihara, 2000).

In this short paper, we introduce a biologically inspired, but simple, resonate-and-fire model that illustrates how subthreshold oscillations may affect a neuron's spiking dynamics. The resonate-and-fire model is the simplest possible model to exhibit damped oscillation of membrane potential, and it makes many non-trivial ideas easy to understand and illustrate. Its computational efficiency is comparable with that of the integrate-and-fire model, which makes it suitable for simulations of large networks of spiking neurons.

### 2. Integrators versus resonators

Neurons generate action potentials because their membranes have voltage dependent ionic channels (Johnston & Wu, 1995). Since there are many types of such channels, there could be thousands of different conductance-based mechanisms for excitability and spiking, and, hence, thousands of biophysically accurate models of spiking neurons. Most such models can be studied using dynamical systems theory. For example, a rest state corresponds to an equilibrium attractor, and repetitive spiking to a limit cycle attractor. An important observation is that neurons are excitable because they reside near a bifurcation from equilibrium to a limit cycle attractor (Rinzel & Ermentrout,

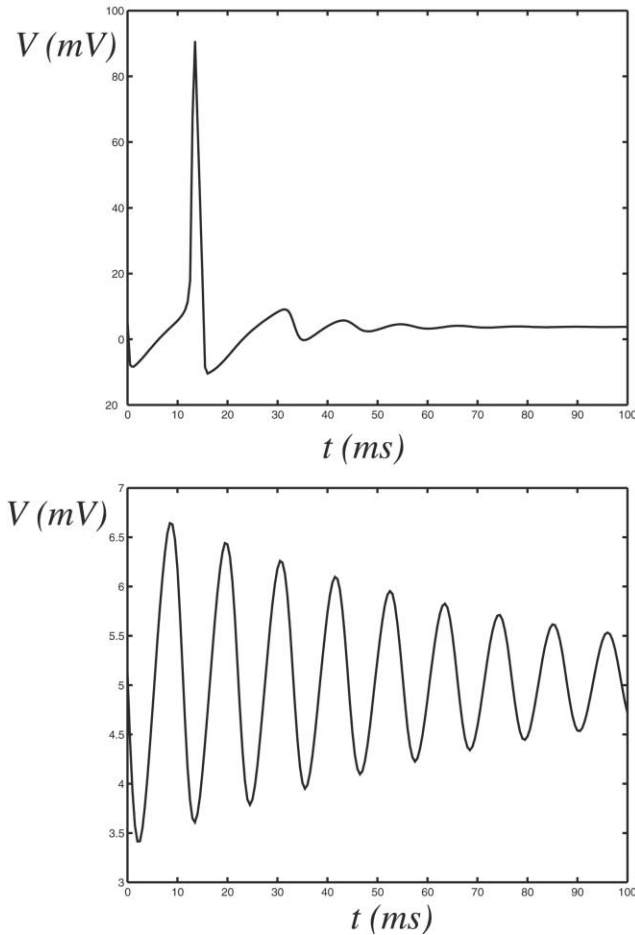


Fig. 1. Examples of damped subthreshold oscillations of membrane potential in the Hodgkin–Huxley model (compare the voltage scales).

1989). Despite the huge number of biophysical mechanisms, there are only two major dynamic mechanisms of excitability: via saddle-node or Andronov–Hopf bifurcations (see review by Izhikevich, 2000).

The two bifurcations frequently result in different subthreshold behavior of the voltage variable after a short pulse of current is applied, see Fig. 2. Voltage exhibits exponential convergence to the rest state in the saddle-node case, and damped *oscillatory* convergence in the Andronov–Hopf case. This results in different neuro-computational properties, as we illustrate in Fig. 3 and discuss below.

2.1. Integrators

Consider Fig. 2a, where the voltage variable exhibits exponential convergence to the rest state after the first pulse was applied. If the second pulse arrives right after the first one, the voltage crosses the threshold and the neuron fires. The shorter the distance between the pulses is, the more likely the neuron fires. Such neurons perform temporal integration of the incoming pulse trains, and they are termed *integrators*. They prefer high frequency of the

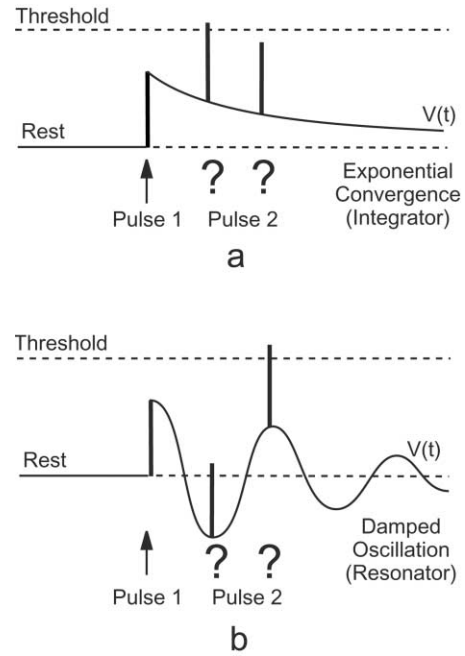


Fig. 2. The neuron membrane potential,  $V(t)$ , is perturbed by a current pulse (pulse 1). (a) Systems having exponential convergence to the rest state: the second pulse (pulse 2) can make the neuron fire if it arrives right after Pulse 1. (b) Systems having damped oscillatory convergence to the rest: to make the neuron fire, the distance between the pulses 1 and 2 should be near the period of the subthreshold oscillation.

input: the higher the frequency, the sooner they fire. Decreasing the frequency of the input delays or even terminates their firing, as one can see in Fig. 3a. Many cortical neurons are integrators.

2.2. Resonators

In contrast, neurons near an Andronov–Hopf bifurcation exhibit damped oscillation of the membrane potential, which changes the distance to the threshold. The effect of the second pulse depends on its timing relative to the period of the oscillation. If the timing between the two pulses is near half the period, the pulses effectively cancel each other, see Fig. 2b. If the timing is near one period, the pulses add up. Such neurons prefer inputs having a certain resonant frequency that is equal to the frequency of the subthreshold oscillation. That is, in order to evoke a response, one should stimulate such a neuron at the resonant frequency, as we illustrate in Fig. 3b using various conductance-based Hodgkin–Huxley-type models. This resonant behavior has been described in thalamic (Hutcheon, Miura, Yarom, & Puil, 1994; Puil, Meiri, & Yarom, 1994) and cortical neurons (Gutfreund, Yarom, & Segev, 1995; Hutcheon et al., 1996a,b; Jansen & Karnup, 1994). Such neurons are referred to as being *resonators* (Izhikevich, 2000; Llinas, 1988). In contrast to integrators, increasing the frequency of stimulation may delay or even terminate firing of a resonator neuron (see middle of Fig. 3b).

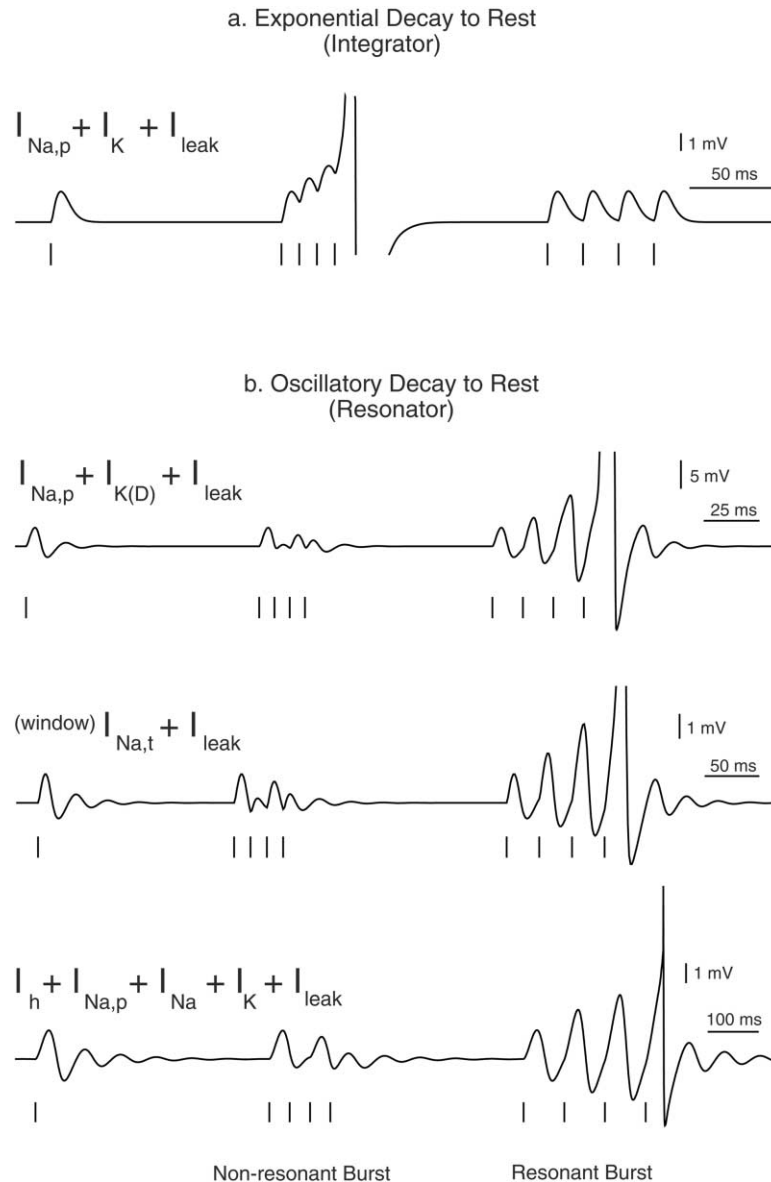


Fig. 3. Neuro-computational properties of neurons depend on whether or not the decay to the rest state is oscillatory. (a) Neurons having exponential (non-oscillatory) decay to the rest state act as integrators—the higher the frequency of the input (vertical bars below the voltage traces) the sooner they fire. An input burst of four spikes is more effective when the interspike interval is small. (b) Neurons having damped oscillations to rest act as resonators—they prefer input having resonant frequency. An input burst of four spikes is more effective when the interspike interval equals the period of the damped oscillation (resonant burst). Shown are voltage traces of various electrophysiological Hodgkin–Huxley-type models possessing the currents listed in each panel.

This dichotomy, i.e. integrators versus resonators, is important to keep in mind when studying spiking neurons. For example, the Hodgkin and Huxley (1952) and FitzHugh (1969) models exhibit Andronov–Hopf bifurcation, and, hence, are resonators. In contrast, the Connor (1977) model exhibits saddle-node bifurcation, and, hence, is an integrator. Many conductance-based models, such as Morris and Lecar (1981), can be integrators or resonators depending on the values of parameters, as we illustrate in Fig. 4. Thus, spiking neurons having similar ionic mechanisms may have quite different neuro-computational properties, and it is important to realize that.

### 2.3. Computational efficiency

Biophysically plausible Hodgkin–Huxley-type neural models have many desirable properties, but they might be computationally inefficient when one needs to simulate a huge network of spiking neurons. A reasonable alternative might be to use the *integrate-and-fire* model, which is simple and linear (except at the firing moments). However, the model is an integrator, and, hence, it is not suitable for simulations of networks of Hodgkin–Huxley or FitzHugh–Nagumo neurons, which are resonators (compare Fig. 4a and c).

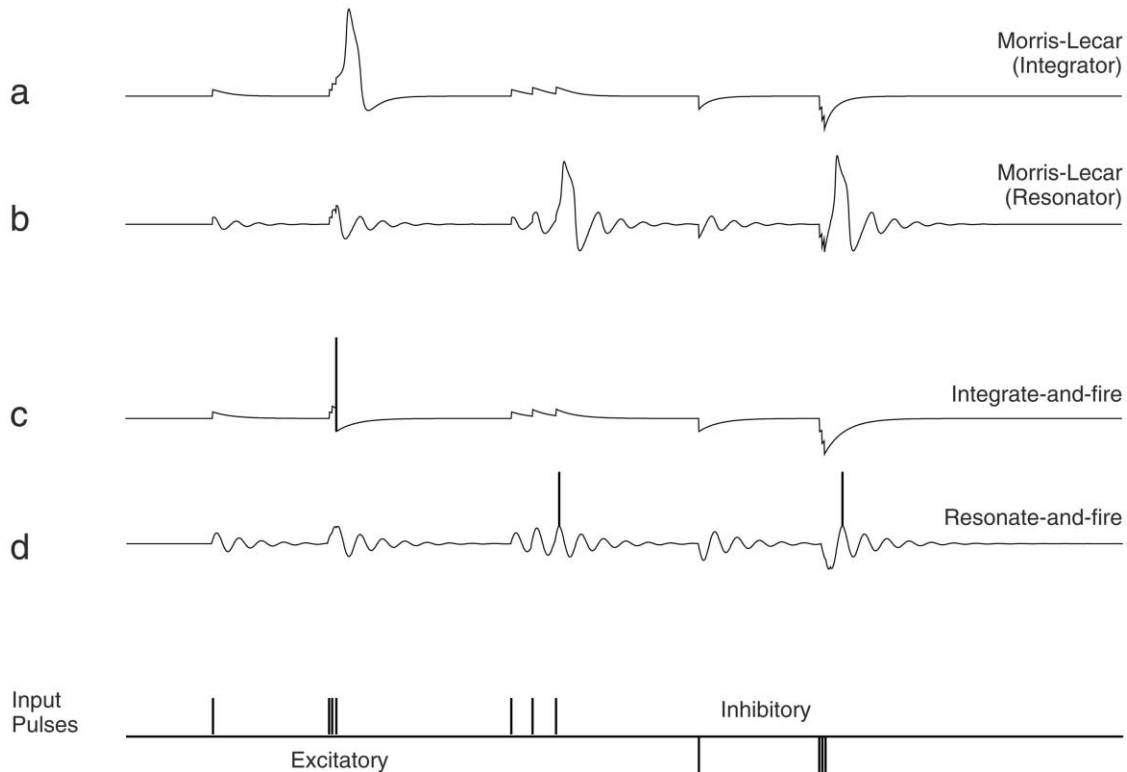


Fig. 4. Top: simulations of the Hodgkin–Huxley-type neural model (Morris & Lecar, 1981) with two sets of parameters corresponding to the integrator (a) and resonator (b) behavior. Notice the differences in the subthreshold and spiking responses. Bottom: integrate-and-fire (c) and resonate-and-fire (d) models describe accurately qualitative the behavior of the Morris–Lecar model. Notice that integrators prefer high frequency of the input, whereas resonators respond to the pulse train having resonant eigenfrequency (middle triplet). Also notice that resonators produce a post-inhibitory spike, while integrators do not.

Below, we introduce an analogue of the integrate-and-fire model—the *resonate-and-fire* neuron, which could be used as a computationally efficient alternative for the Hodgkin–Huxley-type neural models; see Fig. 4b and d. The integrate- and resonate-and-fire models look similar (compare Eqs. (1) and (2) below), and have similar advantages. They are simple, linear and pulse-coupled. Both models share the same drawback. They are extreme caricatures of biological neurons.

### 3. The resonate-and-fire neurons

A salient feature of neural models near Andronov–Hopf bifurcation is the existence of a damped subthreshold oscillation of the membrane potential. This renders a unique neuro-computational property that is not present in the integrate-and-fire model. Our goal is to make a minimal modification to the integrate-and-fire model so that it exhibits damped oscillations.

#### 3.1. Linearization

Any non-linear neuron model exhibiting damped oscillations of membrane potential can be converted into a linear model by a local continuous change of variables. (The linearity assumption is violated during the brief but large

magnitude action potential.) This mathematical result follows from the Hartman–Grobman Theorem and Invariant Manifold Reduction Theorem, and it is discussed in the context of neural systems by Hoppensteadt and Izhikevich (1997). The resulting linear system

$$\dot{x} = bx - \omega y$$

$$\dot{y} = \omega x + by$$

can be written in the equivalent complex form

$$\dot{z} = (b + i\omega)z.$$

Here  $z = x + iy \in \mathbb{C}$  is a complex-valued variable that describes oscillatory activity of the neuron. The real part,  $x$ , is the current-like variable. It describes dynamics of voltage-gated and synaptic currents. The imaginary part,  $y$ , is the voltage-like variable.  $b + i\omega \in \mathbb{C}$  is a parameter, where  $b < 0$  is the rate of attraction to the rest and  $\omega > 0$  is the frequency of the oscillations. We use  $b = -1$  and  $\omega = 10$  in most of our illustrations. The equation above is the simplest model exhibiting damped oscillations. It describes subthreshold behavior of a neuron.

#### 3.2. The model

From now on, we model subthreshold dynamics of each

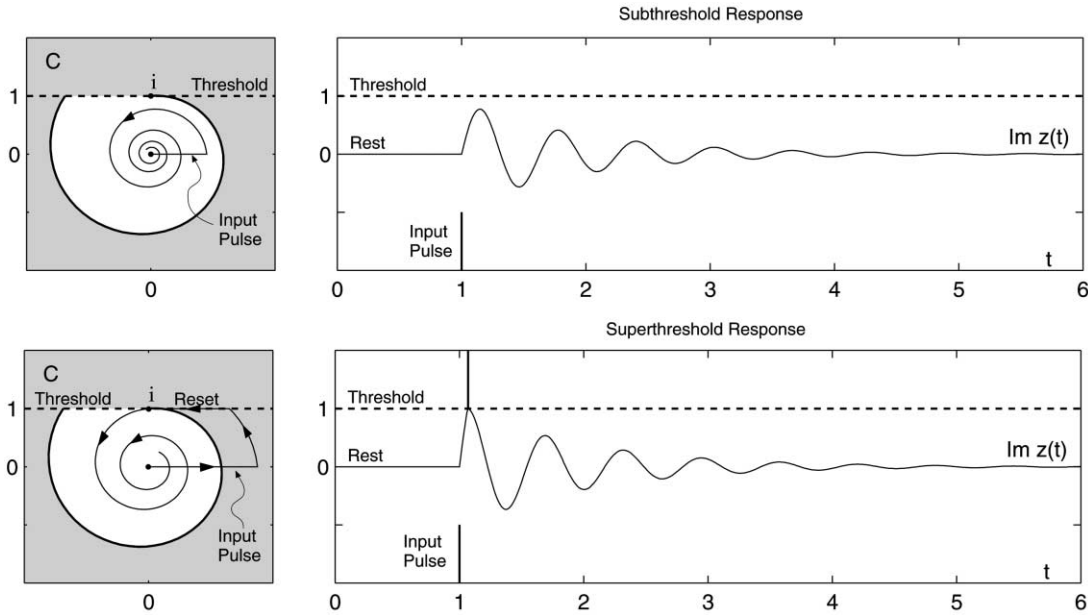


Fig. 5. The resonate-and-fire neuron fires when the solution crosses the threshold  $y = 1$ . To fire, the solution must be pushed into the shaded area.

neuron by the linear model above and say that  $z$  fires an action potential when the voltage variable  $y = \text{Im } z$  crosses the threshold value  $y = 1$ , which is the horizontal line on the complex plane that passes through  $i \in \mathbb{C}$ ; see Fig. 5. To make it fire, external perturbations should push  $z$  beyond the bold curve that encompasses the white area in the figure. The curve is a piece of solution that passes through the point  $i \in \mathbb{C}$ . Any solution starting in the white area will converge to the rest state  $z = 0$  without crossing the threshold. Any solution starting outside the white area will cross the threshold before converging to the rest state.

Similarly to the *integrate-and-fire* model,

$$\dot{y}_i = a_i + b_i y_i + \sum_{j=1}^n s_{ij} \delta(t - t_j^*) \quad (1)$$

the *resonate-and-fire* model can be written in the form

$$\dot{z}_i = (b_i + i\omega_i)z_i + \sum_{j=1}^n c_{ij} \delta(t - t_j^*), \quad (2)$$

where  $z_i \in \mathbb{C}$  describes the state of the  $i$ -th neuron,  $b_i + i\omega_i \in \mathbb{C}$  is its internal parameter, each  $c_{ij} \in \mathbb{C}$  is a synaptic coefficient,  $\delta$  is the Dirac delta function, and  $t_j^*$  is the nearest moment of firing of the  $j$ -th neuron. We see that each firing produces a pulse that displaces activities of the other neurons by the complex-valued constant  $c_{ij}$  (we use real  $c_{ij}$  in our illustrations here; complex  $c_{ij}$  are also feasible). After  $z_i$  fires an action potential, it is reset to a new value. We reset it to  $i \in \mathbb{C}$  (see bottom of Fig. 5), although other reset values are also feasible. Even though each equation in (2) is linear, the network behavior is non-linear, due to the connections between the neurons and the reset dynamics.

Systems (1) and (2) may look similar, but they have quite different dynamics, which we contrast in Fig. 6. Each

incoming pulse displaces activities of the integrate- and resonate-and-fire models. Whenever they cross the threshold  $y = 1$ , the neurons are said to fire a spike. After the spike, the variables are reset to certain values. Both variables decay exponentially to the rest state  $y = -a/b$  and  $z = 0$ , respectively, but the latter exhibits dampened oscillation. In the rest of the paper, we show how this property endows the resonate-and-fire model with many features that cannot exist in the integrate-and-fire model. This emphasizes the difference between neuro-computational properties of integrators and resonators (Izhikevich, 2000).

### 3.3. Firing probability

In Fig. 7 (top) we perturb a quiescent integrate-and-fire neuron by an excitatory pulse so that its activity,  $y(t)$ , exhibits exponential decay to rest. The minimal amplitude of the next excitatory pulse,  $A(t)$ , necessary to excite the cell past the threshold is depicted in the same figure. Since  $A(t) = 1 - y(t)$ , it also exhibits exponential decay. One can see that the larger the distance between the pulses is, the stronger the second pulse should be to elicit a response.

In the middle of Fig. 7 we perturb a quiescent resonate-and-fire neuron by an excitatory pulse and plot  $A(t)$ , which exhibits dampened oscillation with the neuron's eigenfrequency  $\omega$  (eigenperiod  $T = 2\pi/\omega$ ). The minima of  $A(t)$  correspond to the moments the cell is most vulnerable to the second pulse. These are the windows of opportunity for other neurons to elicit response. The first window is right after the pulse. The next window is eigenperiod  $T$  away from the first one. Thus, the second pulse has the greatest effect when it arrives with the first one (coincidence detection) or  $T$  units after the first one (resonance detection). It has the least effect when it arrives  $T/2$  units after the first

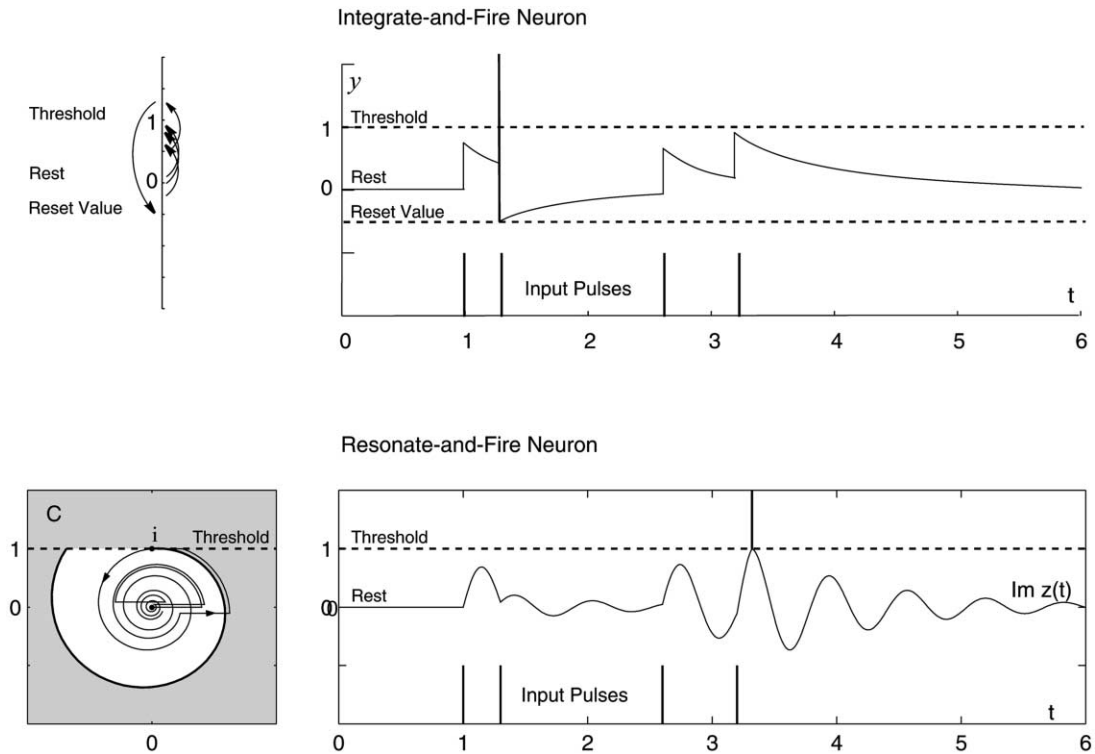


Fig. 6. Typical response of the integrate-and-fire (top) and the resonate-and-fire (bottom) neurons to an input pulse train.

pulse. This observation will be important when we consider below the effect of a doublet stimulation.

In the bottom of Fig. 7 we apply an inhibitory pulse.  $A(t)$  first increases, then decreases below the steady state value. Thus, the inhibitory pulse enhances sensitivity of the resonate-and-fire neuron to subsequent excitatory stimulation having appropriate timing. This is a prominent property of resonators which can be observed in Hodgkin–Huxley-type models (Luk & Aihara, 2000) as well as in simple resonate-and-fire models.

### 3.4. Post-inhibitory spikes

Unlike integrators, resonators can easily fire a spike in response to an inhibitory stimulation. This phenomenon can be seen in biophysically detailed and simplified models, as we illustrate in Figs. 4 and 8. The existence of post-inhibitory spikes is a salient property of resonators, and it is closely related to the rebound or anodal break excitation. Integrate-and-fire neurons do not exhibit such a neuro-computational property (Izhikevich, 2000).

### 3.5. Doublets

Suppose a neuron receives a pair of pulses, which is frequently referred to as being a *doublet*. We consider the effect of such an input geometrically in Fig. 9. We take  $c = 0.8$  so that each pulse alone cannot evoke an action potential, but both can, provided that they have appropriate timing.

The first spike evokes a damped oscillation, as seen in Figs. 5 and 7 (middle). Whether the second pulse can push the solution beyond the threshold depends on its timing relative to the phase of the oscillation. The neuron oscillations with the eigenperiod  $T = 2\pi/\omega$ . If the interspike interval is infinitesimal, as in Fig. 9a, or near the eigenperiod  $T$ , as in Fig. 9c, then the neuron fires. In these cases, the effect of the second pulse adds to that of the first pulse. If the interval is significantly less or greater than the eigenperiod, the neuron may not fire as we illustrate in Fig. 9b and d. In these cases, the effect of the second pulse cancels that of the first pulse. We refer to the doublet having interspike interval equal to the eigenperiod of the postsynaptic neuron as being *resonant* for that neuron. The other doublets in Fig. 9 are *non-resonant*. This result can easily be generated for triplets and bursts of pulses (the case of quadruplets is depicted in Fig. 3).

We see that incoming pulses may add up or cancel each other depending on whether the input is resonant or not. Hence, the name *resonate-and-fire*.

### 3.6. Multiplexing

The same doublet may be resonant for some neurons and non-resonant for others. Resonate-and-fire neurons having eigenfrequency  $\omega$  tend to send doublets, triplets, etc., having the same interspike frequency  $\omega$ . (The frequency may change, though, due to the dispersion properties of axons.) Such doublets are resonant for neurons having

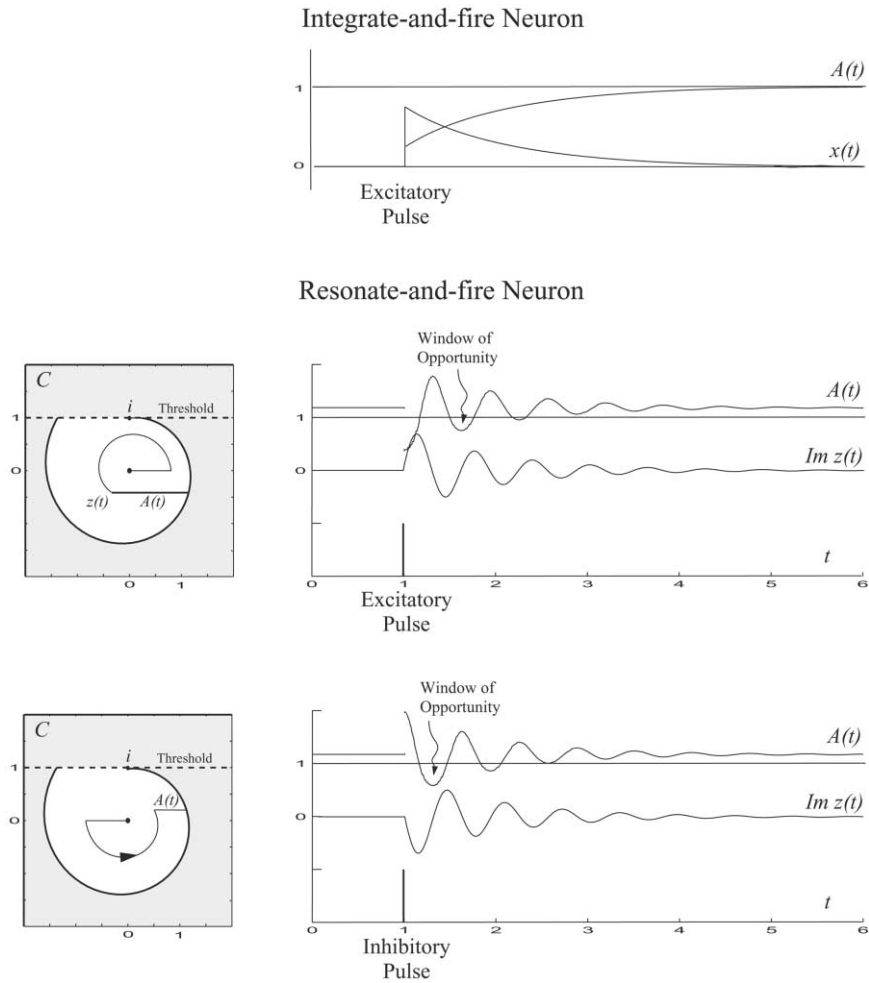


Fig. 7. The minimal amplitude,  $A(t)$ , of the second pulse necessary to discharge the cell as a function of time.

similar eigenfrequencies, and non-resonant for others. This provides an effective tool for selective communication, see Fig. 10. In particular, the network can multiplex: send many message via a single transmission line, as we illustrate in Fig. 11.

In Figs. 10 and 11 we implicitly assume that axonal propagation does not alter the timing of spikes. If it does, then the set of postsynaptic neurons with which a given neuron can communicate selectively is determined by the

interspike frequency at the axonal terminals, and not at the axonal hillock.

### 3.7. Periodic stimulation

We see that if pulses arrive with a wrong interval, they may cancel each other. Thus, a periodically stimulated neuron may never fire, as we illustrate in Fig. 12, despite the fact that the frequency of stimulation is high. To make

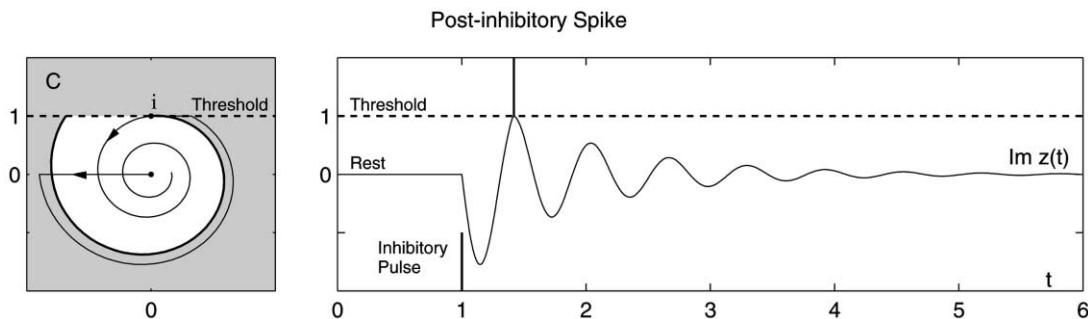


Fig. 8. The resonate-and-fire model illustrates how an inhibitory pulse can lead to an action potential.

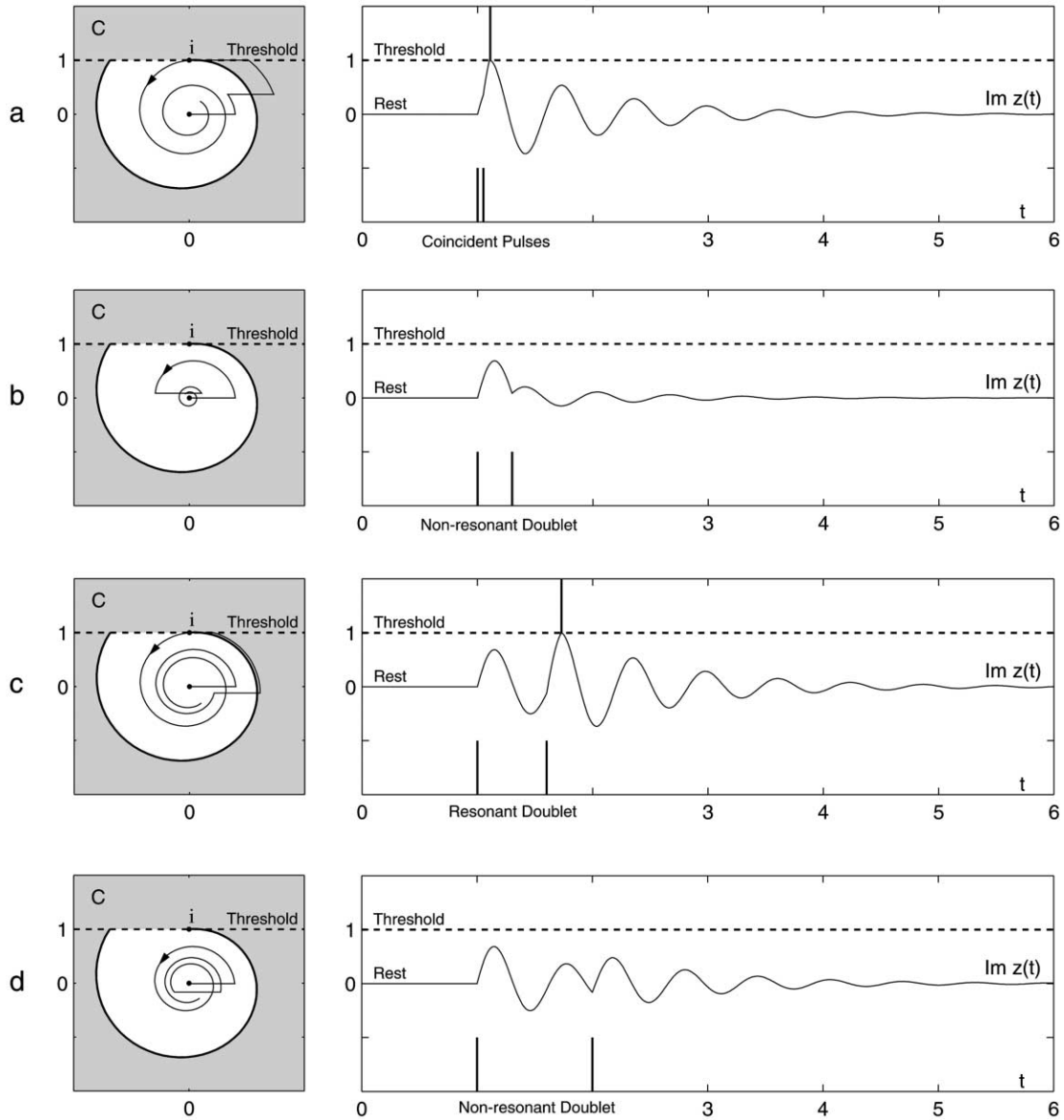


Fig. 9. A doublet may or may not make the postsynaptic neuron fire depending on the interspike interval. (a) The interspike interval is extremely short; the resonate-and-fire model acts as a coincidence detector. (b) The interspike interval is equal to the half of the cell’s eigenperiod. (c) The interspike interval is nearly equal to the eigenperiod. (d) It is too long.

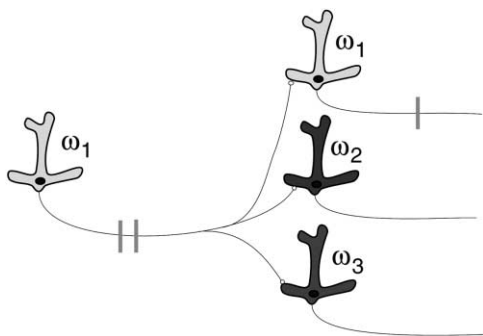


Fig. 10. Selective interaction: a doublet sent by a resonate-and-fire neuron having eigenfrequency  $\omega_1$  is resonant for another neuron having similar eigenfrequency and non-resonant for the others.

the neuron fire, the input period must be nearly resonant: it must be nearly equal to, or a multiple of, the eigenperiod. In Fig. 13 we illustrate the response to the input having slowly increasing frequency, i.e. the ZAP input. One can clearly see the resonance phenomenon when the input frequency passes the eigenfrequency. Thus, only certain (resonant) frequencies of the input get a super-threshold response. This phenomenon has been seen in many biological neurons (see review by Hutcheon & Yarom, 2000).

### 3.8. Sustained periodic firing

When a dc-current is injected into a neuron, the neuron may generate a sustained firing. This may occur in both



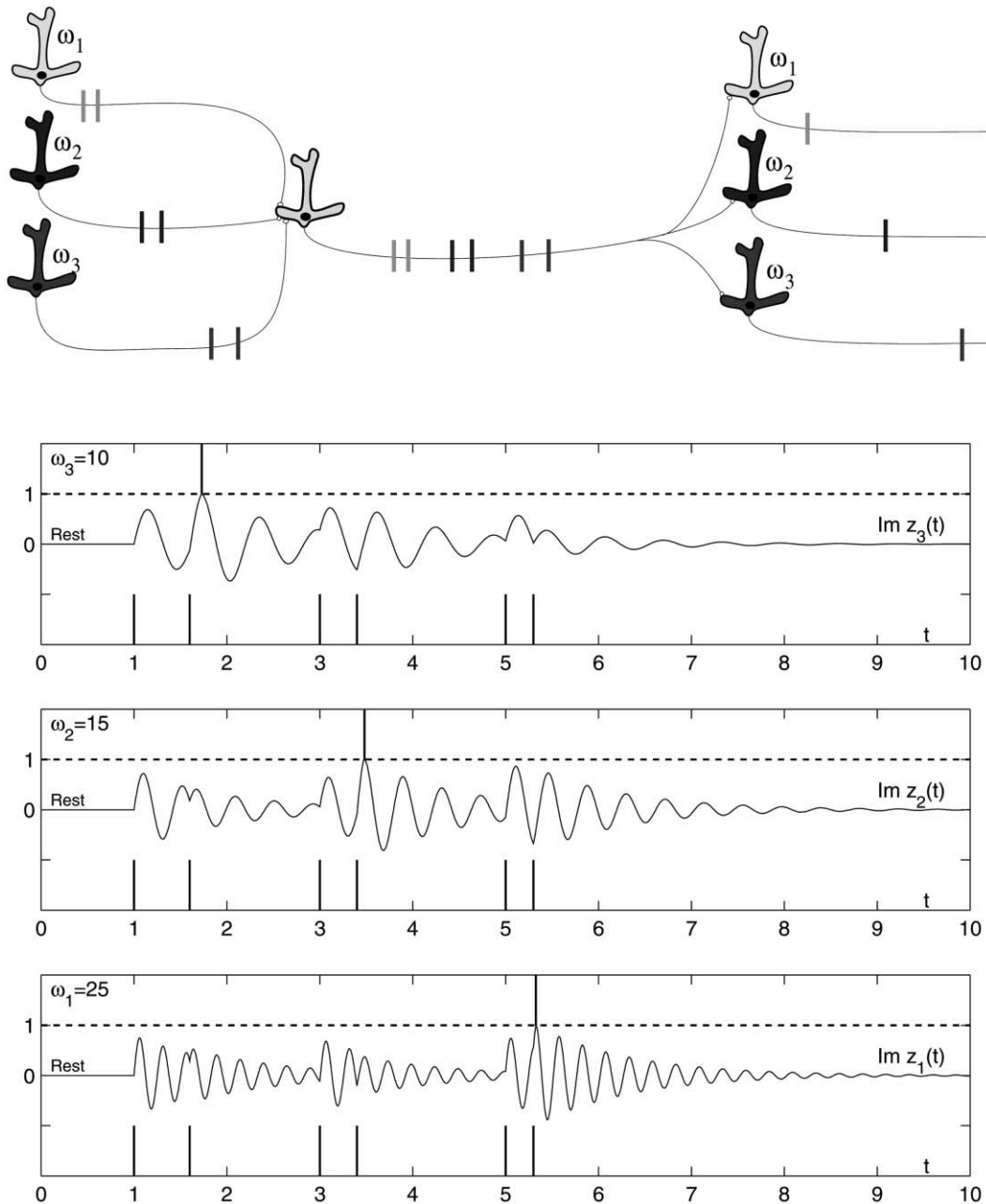


Fig. 11. Multiplexing of neural signals via doublets: resonate-and-fire neurons having equal eigenfrequencies can interact selectively without any cross interference with other neurons.

integrate- and resonate-and-fire neurons. In Fig. 14 we illustrate the behavior of the resonate-and-fire neuron

$$\dot{z} = (b + i\omega)z + I,$$

where  $I \in \mathbb{C}$  is a constant input. The input shifts the equilibrium (rest state) of the model to a new value  $z_0 = -I / (b + i\omega)$ . As soon as the current is turned on, the variable  $z(t)$  starts to approach  $z_0$ . When the value of the current is small, the resonate-and-fire neuron may fire a single transient spike, as in the top of Fig. 14. When the current is strong enough, the neuron becomes a pacemaker. In the bottom of Fig. 14 we depict a magnified phase portrait of the resonate-

and-fire neuron receiving sufficiently large injected dc-current. The new rest state  $z_0$  is still stable, but its basin of attraction, (white area) is small. Such a neuron is susceptible to weak perturbations coming from other neurons.

A peculiar feature of the resonate-and-fire model is that it exhibits a bistability of rest and spiking states. Indeed, the reset value  $i \in \mathbb{C}$  lies outside the basin of attraction of the rest state  $z_0$ . As soon as such a neuron fires its first spike, it continues to fire periodically, until some perturbation pushes the solution inside the white area—the basin of attraction of the rest state. Such a perturbation may be excitatory or inhibitory. It should be relatively weak, and it

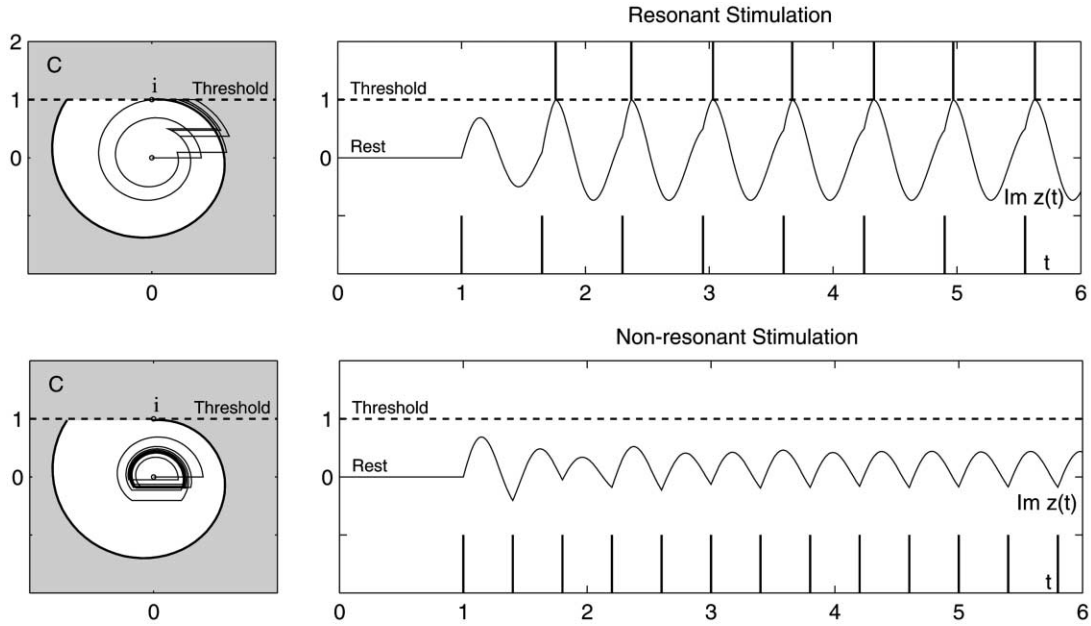


Fig. 12. A periodically stimulated neuron may never fire if the period of stimulation is not resonant, i.e. far from being equal to or a multiple of the eigenperiod.

should have an appropriate timing. This interesting phenomenon has been seen in the Hodgkin–Huxley model (Guttman, Lewis, & Rinzel, 1980), but it cannot occur in the integrate-and-fire model.

Another, simpler way to make the resonate-and-fire neuron fire periodic spike train is to move the reset point into the shaded area, e.g. to  $-2 + i$ .

3.9. Sustained subthreshold oscillation

The resonate-and-fire neuron (2) cannot exhibit sustained subthreshold oscillation of the membrane potential unless  $b = 0$ . However, one can use the topological normal form for the Andronov–Hopf bifurcation

$$\dot{z} = (b + i\omega)z - |z|^2$$

to simulate dynamics of each resonate-and-fire neuron in Eq. (2). When  $0 < b < 1$ , this system exhibits subthreshold oscillations with the amplitude  $\sqrt{b}$  and the frequency  $\omega$ .

When  $b < 0$ , this system is equivalent to the linear one used in Eq. (2).

4. Discussion

We present a simple resonate-and-fire model that illustrates how damped subthreshold oscillations of neuron membrane potential make it sensitive to the fine temporal structure of the input pulse train. This emphasizes the importance of the spike timing code as opposed to the mean firing rate code (Abeles, 1991). How this affects neuro-computational properties of the brain is still unknown. There are a number of hypotheses on the significance of damped or sustained subthreshold oscillations.

- Resonator (Llinas, 1988). A neuron can respond preferably to the input having resonant frequency.
- Rhythm coordinator (Hutcheon et al., 1996a; Lampl & Yarom 1997; Manor, Rinzel, Segev, & Yarom, 1997). Network interactions amplify damped oscillations lead-

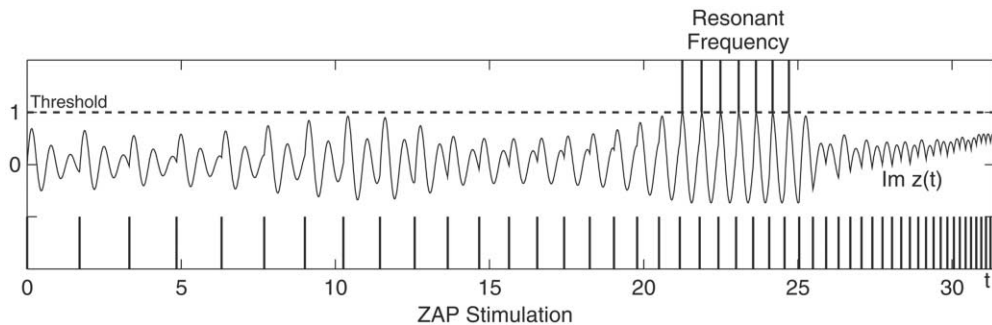


Fig. 13. Response of the resonate-and-fire neuron to a stimulus having slowly increasing frequency.

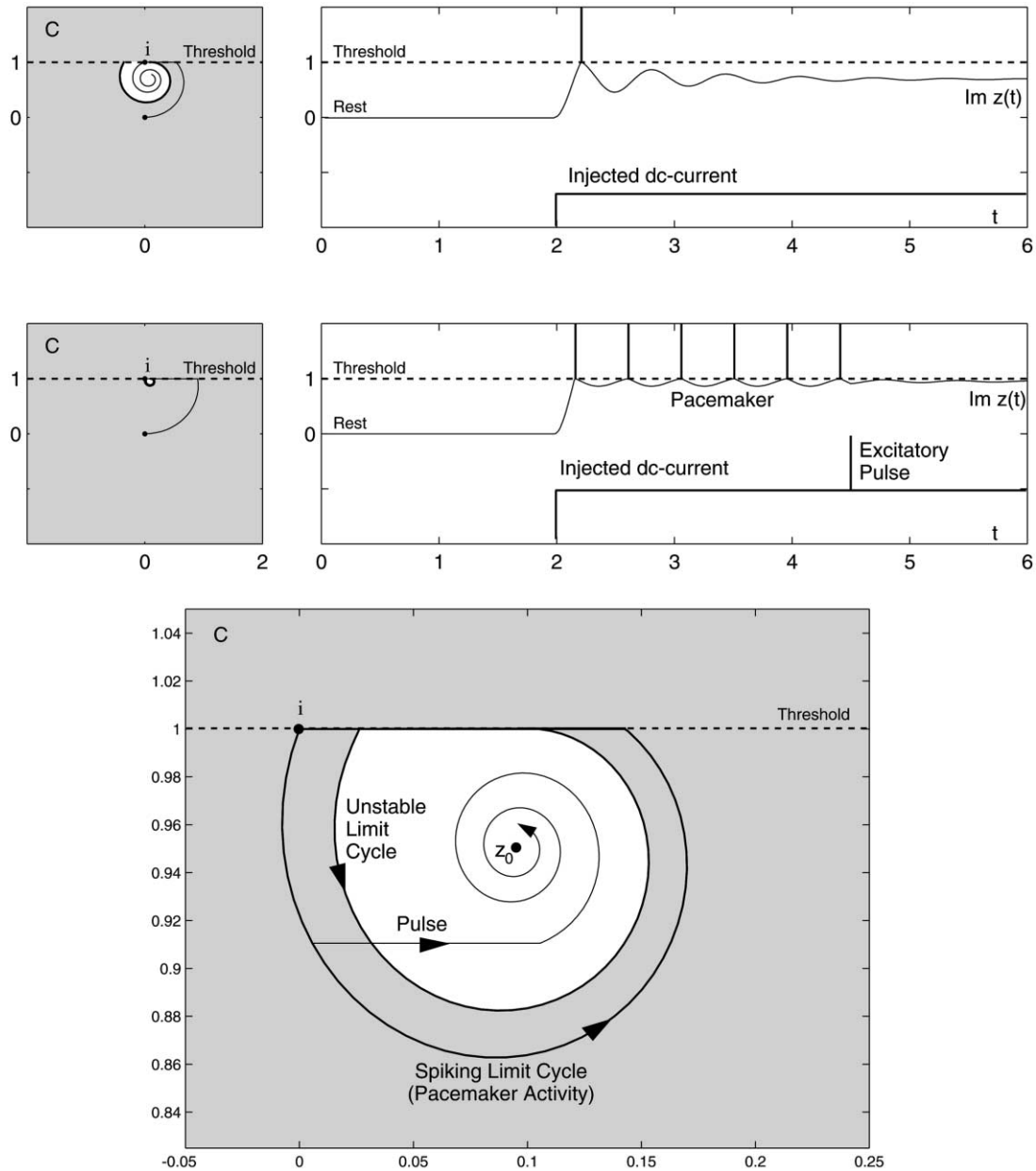


Fig. 14. Behavior of the resonate-and-fire model when a dc-current is injected. When the amplitude of the current is small (top figure), the model fires a transient spike and returns to a new rest state  $z_0$ . When the amplitude of the injected current is large (middle figure), the model exhibits a pacemaker activity. The bottom figure is a magnification of the phase portrait near the rest state. Notice the bistability of the rest state and the spiking limit cycle attractor. An appropriate excitatory stimulus may shut down periodic activity by pushing the solution into the white area, which is the basin of attraction of the rest state.

- ing to a sustained synchronized rhythmic activity.
- Timing device (Lampl & Yarom, 1993). Neurons are logical gates ensuring that the information is added to the system only at a given time.
- Logarithmic encoding (Hopfield, 1995). Relative timing of spikes may be independent of the intensity or scale.
- Generalized coincidence detector. Pulses arriving with the eigenperiod delay may have the same effect as if they arrived simultaneously.
- Selective communications via doublets (Izhikevich, 2000). A neuron innervating thousands of other neurons

- can selectively affect a small subset by sending a doublet, triplet, or burst, having resonant interspike frequency; see Fig. 10.
- FM interaction and multiplexing (Hoppensteadt & Izhikevich, 1997, 1998). The brain can dynamically rewire itself by changing the frequencies of neurons without changing the synaptic connections.

There is a similarity between the well known integrate-and-fire model and the resonate-and-fire model presented here. Both models are simple and linear except at the firing

moments. Both models can be used to speed up simulations of large networks of spiking neurons. However, the models do not repeat, but rather complement each other, since the former is an integrator, and the latter is a resonator.

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