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COMPARATIVE STUDY OF DIVERS OSCILLATORS

ABSTRACT *In this paper several classical neural oscillators (FitzHugh-Nagumo, Van der Pol, Hodgkin-Huxley) were studied. Although there are many known different oscillators, the Hodgkin-Huxley oscillator was more deeply investigated. Systems of two interconnected Hodgkin-Huxley neurons were also analyzed. Relationships between frequency and input current amplitude were found.*

Keywords: *Neuron, Hodgkin-Huxley oscillator, serial interconnection, feedback loop interconnection*

1. INTRODUCTION

The brain is made up of many types of cells, including neurons, neuroglia, and the Shwann cells. The latter two types make up almost one-half of brain's volume, but neurons are believed to be the key elements in signal processing.

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There are as many as 10^{11} neurons in the human brain, and each can have more than 10,000 synaptic connections with other neurons. Neurons are slow, unreliable analog units, yet working together they carry out highly sophisticated computations in cognition and control [10].

Most neurons communicate through action potentials – discrete short pulses of electrochemical activity. Action potentials are generated when the membrane potential of a neuron reaches a threshold value. They propagate along the axon of a cell toward synapses with postsynaptic neurons where they initiate ion currents that trigger (or inhibit) action potentials of the postsynaptic cell [9].

In this paper several classical neural oscillators (FitzHugh-Nagumo, Van der Pol, Hodgkin-Huxley) were studied. Although there are many known different oscillators, the Hodgkin-Huxley oscillator was more deeply investigated. Systems of two interconnected Hodgkin-Huxley neurons were also analyzed. Relationships between frequency and input current amplitude were found.

2. COMPARISON

2.1. FitzHugh-Nagumo oscillator

The FitzHugh [2] and Nagumo et. al. [5] equations describe the interaction between the voltage across the axon membrane, which is created by an input current I_{input} and recovery variable R which mainly reflects the outward potassium ions $\left(K^{+}\right)$ current across the nerve membrane.

These are simplest equations that have been proposed for spike generation. Like Hodgkin--Huxley equations, they have a threshold for generating limit cycles and thus provide a qualitative approximation to spike generation thresholds.

FitzHugh-Nagumo equations can be written as follows:

$$\begin{aligned} \frac{dV}{dt} &= 10\left(V - \frac{V^3}{3} - R + I_{input}\right), \\ \frac{dR}{dt} &= 0.8\left(-R + 1.25V + 1.5\right), \end{aligned} \tag{1}$$

here

V – voltage across the axon membrane,
I_{input} – input current,
R – recovery variable.

In absence of input current, the equilibrium point is an asymptotically stable node. For inhibitory input current I_{input} the equilibrium remains an asymptotically stable node. For excitatory I_{input} (e. g. $I_{input} = 1.5$) value, equilibrium point becomes an unstable node. Phase plane and simulated action potentials for FitzHugh-Nagumo equations are shown in Fig. 1.

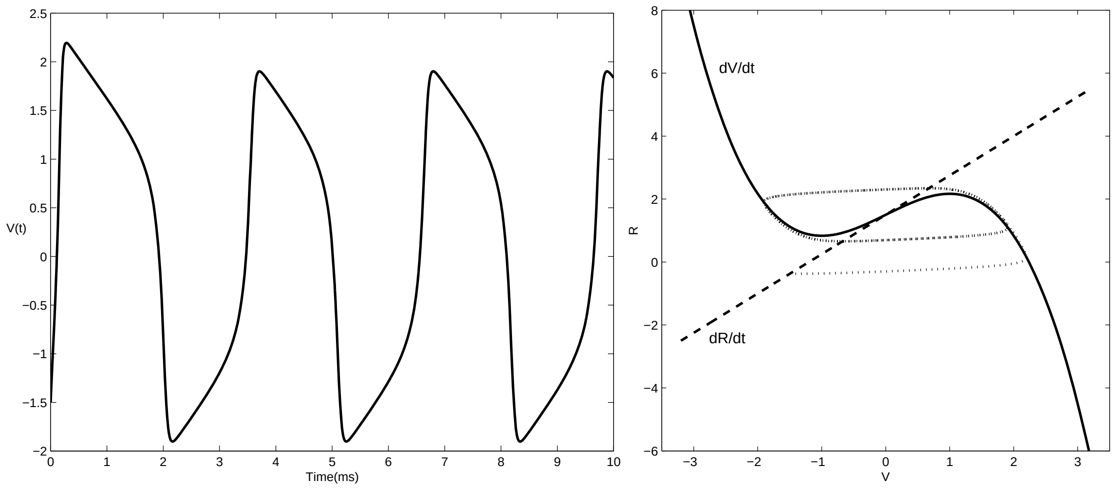

Fig. 1. Spikes and phase plane of FitzHugh-Nagumo oscillator

2.2. Van der Pol oscillator

Van der Pol equations provided the first model of heart rhythms [7]. Its normal form is:

$$\frac{dx}{dt} = y,$$
$$\frac{dy}{dt} = \omega^2 x + y\left(\beta - x^2 + u\right), \tag{2}$$

where

ω – is the frequency.

The only equilibrium point of the system is (0,0). The Jacobian matrix of equilibrium is:

$$\overleftrightarrow{A} = \begin{pmatrix} 0 & 1 \\ -\omega^2 & \beta \end{pmatrix}$$

so the eigenvalues are: $\lambda = \frac{1}{2}\left(\beta \pm \sqrt{\beta^2 - 4\omega^2}\right)$.

For $\beta < 0$ the origin is an asymptotically stable spiral point, and for $\beta > 0$ the origin is an unstable spiral. Phase planes and the response to different β values are shown in Figs. 2, 3, and 4 respectively.

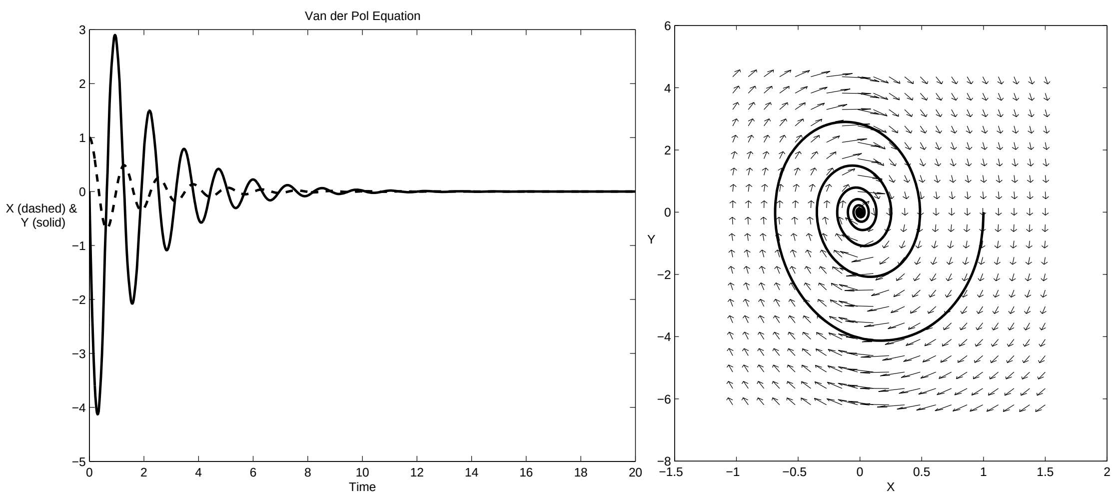

Fig. 2. Van der Pol oscillator when $\beta = -1$

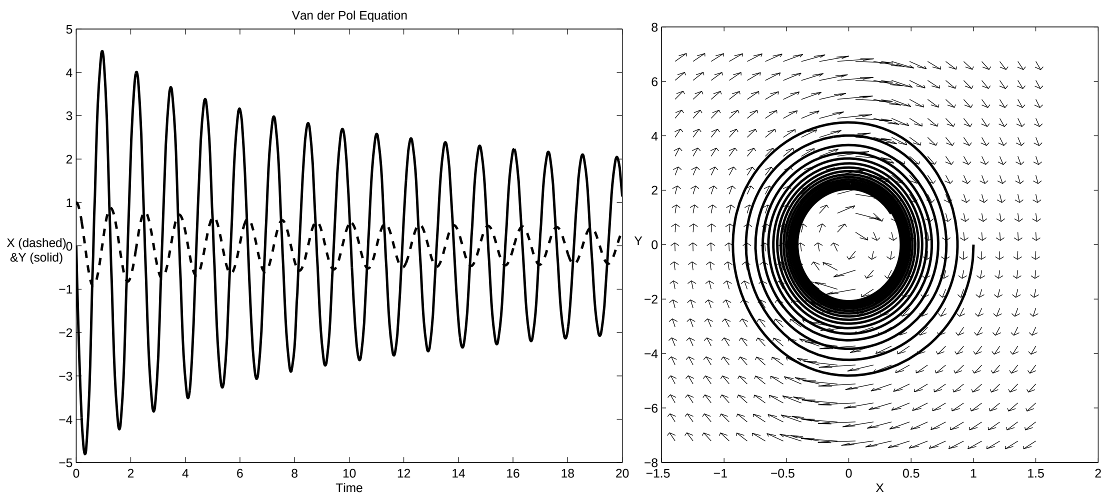

Fig. 3. Van der Pol oscillator when $\beta = 0$

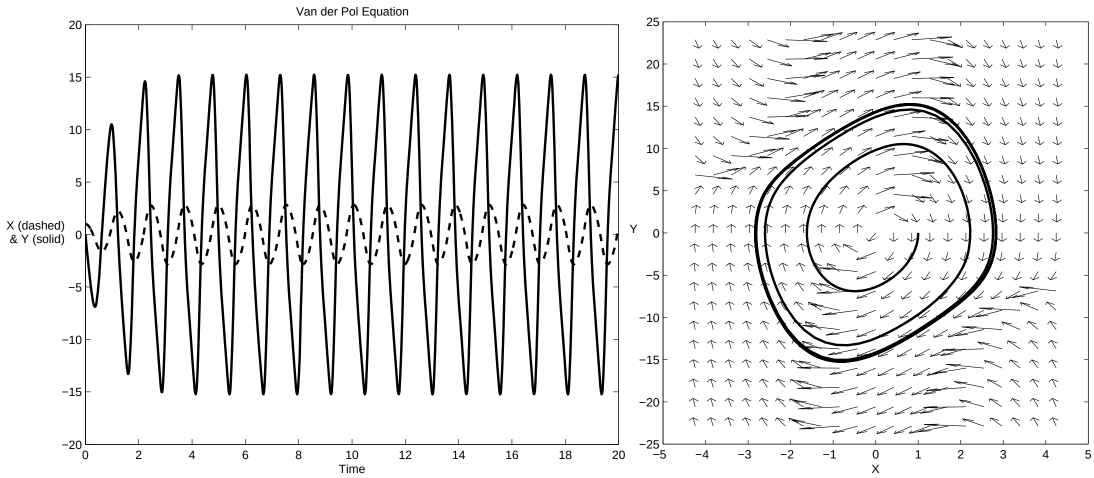

Fig. 4. Van der Pol oscillator when $\beta = 2$

2.3. Hodgkin-Huxley oscillator

The Hodgkin-Huxley [3] equations describe the change in membrane potentials V as a function of the sodium I_{Na}, potassium I_K, leakage I_{leak}, and stimulating I_{input} currents across a nerve membrane as well as membrane capacitance C:

$$C\frac{dV}{dt} = -I_{Na} - I_K - I_{leak} + I_{input} \tag{3}$$

here

$C(\mu F/cm^2)$ – axon membrane capacitance.

For each current $I = g(V - E)$, where g is the electrical conductance, V is the voltage across the membrane, and E is the equilibrium potential of the ion, computed from the Nernst equation [8].

Therefore the equation can be rewritten as:

$$\begin{aligned}
C\frac{dV}{dt} &= -g_{Na}m^3h(V - E_{Na}) - g_K n^4(V - E_K) - g_{leak}(V - E_{leak}) + I_{input} \\
\frac{dm}{dt} &= \frac{1}{\tau_m(V)}(-m + M(V)) \\
\frac{dh}{dt} &= \frac{1}{\tau_h(V)}(-h + H(V)) \\
\frac{dn}{dt} &= \frac{1}{\tau_n(V)}(-n + N(V))
\end{aligned} \tag{4}$$

Here m, h, and n represent the rates of Na conductance channel activation, Na channel inactivation, and K channel activation respectively [1, 3, 4].

As shown in [6] equations (4) can be approximately written in the form:

$$C\frac{dV}{dt} = -g_{Na}M(V)^3(1-R)(V-E_{Na}) - g_K R^4 (V-E_K) - g_{leak}(V-E_{leak}) + I_{input}$$
$$\frac{dR}{dt} = \frac{1}{\tau_R(V)}(-R+G(V))$$
$$\tau_R(V) = 1 + 5\exp\left(\frac{-(V+60)^2}{55^2}\right) \qquad (5)$$

Equations (5) can be simplified still further [2] which leads to equations of the form:

$$C\frac{dV}{dt} = -g_{Na}(V)(V-E_{Na}) - R(V-E_K) + I_{input}$$
$$\frac{dR}{dt} = \frac{1}{\tau_R(V)}(-R+G(V)) \qquad (6)$$

The phase planes and action potentials of (6) are shown in Fig. 5.

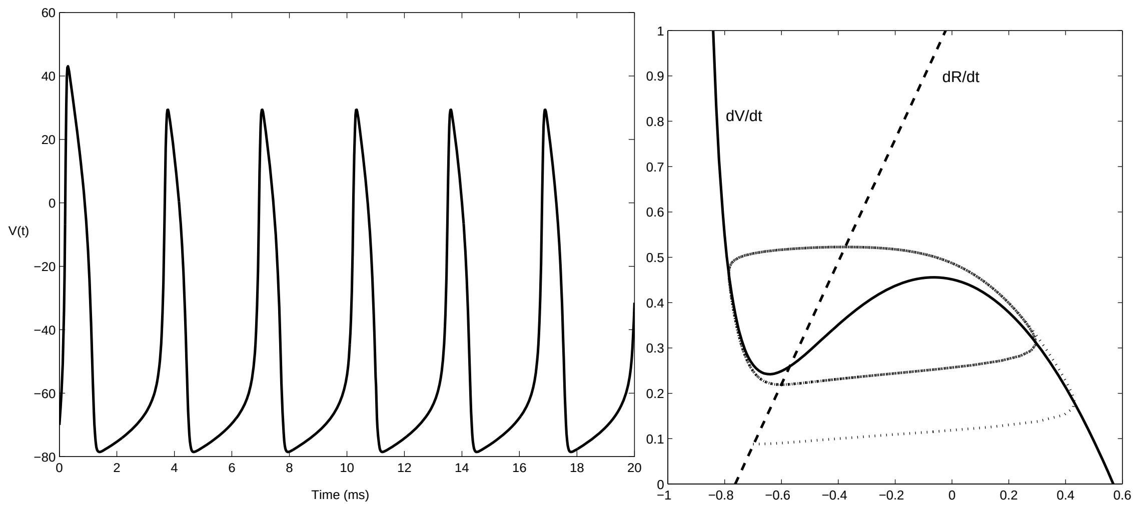

Fig. 5. Action potentials and the phase plane of Hodgkin-Huxley oscillator

3. RESPONSE TO INPUT CURRENT

3.1. FitzHugh-Nagumo oscillator

Here the threshold for input current is $I = 1$, so when I = 0.9 < 1, the system does not generate spikes (Fig. 6).

When input current is greater then the threshold value, action potentials are generated (Fig. 7).

Increasing input from I = 1 to I = 2, yields generation of action potentials with the same frequency, only the spike width is increased (Fig. 8).

When the input current surpasses the saturation level (I = 2.1 - see Fig. 9), spikes are not generated.

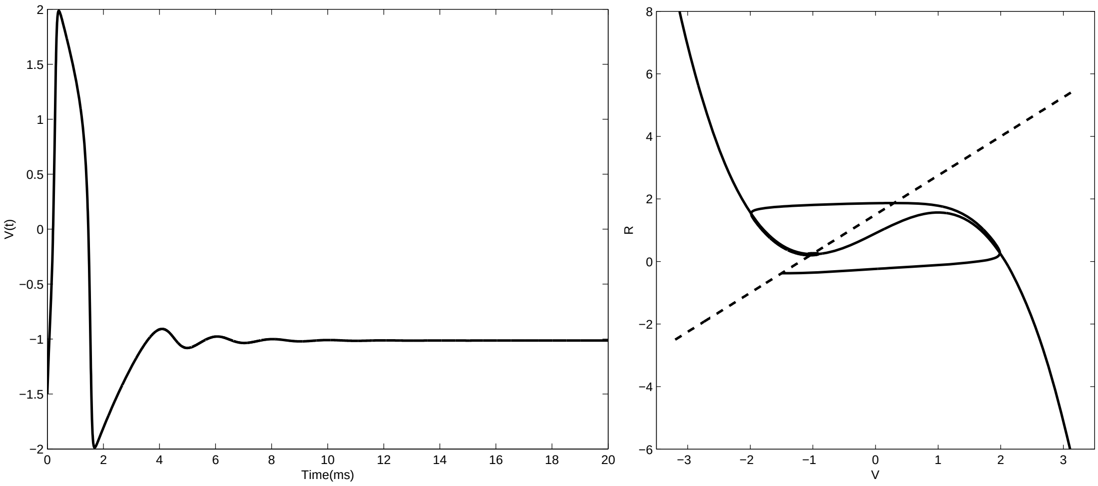

Fig. 6. FitzHugh-Nagumo oscillator when $I = 0.9$

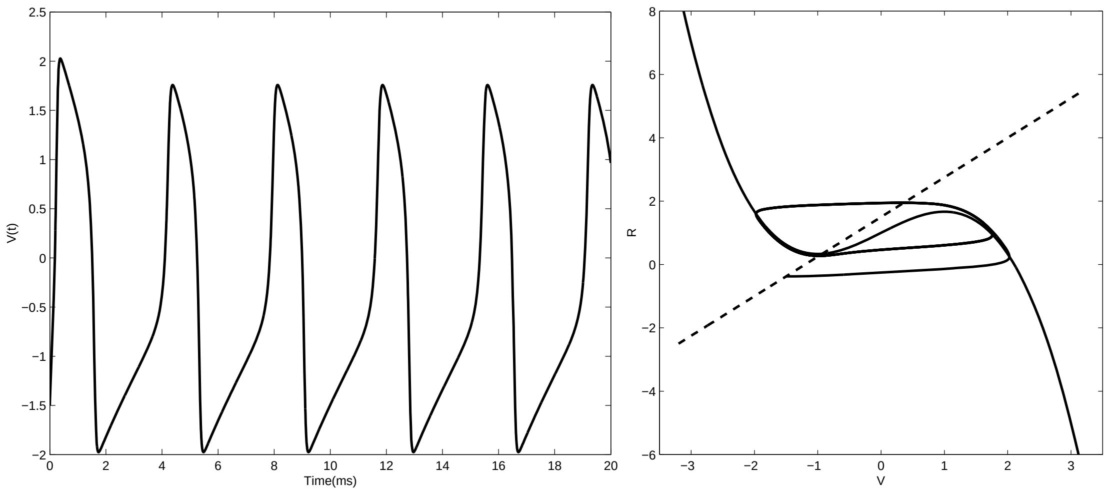

Fig. 7. FitzHugh-Nagumo oscillator when $I = 1$

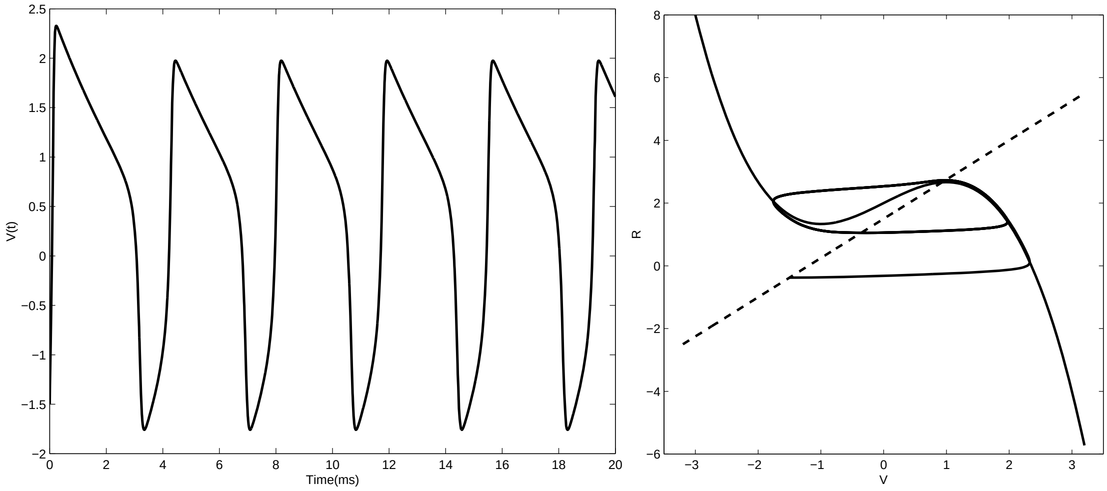

Fig. 8. FitzHugh-Nagumo oscillator when $I = 2$

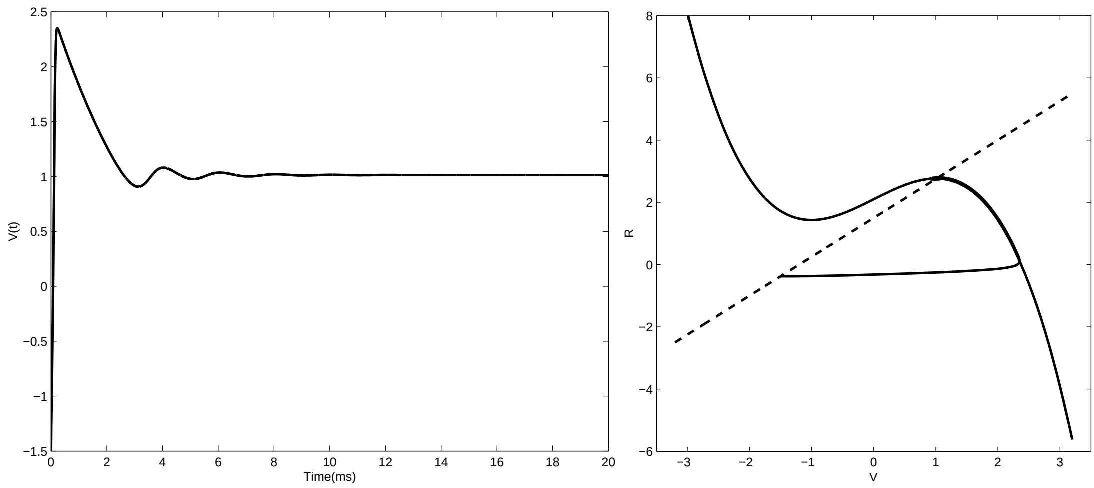

Fig. 9. FitzHugh-Nagumo oscillator when $I = 2.1$

3.2. Van der Pol oscillator

When step input $u = 1$ is applied, and parameter $\beta = -1$, the equilibrium point is no more an origin, but it is still an asymptotically stable spiral point, and, as shown in Fig. 10, the system decays faster to steady state with less oscillations .

When step input $u = 1$ is applied to the system with $\beta = 0$, the system's oscillations are roughly the same as in previous example when $\beta = -1$ and $u = 1$ (Fig. 11).

If a step input is applied to the system, when $\beta = 1$, the phase trajectory becomes an asymptotically stable spiral, like in the examples above, but slightly greater oscillations are observed (Fig. 12).

Thus, comparing Figs. 2, 3, 4 and 10, 11, 12 we can conclude, that application of a step input $u = 1$ to the system makes it more stable and less oscillating. Even when the initial system is unstable (with $u = 0$ and $\beta = 1$, see Fig. 3), setting $u = 1$ makes it stable (Fig. 11).

Changing the input signal from $u = 0$ to $u = 1$ with $\Delta u = 0.1$ shows, that when increasing u, amplitude of oscillations decreases until $u = 0.5$. If $u = 0.5$, the output signal $V = 0$. Further increasing of u leads to decreasing the number of oscillations and increasing the amplitude of the first oscillation (Fig. 13).

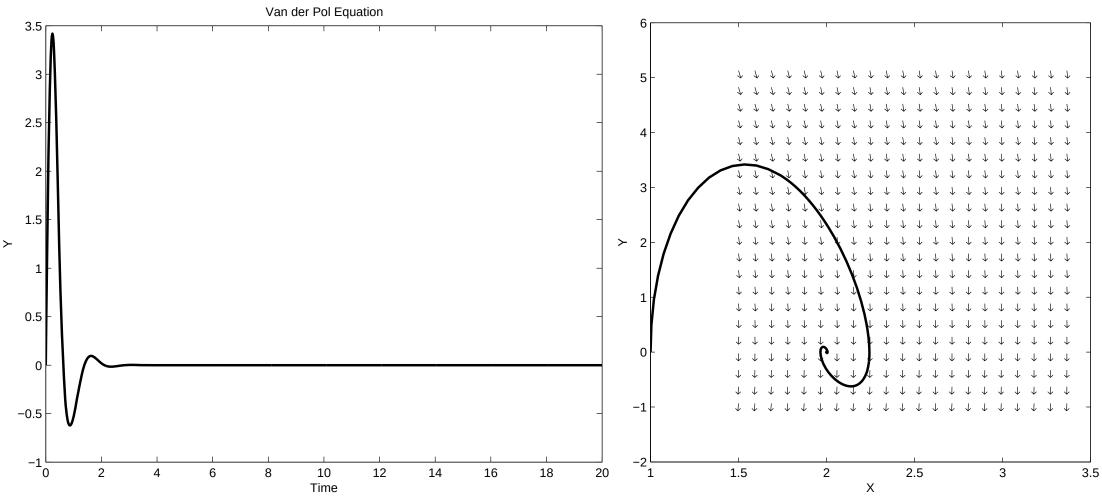

Fig. 10. Van der Pol oscillator when $\beta = -1,\ u = 1$

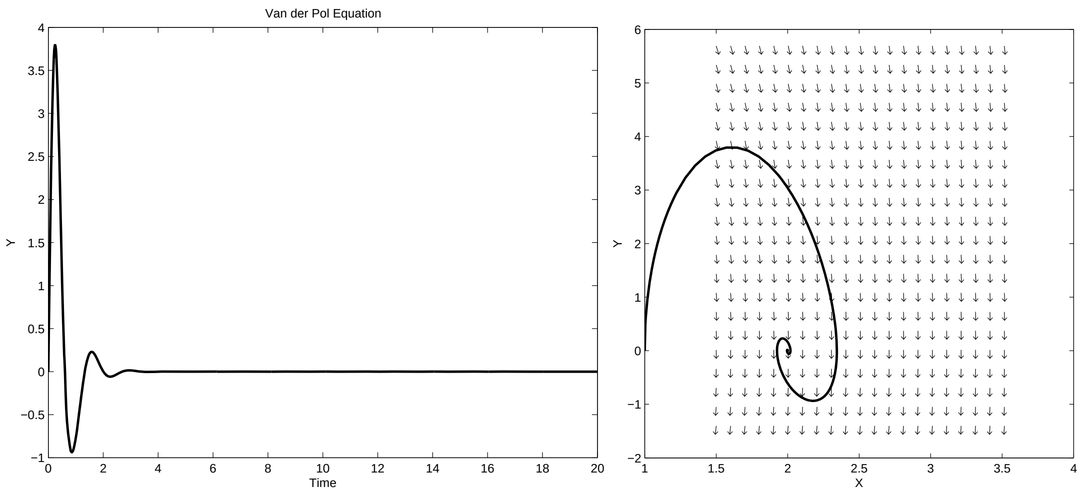

Fig. 11. Van der Pol oscillator when $\beta = 0,\ u = 1$

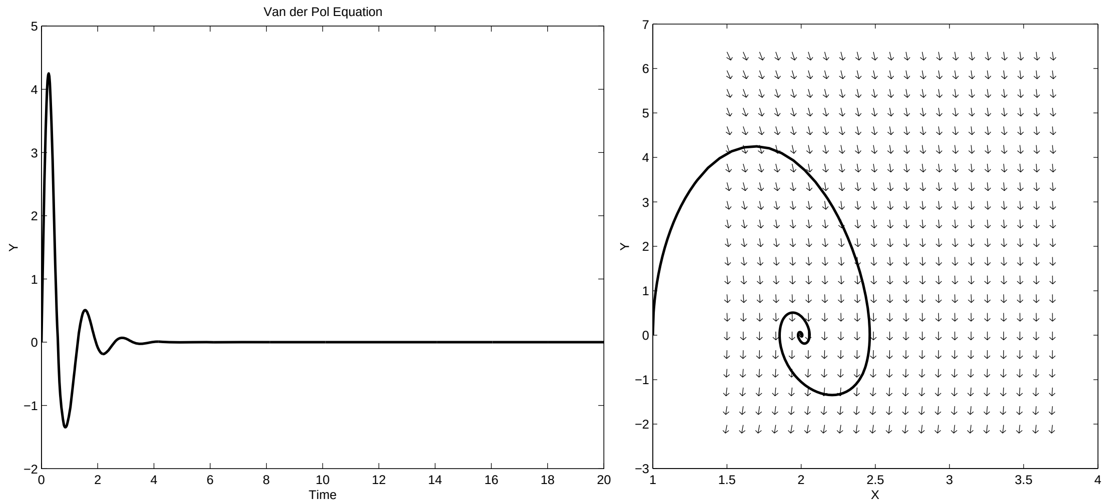

Fig. 12. Van der Pol oscillator when $\beta = 1,\ u = 1$

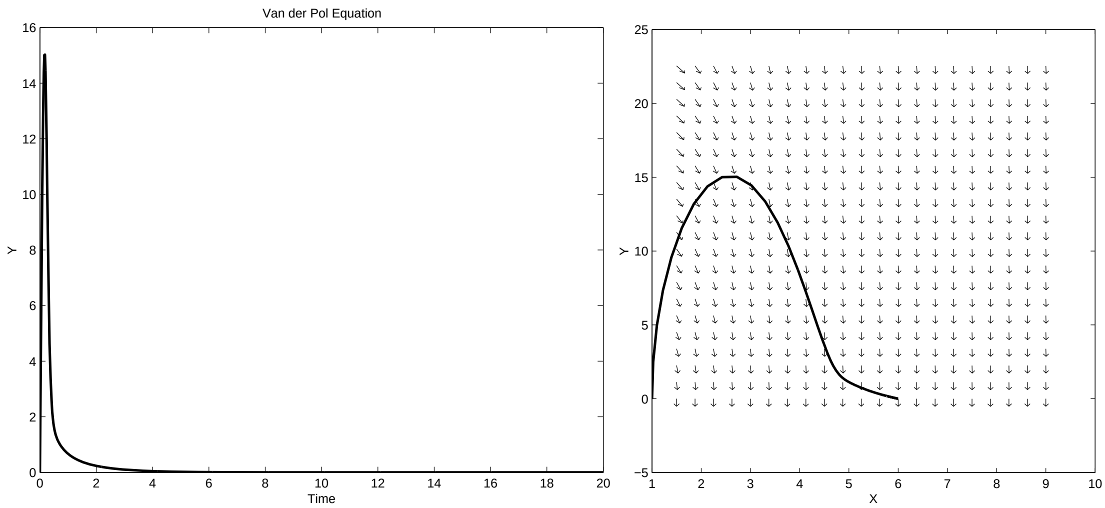

Fig. 13. Van der Pol oscillator when $\beta = 1,\ u = 3$

3.3. Hodgkin-Huxley oscillators

When $I = 0$ there are no action potentials, because the input parameter I is below the threshold, so the system is in resting state (Fig. 14). When $I = 0.1$, the limit cycle exist and spikes are generated. (Fig. 15). As the input current is increased from $I = 0.1$ to 5, the spike frequency is also increased and the amplitude (except first spike) is decreased (Figs. 16, 17, 18, 19, 20). At $I = 6$, the limit cycle is very small in comparison with the input current amplitude, so only one spike is visible as the system follows phase trajectories. In this case the system is similar to the one which has an asymptotically stable spiral point as shown in Fig. 21.

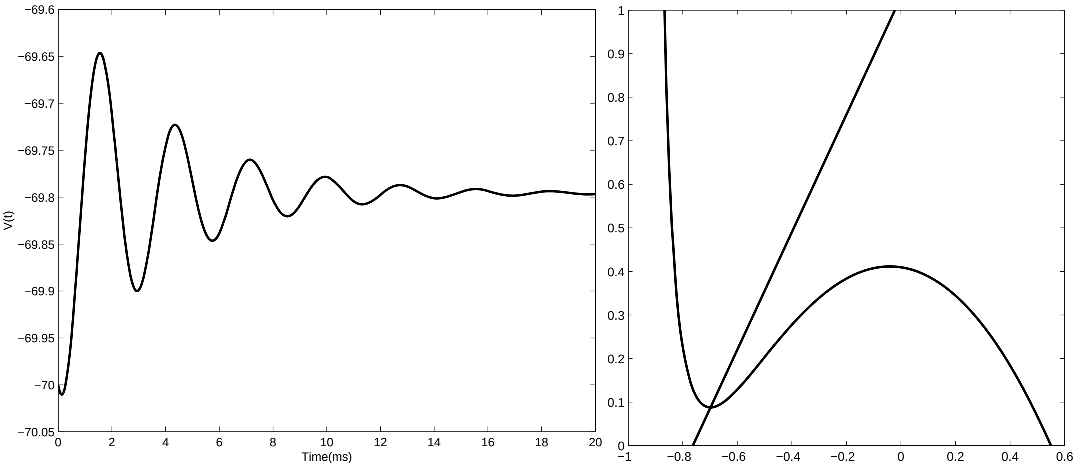

Fig. 14. Hodgkin-Huxley oscillator when $I = 0$

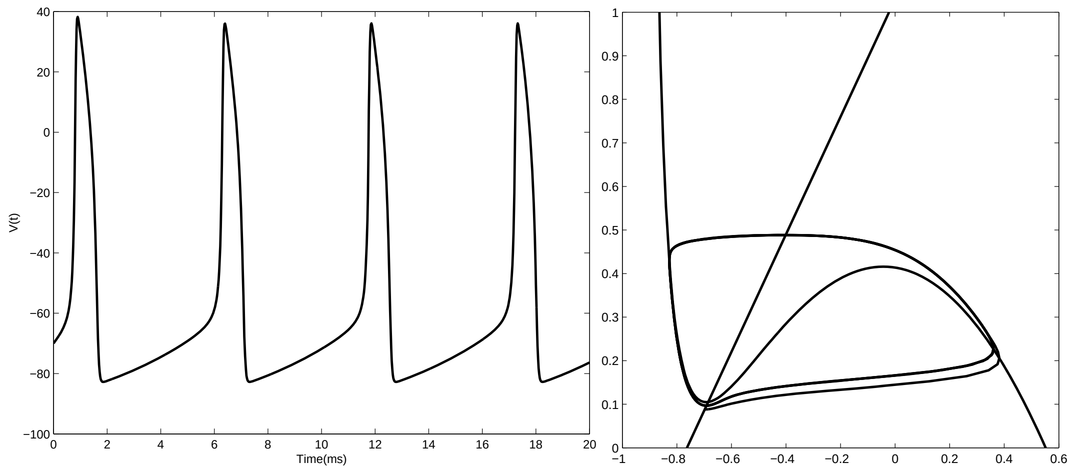

Fig. 15. Hodgkin-Huxley oscillator when $I = 0.1$

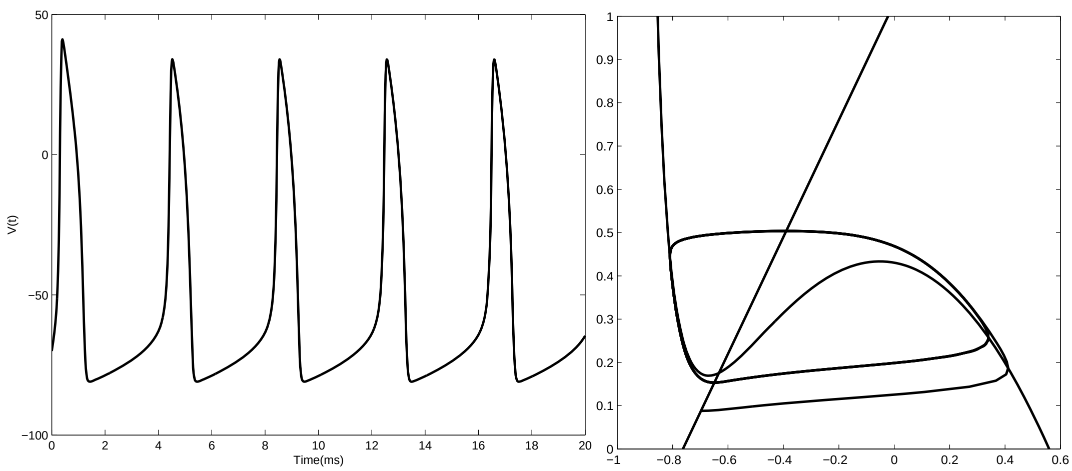

Fig. 16. Hodgkin-Huxley oscillator when $I = 0.5$

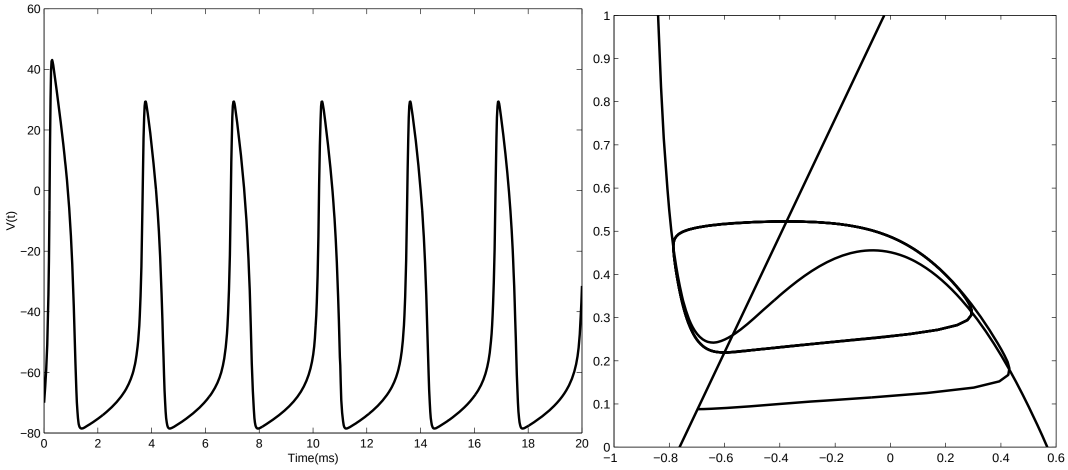

Fig. 17. Hodgkin-Huxley oscillator when $I = 1$

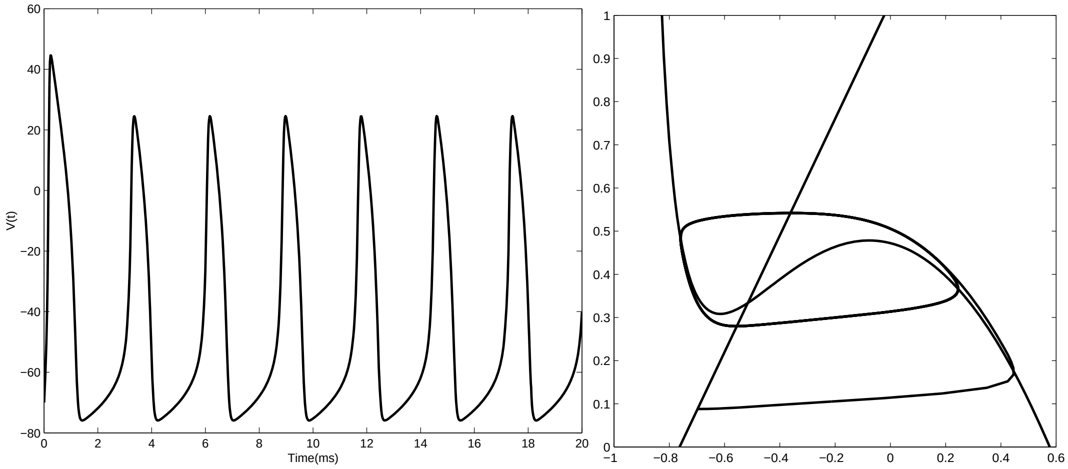

Fig. 18. Hodgkin-Huxley oscillator when $I = 1.5$

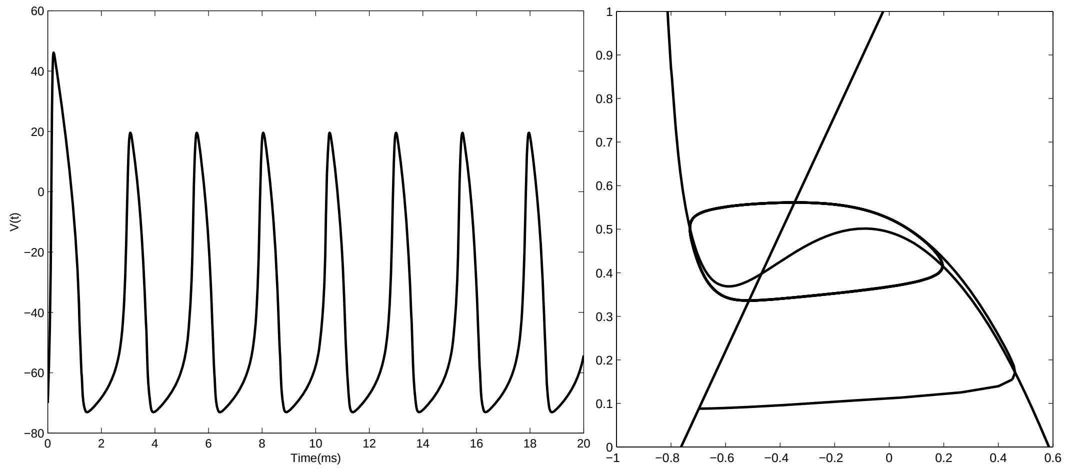

Fig. 19. Hodgkin-Huxley oscillator when $I = 2$

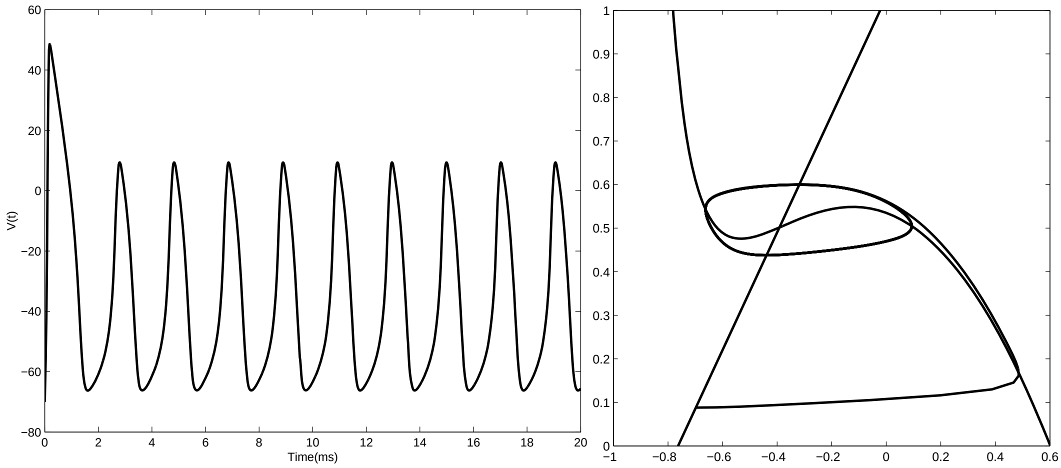

Fig. 20. Hodgkin-Huxley oscillator when $I=3$

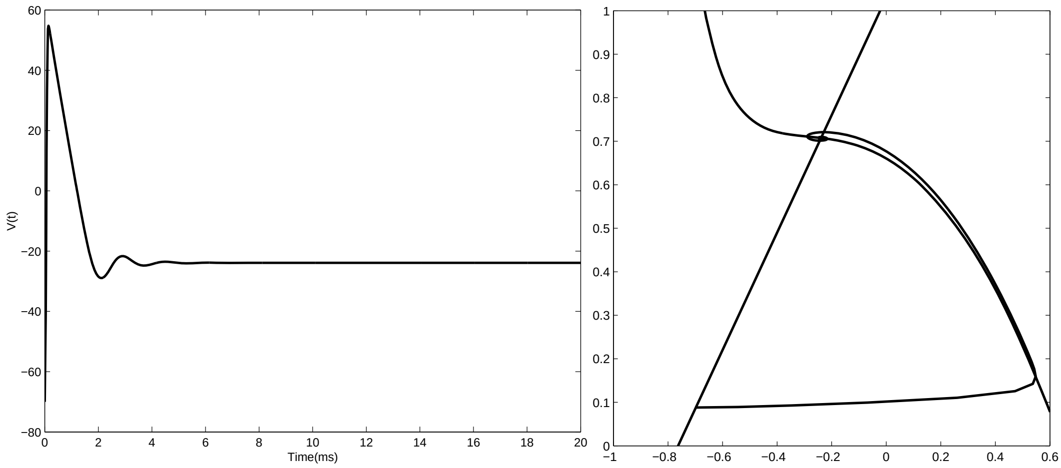

Fig. 21. Hodgkin-Huxley oscillator when $I=6$

4. INTERCONNECTIONS

4.1. Serial interconnection of two neurons

There are two identical neurons described by Hodgkin-Huxley equations. The neurons also have identical initial conditions. The first neuron's input signal is the input current I, however the second neuron's input signal is the train of action potentials generated by the first neuron as depicted in Fig. 22.

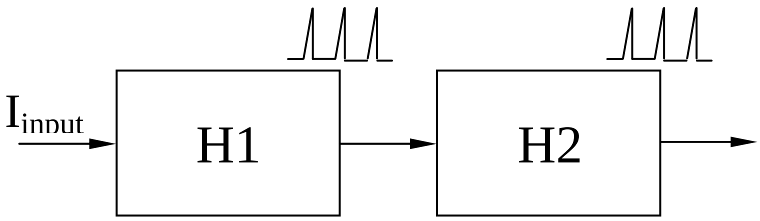

Fig. 22. Serial interconnection of two neurons

When the input current $I_{input} = 0$, the first neuron generates no spikes (see Fig. 14). The response and the phase plane of H2 are shown in Fig. 23.

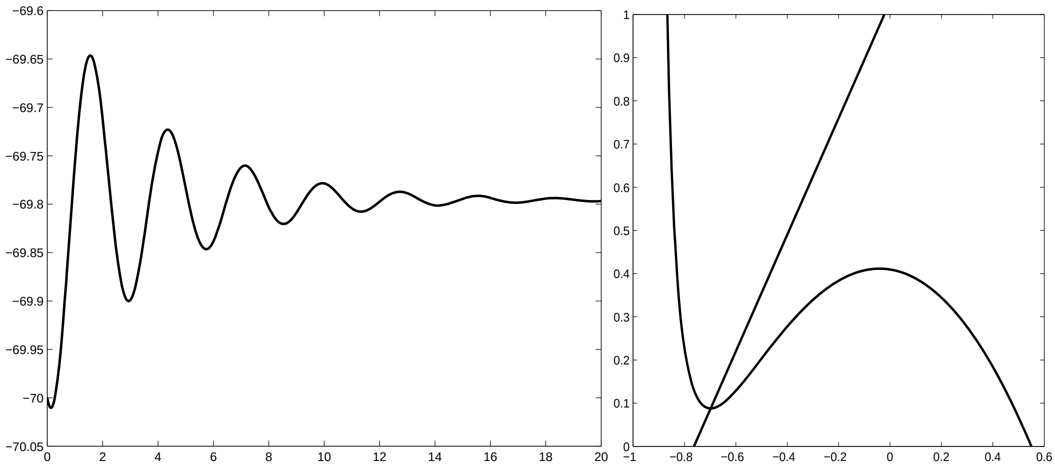

Fig. 23. Response and phase plane of the system when $I_{input} = 0$

If the input current becomes $I_{input} = 0.1$, then the first neuron begins to fire spikes, as shown in Fig. 15. In response to the periodic spike train, generated by the first neuron, the second neuron generates a similar spike train, only these spikes have slightly different shape (fig. 24).

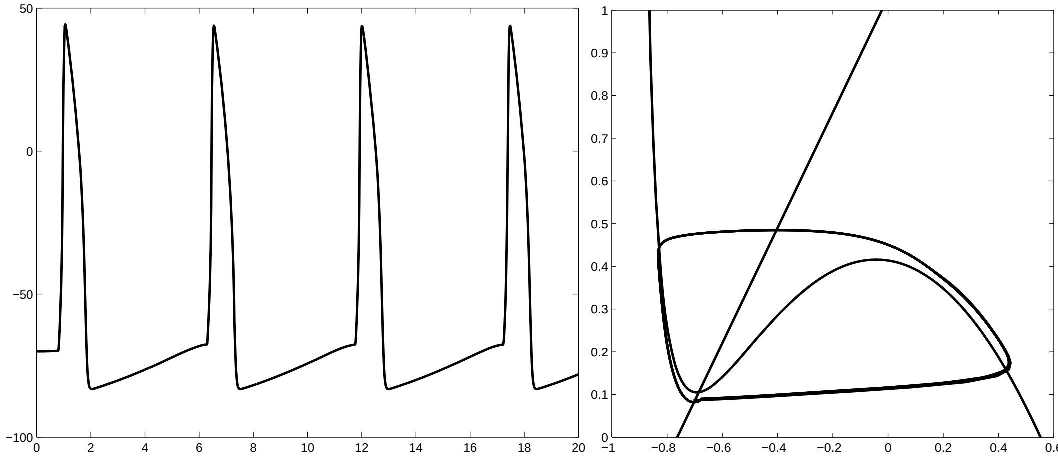

Fig. 24. Response and phase plane of the system when $I_{input} = 0.1$

When $I_{input} = 0.5$ and $I_{input} = 0.7$ the system response is shown in Figs. 25 and 26 respectively.

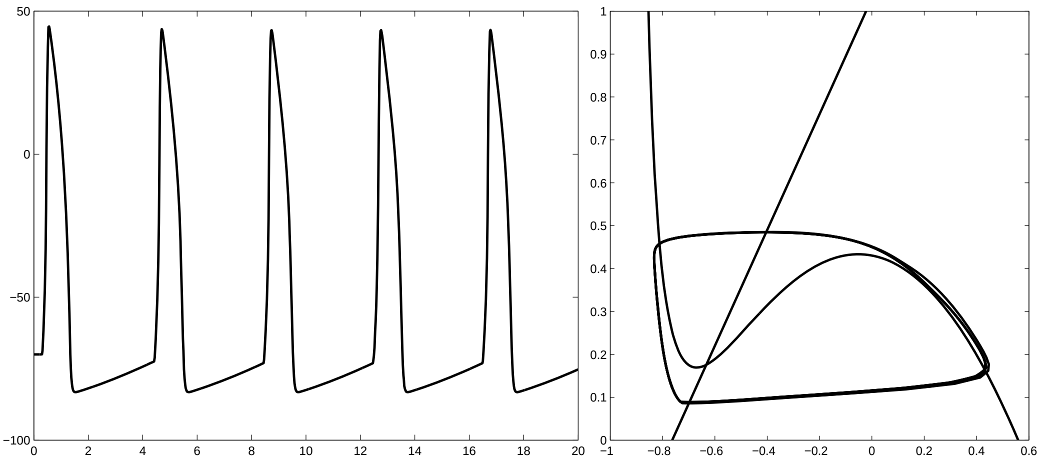

Fig. 25. Response and phase plane of the system when $I_{input} = 0.5$

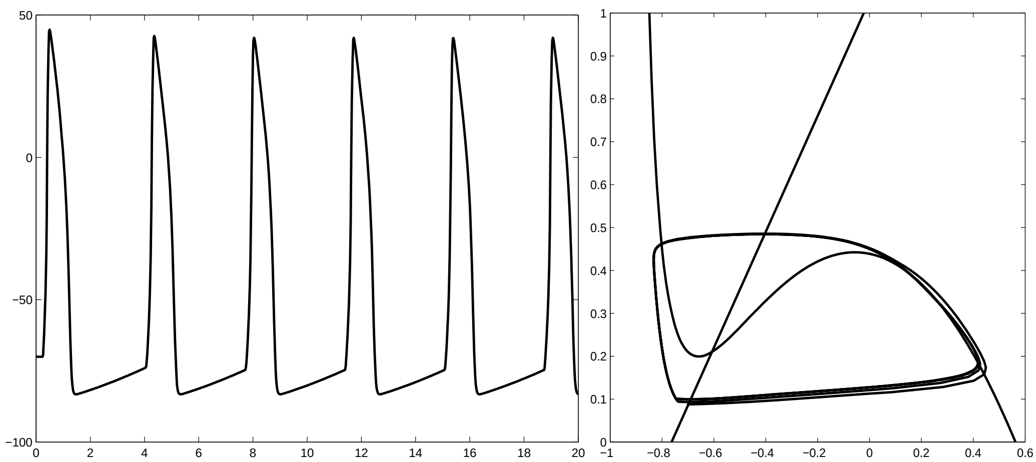

Fig. 26. Response and phase plane of the system when $I_{input} = 0.7$

Similar behaviour of the system is observed until the input current value is below 1.4 (see Figs. 27, 28). A remarkable fact is that for obtaining spikes from a single neuron we must destabilize the system with a large input signal value. And this value must be bigger if we want have a higher frequency of spikes. However when a neuron is excited by another neuron, these disturbances are smaller (see phase planes in Figs. 18 and 28 respectively).

Also when input current $I_{input} = 1.4$, the second neuron fails to respond to the sixth input spike as shown in Fig. 29. When the input current $I_{input} = 2$ the phase shift phenomenon [8] is observed as shown in Fig. 30.

Figure 31 shows how the frequency of spikes depends on the input current value. Here we can see, that the frequency of spikes increases quasi-exponentially, until the input value reaches about 1.4. Figure 32 shows a part of Fig. 31 emphasizing the interval 0...1.4 of the input current.

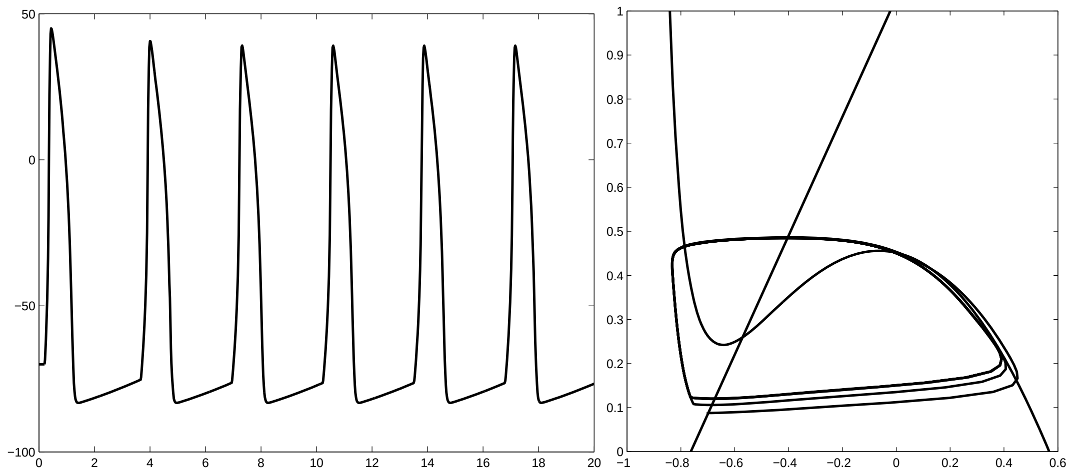

Fig. 27. Response and phase plane of the system when $I_{input} = 1$

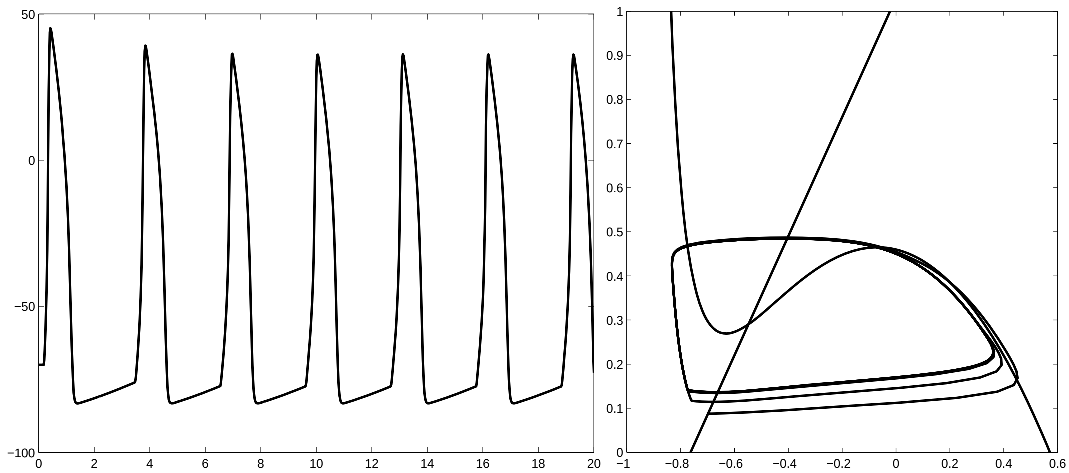

Fig. 28. Response and phase plane of the system when $I_{input} = 1.2$

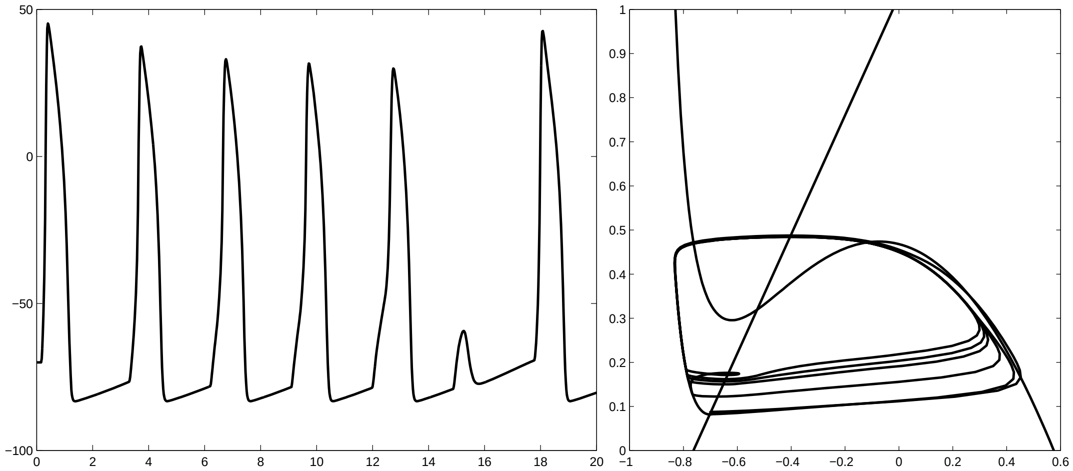

Fig. 29. Response and phase plane of the system when $I_{input} = 1.4$

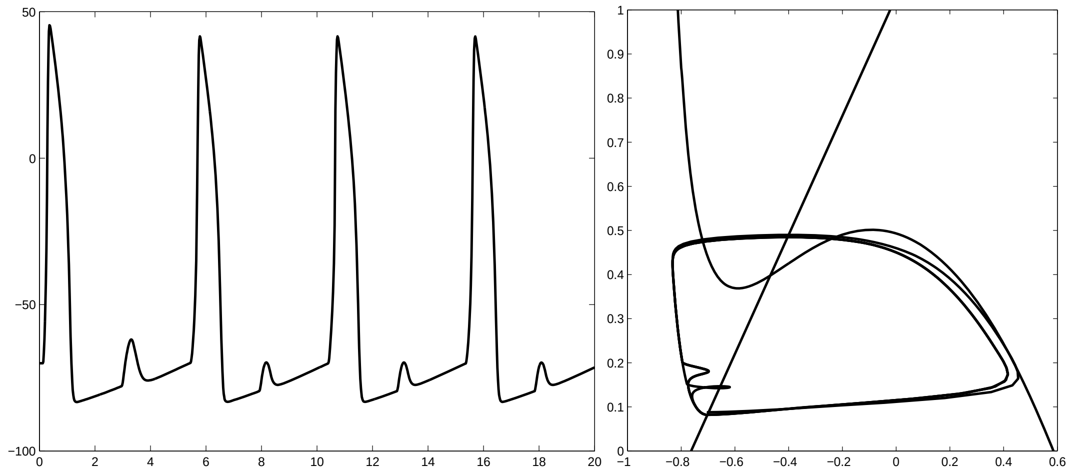

Fig. 30. Response and phase plane of the system when $I_{input} = 2$

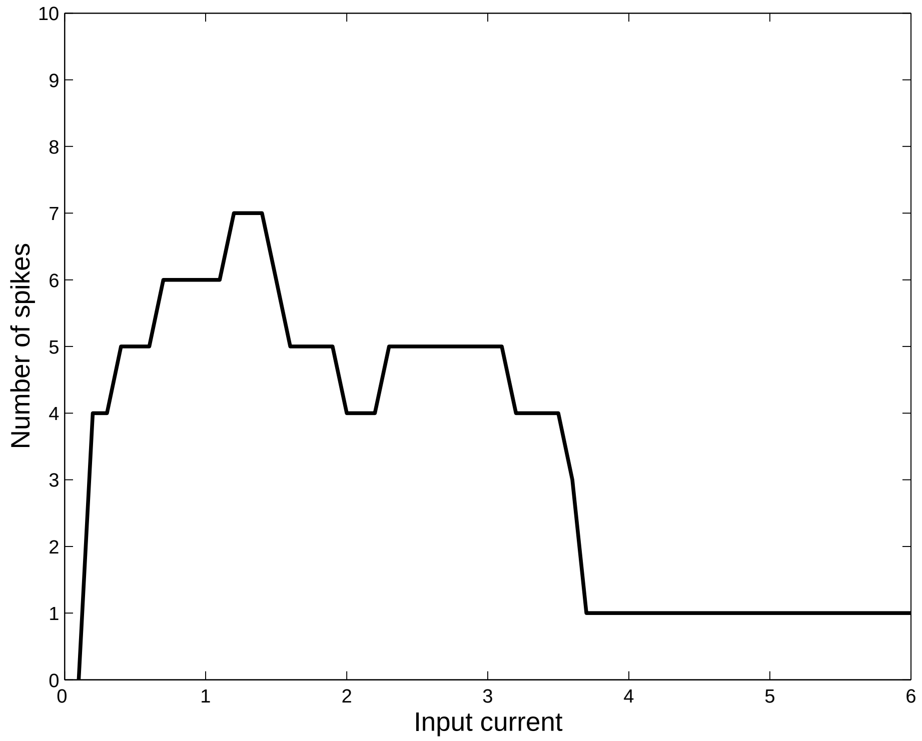

Fig. 31. Dependency of frequency on the input current when $I_{input} = 0...6$

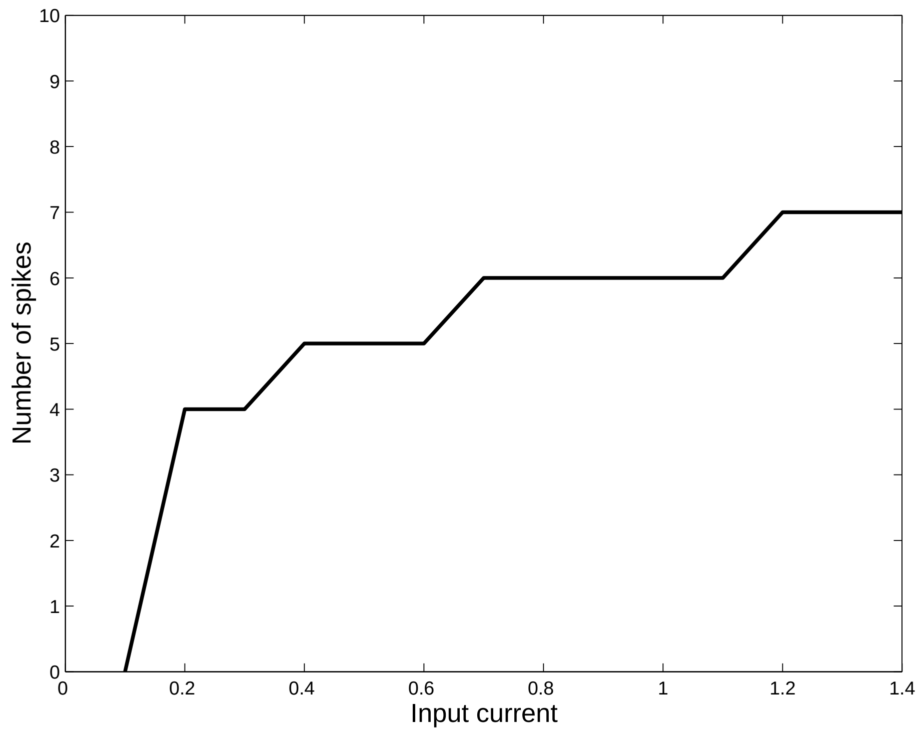

Fig. 32. Dependency of frequency on the input current when $I_{input} = 0...1.4$

4.2. Negative feedback loop interconnection of two neurons

When neurons H1 and H2 are connected in a negative feedback loop, as shown in Fig. 33, additional time constant is needed to slow down the neuron's H2 response, because when neuron, H2 excites neuron H1 equally fast, both spike trains stop very fast.

The Behavior of the system according to input currents $I_{input} = 1$ and $I_{input} = 2$ is shown in Figs. 34, 35, 36, 37 respectively.

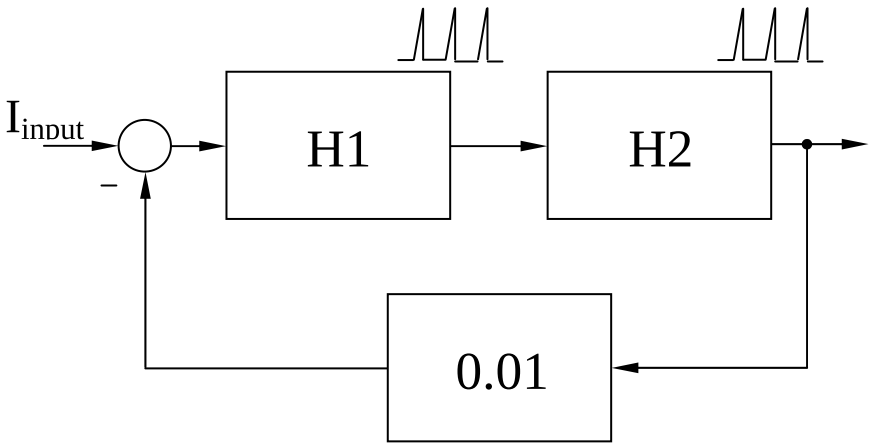

Fig. 33. Negative feedback loop interconnection of two neurons

Figure 38 shows how the frequency of spikes depends on the input current value. Figure 39 shows a part of Fig. 38 emphasizing the interval 0...2 of the input current. In this interval the last spikes are inhibited by means of negative feedback loop. The increase in the frequency of spikes is linear when the value of the input current is 0...2.

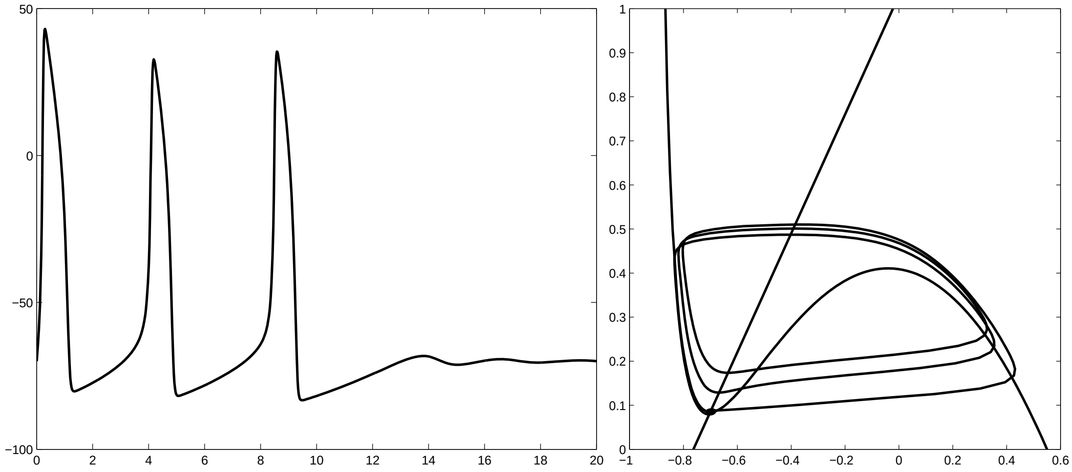

Fig. 34. Response of the H1 when $I_{input} = 1$

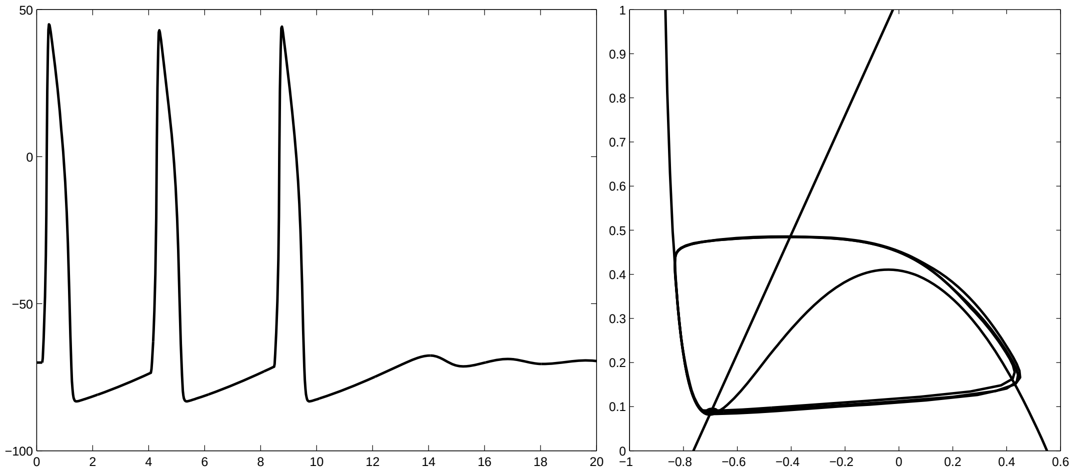

Fig. 35. Response of the H2 when $I_{input} = 1$

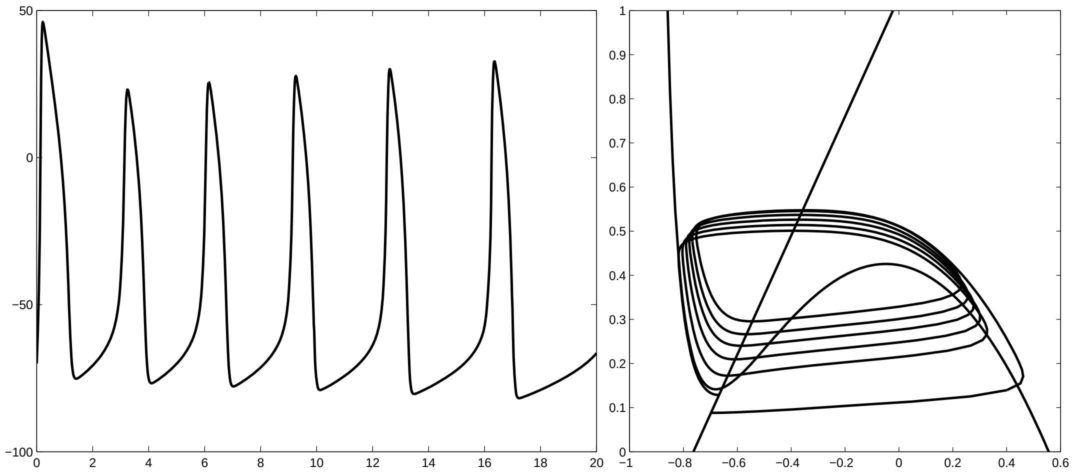

Fig. 36. Response of the H1 when $I_{input} = 2$

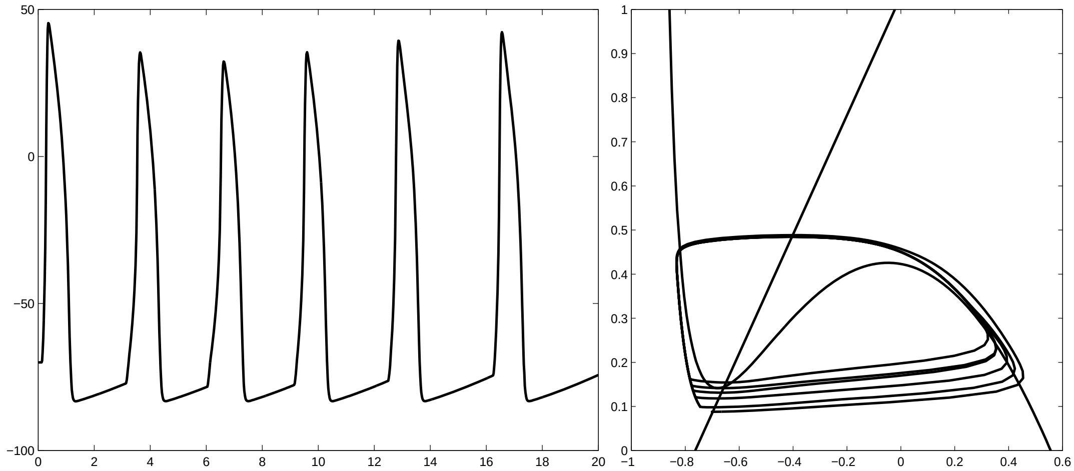

Fig. 37. Response of the H2 when $I_{input} = 2$

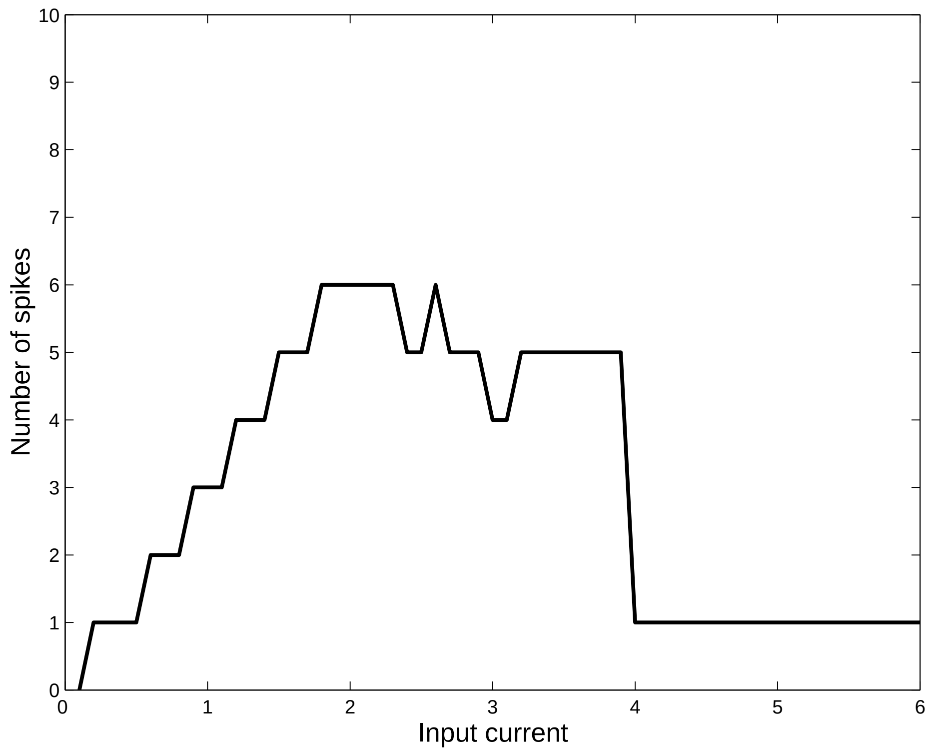

Fig. 38. Dependency of frequency on the input current when $I_{input} = 0...6$

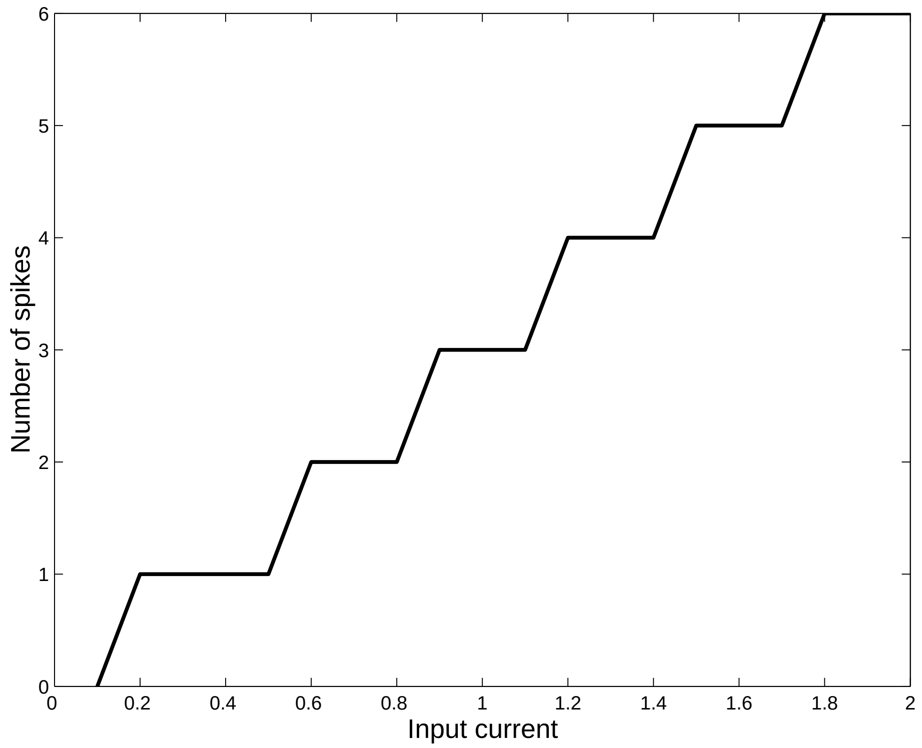

Fig. 39. Dependency of frequency on the input current when $I_{input} = 0...2$

4.3. Positive feedback loop interconnection of two neurons

When neurons H1 and H2 are connected in positive feedback loop, as shown in Fig. 40, additional time constant is needed to slow down neuron's H2 response. Behavior of the system according to input currents $I_{input} = 1$ and $I_{input} = 2$ is shown in Figs. 41, 42, 43, 44 respectively.

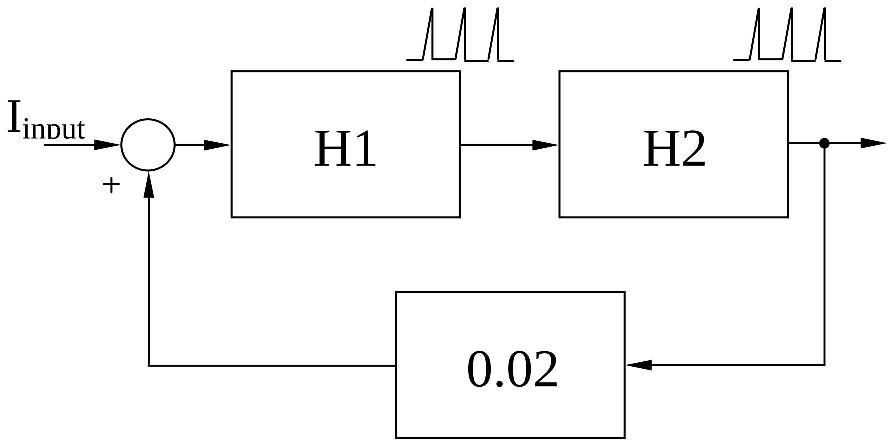

Fig. 40. Positive feedback loop interconnection of two neurons

Figure 45 shows how the frequency of spikes depends on the input current value when neurons are connected as shown in Fig. 40.

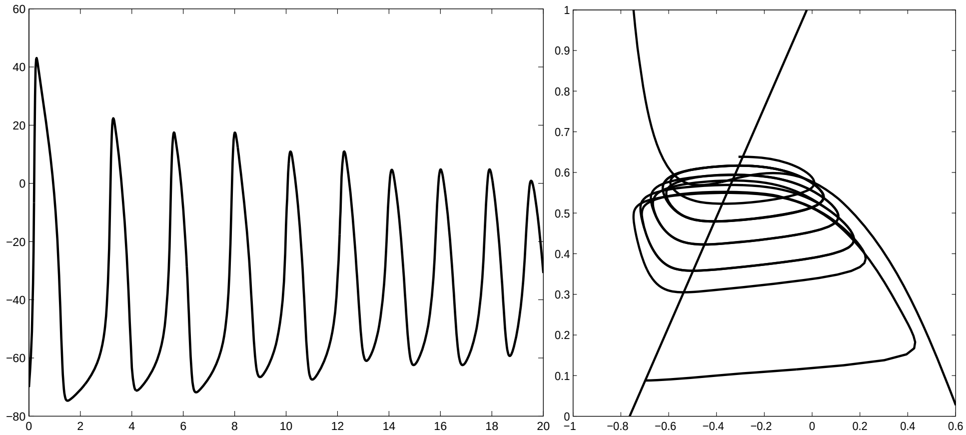

Fig. 41. Response of the H1 when $I_{input} = 1$

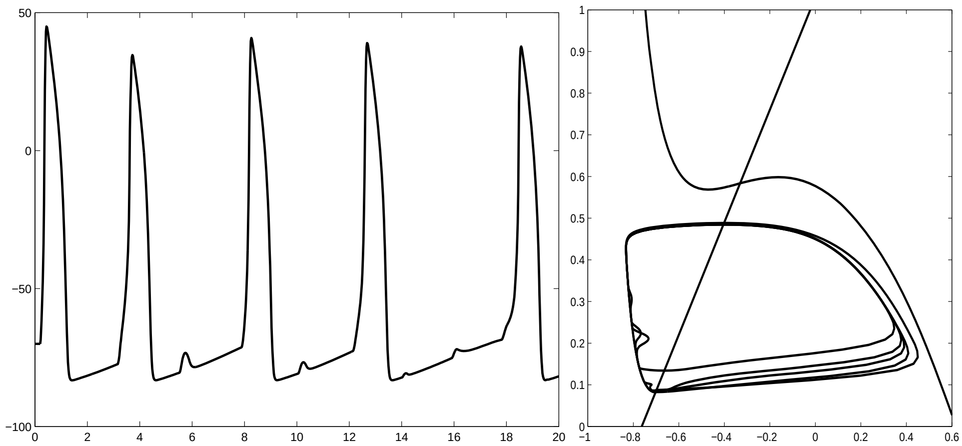

Fig. 42. Response of the H2 when $I_{input} = 1$

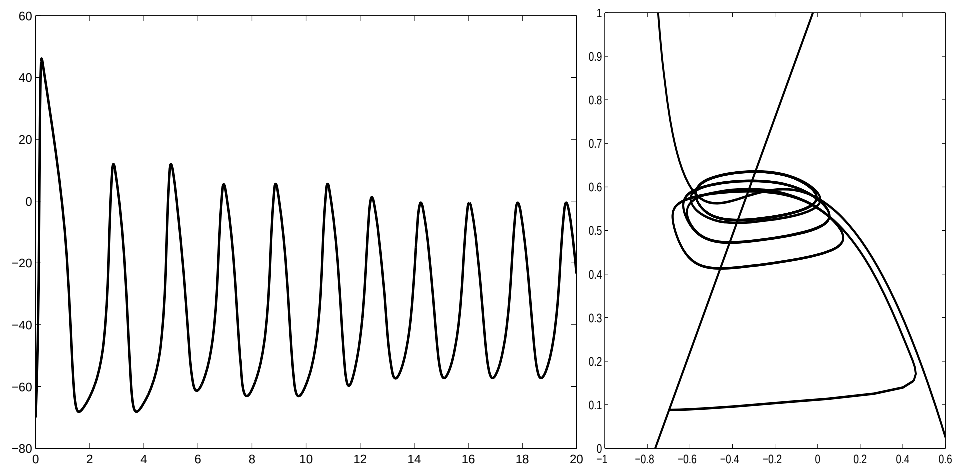

Fig. 43. Response of the H1 when $I_{input} = 2$

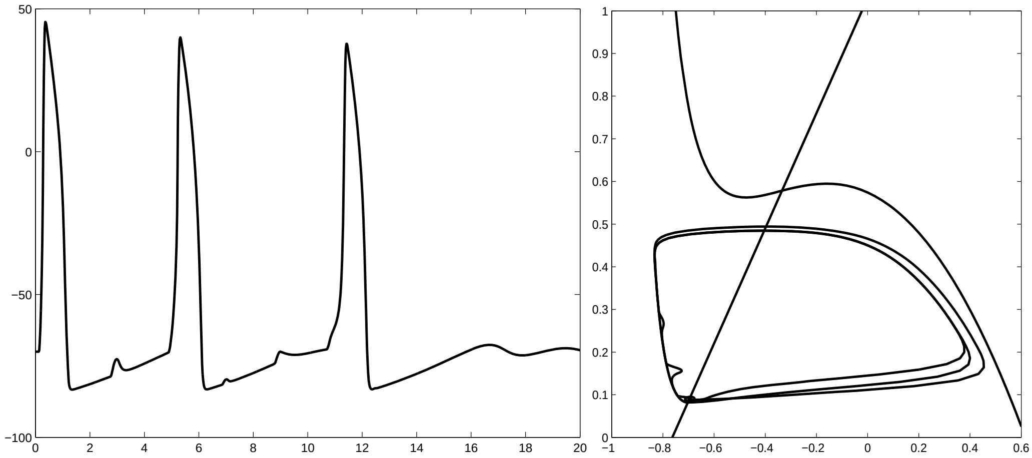

Fig. 44. Response of the H2 when $I_{input} = 2$

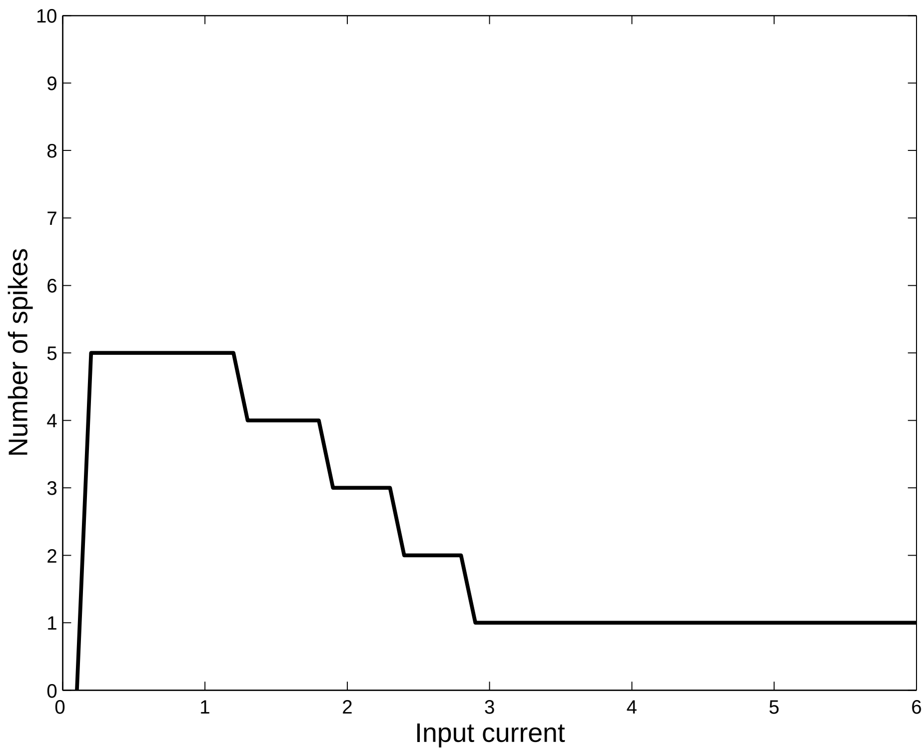

Fig. 45. Dependency of frequency on the input current when $I_{input} = 0...6$

5. CONCLUSION

1. Three classical oscillators: FitzHugh-Nagumo, Van der Pol, Hodgkin-Huxley were compared.
2. Serial and parallel interconnections of two neurons, described by Hodgkin-Huxley differential equations were analyzed. Graph of firing frequency versus input current was plotted. When neurons are connected in series, growth of frequency of spikes vs. input current is similar to exponential. When neurons are connected in parallel, growth of frequency is linear.
3. When input current of the system of two neurons exceeds a particular value, then the phase shift phenomenon and a behavior similar to chaos is observed.

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PORÓWNAWCZE BADANIA RÓŻNYCH OSCYLATORÓW

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STRESZCZENIE *Artykuł omawia kilka klasycznych oscylatorów neutralnych (FitzHug-Nagumo, Van der Pol, Hodgkin-Huxley). Jakkolwiek znanych jest wiele różnych oscylatorów, jednak oscylator Hodgkin-Huxley został zbadany dokładniej. Przeanalizowano też układy dwu połączonych neuronów Hodgkin-Huxley. Podano zależność częstotliwości od amplitudy prądu wejściowego.*