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THE LUR'E MODEL FOR NEURONAL DYNAMICS

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Abstract: The long term objective of our research is to use the knowledge from biological studies on animal locomotion and establish a new paradigm for control design that realizes robust, adaptive, and autonomous systems. As a very first step, this paper proposes a new dynamical model of a single neuron, given by a specific class of the Lur'e systems, and show that the model makes a good tradeoff between the simplicity and the accuracy when compared with the existing models. The Lur'e neuron model is intended for adoption as a basic unit in biologically inspired control systems.

Keywords: Neuronal modeling, Feedback control, Biological oscillator

1. INTRODUCTION

Animal motions are controlled by neuronal circuits in the central nervous system. In view of a wide variety of functionalities and autonomy of animal motions, it is natural to ask how the knowledge from biology can be exploited to make a qualitative difference in the performance achievable by feedback control. As is well known, the use of neuronal basis for automatic control of physical systems has been investigated in the literature related to artificial neural networks (ANNs); Hunt et al. (1992); Narendra (1996); Narendra and Lewis (2001). Many of these approaches are based on a fundamental result by Funahashi (1989); Hornik (1989) that the ANN architecture is capable of approximating any continuous function with an arbitrarily high accuracy. This result, together with the parameter optimization techniques such as the back propagation, constituted a new paradigm for general nonlinear adaptive control. Thus, the ANN approach successfully generalized the biological knowledge on neural networks into mathematical abstraction which is useful for development of practical design methodologies.

On the other hand, it is perhaps fair to say that the generality of the ANN approach has been gained at the expense of oversimplified models for neuronal dynamics, and hence the approach may have strayed too far away from physiological evidences [1] . For instance, a class of popular neuron models is given by, Hunt et al. (1992);

$$y = \phi(H(s)(w^{\mathsf{T}}u + \theta)) \tag{1}$$

where $u(t) \in \mathbb{R}^n$ and $y(t) \in \mathbb{R}$ are the input and the output of the neuron, $w \in \mathbb{R}^n$ and $\theta \in \mathbb{R}$ are the synaptic weight and the bias, $H(s)$ is a transfer function, and ϕ is a static nonlinearity. Typically, $H(s)$ is chosen to be a constant or a first order lag $1/(1+\tau s)$, and ϕ is set to a sigmoid function. This model may capture the most basic neuronal dynamics such as the threshold and the processing delay, but the variable y often stands for the "firing rate" and thus the model ignores the dynamical mechanism underlying the generation of spike trains which constitute the identity of a neuron from a physiological point of view. The question is: *Does this simplification in neuronal modeling sacrifice desirable properties of real neuronal controls such as robustness and autonomy?*

The objective of this paper is to provide a basis for investigating such question. We propose a neuron model that is *simple* enough to allow for theoretical analysis but also *accurate* enough to reproduce a variety of

[1] See the special issue of IEEE Control Systems Magazine; Ghosh and He (2001), and the proceedings of ACC 2001 e.g. Nenadic and Ghosh (2001) for recent approaches from neuroscience view point.

neuronal functionalities. The model can be considered as a simplified version of Hodgkin and Huxley (1952) model, and is given as a special class of the systems considered in Lur'e (1957), i.e. a feedback connection of a linear time-invariant system and a static nonlinearity. The Lur'e neuron model we propose is shown to possess various dynamic properties of a neuron, such as threshold, refractory period, frequency modulation (or rate coding), and mode switching (or bistability).

2. NEURONAL MODELING

2.1 Brief review of existing models

The input-output properties of neurons are usually modeled by an electrical circuit consisting of parallel connections of the membrane capacitance and ion channel conductances. A relatively complete mathematical model of a nerve membrane was first obtained by Hodgkin and Huxley (1952) for a squid giant axon. The Hodgkin-Huxley (HH) model is capable of generating various typical properties of generic neurons, and still remains, after a half century, to provide the essential structure of most sophisticated neuron models available to date. The HH model is of fourth order and is highly nonlinear. Rigorous mathematical analysis of the HH model is extremely difficult and thus its behavior has been analyzed either by simulations or by simplifying the model.

Several simpler models of the second order have been obtained and their dynamical behavior analyzed in a more precise manner. Nagumo et al. (1962) modeled a nerve axon by a negative resistance (tunnel diode) circuit to capture the essential dynamics of various ion channels. FitzHugh (1969) showed that this model can be obtained by modifying the van der Pol oscillator. Thus, it is called the FitzHugh-Nagumo (FHN) model. Another model has been introduced by Morris and Lecar (1981) in the context of electrical activity of the barnacle muscle fiber. The Morris-Lecar (ML) model has an increased complexity in nonlinear terms when compared with the FHN model. An analysis of the ML model based on isocline methods by Rinzel and Ermentrout (1989) showed that the model has dynamics rich enough to reproduce various generic neuronal properties including the frequency modulation, which the FHN model does not possess.

2.2 Lur'e model

We propose the following model obtained by simplifying the ML model, extracting the essential dynamics in terms of the isocline profile:

$$\begin{aligned} \dot{v} &= \psi_1(v) - w + u \\ \dot{w} &= \rho(\psi_2(v) - w) \end{aligned} \tag{2}$$

where v is the membrane potential, w represents dynamics of voltage gated Na^+ and K^+ channels, u is the current input, ρ is the speed of K^+ channels opening (temperature dependent), and $\psi_i(v)$ are the static nonlinearities such that $-\psi_1(v)$ is "N–shaped" and $\psi_2(v)$ is saturation-like (see Fig. 1). The shapes of the functions $\psi_i(v)$ are motivated by the isoclines of the ML model.

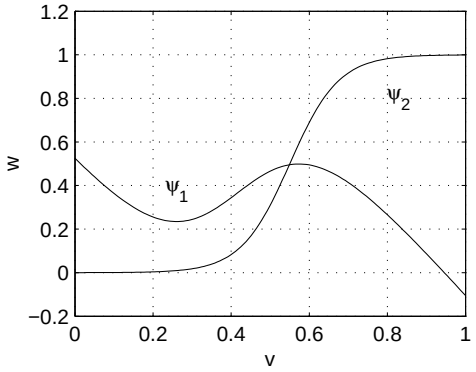

Fig. 1. Typical shapes of $\psi_1(v)$ and $\psi_2(v)$

Next we show that an additional structure, useful for simplifying the analysis, can be embedded into the model. In particular, both nonlinearities $\psi_i(v)$ can be generated by shifting/scaling a single basic nonlinearity $\phi(x)$. To this end, let $\phi(x)$ be a monotonically nondecreasing bounded function. For instance, $\phi(x)$ may be chosen as either piecewise linear

$$\phi(x) := \begin{cases} 0 & (x < 0) \\ x & (0 \le x \le 1) \\ 1 & (x > 1) \end{cases} \tag{3}$$

or sigmoidal

$$\phi(x) := \frac{1}{1 + e^{2-4x}}. \tag{4}$$

Then we can realize $\psi_i(v)$ as

$$\begin{aligned} \psi_1(v) &= c\phi(av) - bv + u_o \\ \psi_2(v) &= \phi(d(v + v_o)) \end{aligned}$$

where $a, b, c, d > 0$ are the parameters that determine the shape of $\psi_i(v)$ and u_o and v_o are vertical and horizontal bias terms to adjust the relative positioning of $\psi_1(v)$ and $\psi_2(v)$. These functions are plotted in Fig. 2 for the case of piecewise linear basis function $\phi(x)$. The curves for the sigmoidal basis are similar but smooth.

With these choices of $\psi_i(v)$, we have

$$\begin{aligned} \dot{v} &= c\phi(av) - bv - w + u_o + u \\ \dot{w} &= \rho(\phi(d(v + v_o)) - w). \end{aligned} \tag{5}$$

By pulling out the basic nonlinearity $\phi(\cdot)$, this can be written as the Lur'e system in Fig. 3 where $\beta := [\ u_o \quad v_o\ ]^{\mathrm{T}}$ is the constant bias input vector, $\phi I := \mathrm{diag}(\phi, \phi)$ is the repeated static nonlinearity, and

$$G(s) := C(sI - A)^{-1}B + D, \tag{6}$$

$$\left[\begin{array}{cc} A & B \\ C & D \end{array}\right] := \left[\begin{array}{cc|ccccc} -b & -1 & c & 0 & 1 & 1 & 0 \\ 0 & -\rho & 0 & \rho & 0 & 0 & 0 \\ \hline a & 0 & 0 & 0 & 0 & 0 & 0 \\ d & 0 & 0 & 0 & 0 & 0 & d \\ 1 & 0 & 0 & 0 & 0 & 0 & 0 \end{array}\right]$$

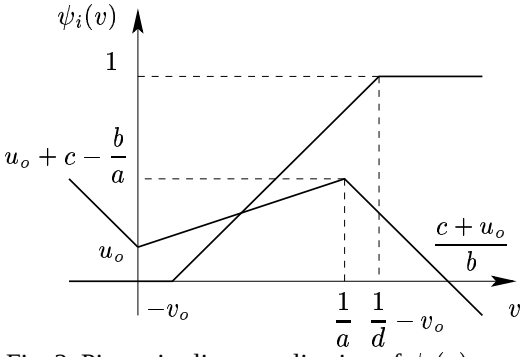

Fig. 2. Piecewise linear realization of $\psi_i(v)$

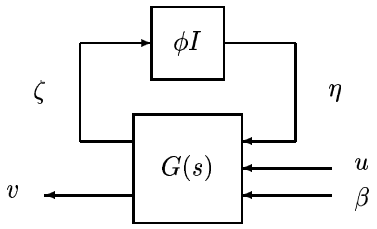

Fig. 3. Lur'e system

with the state vector $[\ v \quad w\ ]^{\mathrm{T}}$. Thus, the complexity of our Lur'e neuron model is comparable to the FHN model discussed earlier in that both belong to the class of systems in Fig. 3 with a second order linear part $G(s)$. The essential difference between this model and the FHN model is the nonlinearity of $\psi_2(v)$. We will show later that the new model can perform frequency modulation, which the FHN model cannot, due to this additional nonlinearity.

3. ANALYSIS OF NEURONAL DYNAMICS

3.1 Stability analysis

In this section, we shall analyze stability properties of the Lur'e neuron model in (2). Our first result states bounded-input bounded-output stability of the Lur'e system.

Proposition 1. Consider the Lur'e system in (5). Suppose the parameters b and ρ are positive, and $\phi(x)$ is globally Lipschitz and bounded. Then, for any piecewise continuous, bounded input u and for any initial states $v(0)$ and $w(0)$, there exists a unique bounded solution (v, w) to (5).

Proof. The existence and uniqueness of the solution follows from Lipschitz continuity of ϕ and piecewise continuity of u (see Khalil (1996)). Now, recall that the system can be expressed as the feedback system in Fig. 3 where $G(s)$ is given by (6). Since ϕ is a bounded function, all the input signals to $G(s)$ are bounded. Moreover, positivity of b and ρ means stability of the linear system $G(s)$. Hence, all the states of any minimal realization of $G(s)$ must be bounded. ■

We now consider the Lur'e model in (2) with *constant* input u and examine stability of equilibrium points via the Lyapunov's indirect method. The result is summarized as follows:

Proposition 2. Let (v_e, w_e) be an equilibrium point of (2) with a given constant input u. Suppose the linearized system around the equilibrium point has no eigenvalues on the imaginary axis. Then the equilibrium point is

$$\begin{aligned} \text{a saddle point} &\Leftrightarrow \psi_2' < \psi_1' \\ \text{an unstable node/focus} &\Leftrightarrow \psi_2' > \psi_1', \quad \rho < \psi_1' \\ \text{a stable node/focus} &\Leftrightarrow \psi_2' > \psi_1', \quad \rho > \psi_1' \end{aligned}$$

where ψ_i' $(i = 1, 2)$ are the derivatives of ψ_i evaluated at $v = v_e$.

Proof. The linearization of (2) around the equilibrium point is given by $\dot{x} = Ax$ where

$$A := \begin{bmatrix} \psi_1' & -1 \\ \rho\psi_2' & -\rho \end{bmatrix}.$$

The corresponding characteristic equation is

$$\lambda^2 + (\rho - \psi_1')\lambda + \rho(\psi_2' - \psi_1') = 0.$$

The result then follows immediately from the following fact: Let the roots of equation

$$\lambda^2 + \alpha\lambda + \beta = 0$$

with unknown λ be denoted by λ_i $(i = 1, 2)$. Then under the assumption $\mathrm{Re}(\lambda_i) \neq 0$ for $i = 1, 2$, we have

$$\begin{aligned} & \lambda_1\lambda_2 < 0 \Leftrightarrow \beta < 0 \\ \mathrm{Re}(\lambda_i) > 0, \quad & (i = 1, 2) \Leftrightarrow \beta > 0, \quad \alpha < 0 \\ \mathrm{Re}(\lambda_i) < 0, \quad & (i = 1, 2) \Leftrightarrow \beta > 0, \quad \alpha > 0 \end{aligned}$$ ■

3.2 Functional properties of the Lur'e model

We now show by simulations that the Lur'e model captures a variety of neuronal properties. We consider the sigmoid basis function (4) for ϕ and use the following values of the parameters in (5):

$$u_o = -0.2, \quad v_o = -0.35, \quad \rho = 0.3,$$
$$a = 1.8, \quad b = 3, \quad c = 2.2, \quad d = 5,$$

Similar results can be obtained if we use the piecewise linear basis function (3) instead of the sigmoid function.

When $u = 0$, the isoclines are given by the light curves in Fig. 4 (above). Note that there are three equilibrium points X, Y, and Z. From the earlier stability analysis, it can readily be found that X is stable, Y is a saddle, and Z is an unstable node/focus. The resting values of v and w (i.e. the unique stable equilibrium point when $u = 0$) are found to be

$$v_{\mathrm{rest}} = 5.88 \times 10^{-2}, \quad w_{\mathrm{rest}} = 4.00 \times 10^{-4}$$

and are used as the initial states for all simulations that follow.

Threshold: Short pulse inputs of duration 0.2 with various heights are applied to the Lur'e model when it is at rest. We see from Fig. 4 (below) that an action

potential is generated if and only if the pulse height is larger than a threshold value ($\cong 0.74$). The underlying mechanism for the threshold phenomenon can be explained as follows. In Fig. 4 (above), the pulse input makes the state (v, w) jump (or rapidly move) from the resting point X to the right by a distance roughly equal to the product of the pulse duration and the height. If the jump is small, then the state simply goes back to the resting point X. If the jump is big enough to go beyond the separatorix [2], then the state trajectory goes around the unstable equilibrium point Z and eventually converges to X. Thus, the threshold is determined by the horizontal distance between X and the separatorix.

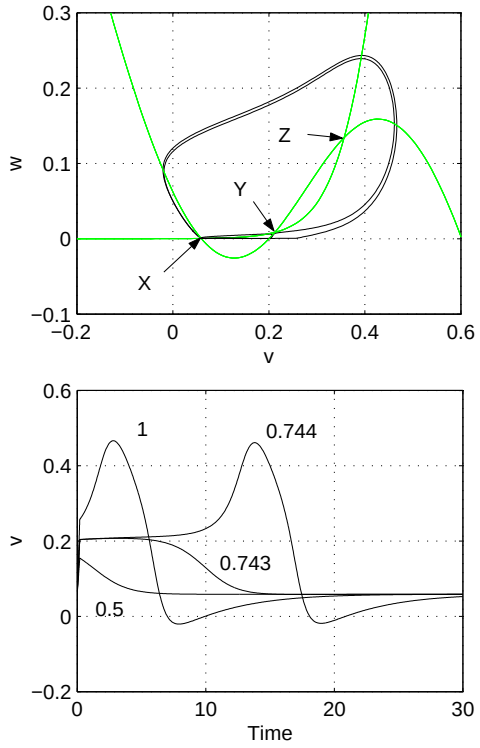

Fig. 4. Threshold phenomenon of the Lur'e model

Frequency modulation: Fig. 5 shows the response of the Lur'e model when the following two-stage step input is applied:

$$u(t) = \begin{cases} 0.03 & (0 \le t < 100) \\ 0.08 & (100 \le t) \end{cases}$$

The figure clearly shows that the frequency of the spiky limit cycle changes with the magnitude of the constant input. Rinzel and Ermentrout (1989) showed by phase plane analysis that the cause of the frequency modulation in the ML model is the saddle-node bifurcation. In the case of our Lur'e model, exactly the same argument can be made to explain the frequency modulation phenomenon. We shall briefly repeat the analysis for completeness using Fig. 5 (above). Note that the two state trajectories coming out of the saddle point Y along its unstable eigenvectors must terminate at the unique stable equilibrium point X, for the boundedness of the trajectories are guaranteed by Proposition 1. One of these heteroclinic trajectories coming out of Y to the left goes directly to X, while the other one goes around Z and converges to X. Now, as the input magnitude increases from zero, the equilibrium points X and Y come closer to each other. When they meet, a saddle-node bifurcation occurs and the pair of heteroclinic orbits becomes a homoclinic orbit which is a limit cycle with infinite period. If the input magnitude is a bit further increased, then Z becomes the only equilibrium point. Since Z is unstable and every trajectory is bounded, there must exist a periodic orbit (Poincare–Bendixson theorem, Khalil (1996)). The frequency of the periodic orbit increases from zero to some finite value as the input magnitude increases, exhibiting the frequency modulation. Finally, it should be noted that the FHN model can have only one equilibrium point for any input value and thus the saddle-node bifurcation, which is responsible for the frequency modulation, can never happen.

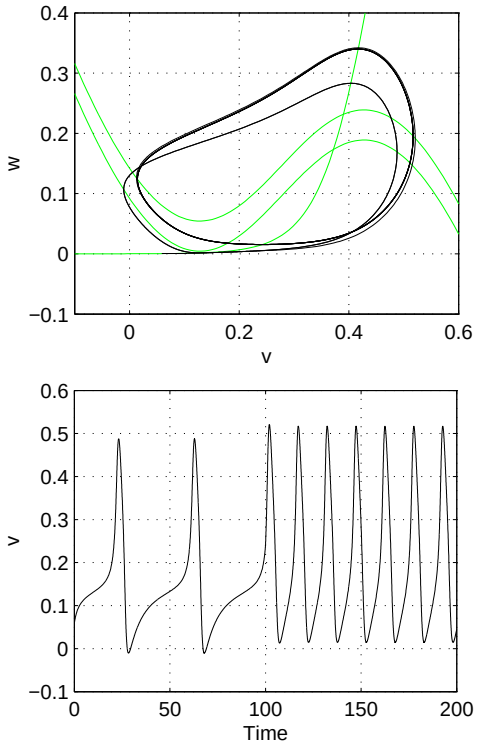

Fig. 5. Frequency modulation of the Lur'e model

Mode switching: A constant input u of magnitude 0.15 is applied to the Lur'e model at $t = 0$ when the system is at rest. Then the system enters a limit cycle as shown in Fig. 6 (above). If a short pulse of duration 0.2 and height 0.5 is superimposed on the constant input at $t = 50$, the periodic firing is "turned off" and the membrane potential v converges to a constant value.

[2] A pair of state trajectories that converge exactly to the saddle point Y. In Fig. 4 (above), it is roughly given by the part of the vertical isocline from Z to Y and its smooth extension to the point $(0, -0.1)$.

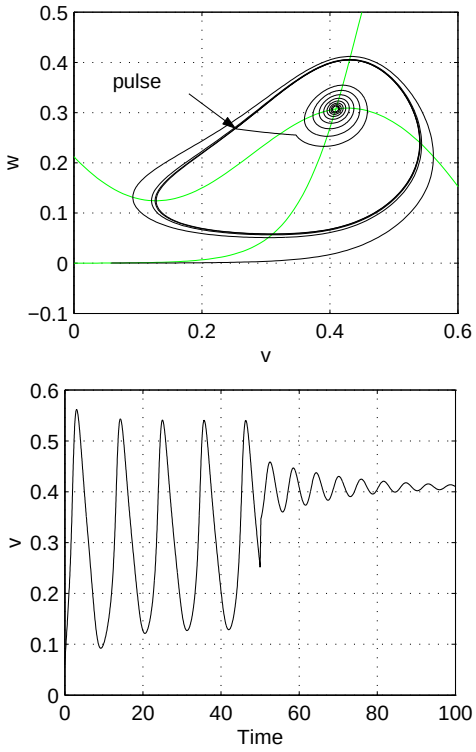

Fig. 6. Bistability of the Lur'e model

This mode switching phenomenon is explained as a result of bistability. As shown before, for the value of constant input u just above the saddle-node bifurcation, the equilibrium point Z is an unstable focus/node and a stable limit cycle is generated. If u is further increased, the slope of the vertical isocline ψ_1' at Z eventually becomes smaller than ρ. This means, according to Proposition 2, that Z becomes a stable equilibrium point. At this point, the stable limit cycle and the stable equilibrium point coexist, and the system exhibits bistability. These two are separated by an invisible unstable limit cycle. If a short pulse of input makes the state jump to the inside of this unstable periodic orbit, then the state is attracted to the stable equilibrium point as shown in Fig. 6.

3.3 Further refinement of the Lur'e model

The Lur'e model we have developed and analyzed so far captures the dynamics of the axon, a neuronal component responsible for generation of action potentials. The dynamics and functions of other components, such as the dendrite and the soma, also play an important role in emerging high functionality of networked neuronal oscillators. Another crucial dynamics is due to the information transfer between neurons via the synaptic connections. The objective of this section is to add the relevant dynamics to complete the neuronal modeling.

Adaptation: An important characteristic missing in the Lur'e model is the *adaptation*. In fact, all of the HH, ML, and FHN models lack this property, probably because this property is due to the dynamics of the soma and/or the dendrite. It is characterized by the

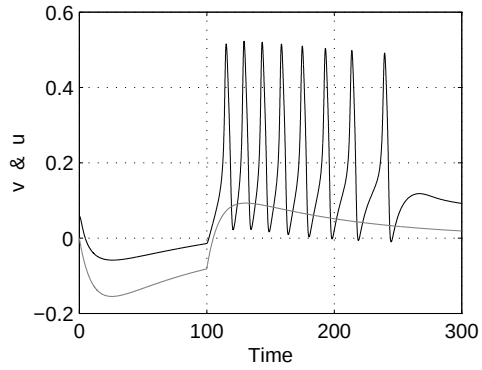

Fig. 7. PIR phenomenon of $\mathcal{N}$

following phenomenon. When a step current input of sufficiently large amplitude is applied to a neuron, a train of action potentials is generated. For the neuron models, the action potentials persist forever with a fixed frequency. For the actual neurons, however, the frequency gradually decreases and eventually the neuron stops firing; FitzHugh (1969).

From a systems point of view, the above observation suggests that the neuronal dynamics seem to involve a filter with a zero at the origin, not to pass through the step input. Hence we propose to add the following linear filter at the input port of the Lur'e model:

$$F(s) = \frac{ks}{(s+p_1)(s+p_2)} \tag{7}$$

where k, p_1 and p_2 are some positive constants. The complete description of our neuron model is given by (2) and $u = F(s)\nu$ where ν is the input to the model. Let us denote this model by $v = \mathcal{N}(\nu)$. The input ν has the physical significance of the electrical current injected into the soma and/or the dendrite. A simulation of step response shows that spikes are generated but are terminated within a finite time interval with gradually decreasing frequency, indicating the adaptation phenomenon.

Post-inhibitory rebound (PIR): Another important property missing in the original Lur'e model (2) is the *PIR*; Friesen and Friesen (1994). It is observed in real neurons that action potentials are generated after an inhibitory (negative) current input is applied for a while and then cut off. It turns out that the PIR property can be incorporated into our neuron model by exactly the same filtering mechanism as above. Fig. 7 shows the response of our model $\mathcal{N}$ when a current pulse

$$\nu(t) = \begin{cases} -1 & (0 \le t < 100) \\ 0 & (t \ge 100) \end{cases}$$

is applied. We see that the current input u from the soma to the axon (light curve) bounces back to take on positive values after the end of the inhibitory input. Because of this, a finite train of action potentials are generated (dark curve), indicating the PIR property.

Synaptic fatigue: Let us consider the effect of a firing neuron $\mathcal{N}_{\rm pre}$ connected through a synapse to

another neuron $\mathcal{N}_{\rm post}$. The membrane potential $v_{\rm pre}$ of $\mathcal{N}_{\rm pre}$ induces some ionic current flow through the membrane of $\mathcal{N}_{\rm post}$ at its dendrites. The direction of the overall current flow $\nu_{\rm post}$ depends on the particular synaptic connection: if the induced current $\nu_{\rm post}$ is negative (positive), the synaptic connection is said to be inhibitory (excitatory). Thus, we may view the synaptic connection as a dynamical system with the input $v_{\rm pre}$ and the output $\nu_{\rm post}$. Let us denote this system as $\nu_{\rm post} = \mathcal{S}(v_{\rm pre})$. It is a common practice Friesen and Friesen (1994); Koch and Segev (1989) to model the system $\mathcal{S}$ in terms of varying electrical conductances, leading to a fairly complex nonlinear model.

In the sequel, we argue that the following simple constant gain model can be used for $\mathcal{S}$ for the purpose of devising networked neuronal oscillators:

$$\nu_{\rm post} = \pm\sigma v_{\rm pre}$$

where σ is a positive constant whose value is a measure of the strength of the synaptic connection, and the sign $\pm$ reflects the excitatory or the inhibitory nature of the synapse. Of course, the induced current input to $\mathcal{N}_{\rm post}$ is not at all proportional to the presynaptic potential $v_{\rm pre}$. However, if we look at the effect of $v_{\rm pre}$ on the postsynaptic potential $v_{\rm post}$, the resulting model

$$v_{\rm post} = \mathcal{N}(\pm\sigma v_{\rm pre}) \tag{8}$$

has the right property of our interest — *synaptic fatigue*. In particular, with this model, a persistent excitation by an infinite train of action potentials in $v_{\rm pre}$ results in a *finite* train of action potentials in $v_{\rm post}$.

In summary, the overall neuron model from the presynaptic potential input to the postsynaptic potential output is given by (8) with the linear filter $F(s)$ in (7) and the nonlinear Lur'e system in (2). This model captures various properties of real neurons including the adaptation, post-inhibitory rebound, and synaptic fatigue, in addition to the standard properties summarized in Section 3.2. These additional properties are known to be particularly important for construction of networked neuronal oscillators; Friesen and Friesen (1994); Matsuoka (1985).

4. CONCLUSION

We have proposed a new model for a single neuron. The model is given as a special class of the Lur'e systems for which substantial amount of mathematical analysis tools are available. The complexity of the Lur'e model is shown to be comparable to the FHN model which is one of the simplest neuron models capable of generating spike trains. The accuracy of the Lur'e model is measured by its ability to reproduce typical neuronal responses and is shown qualitatively comparable to the more complex ML model.

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