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Binding Neuron

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INTRODUCTION

Although a neuron requires energy, its main function is to receive signals and to send them out – that is, to handle information. - F. Crick, The Astonishing Hypothesis, 1994

The brain ability to perform meaningful signal processing tasks related to perception, pattern recognition, reasoning is normally attributed to large-scale neuronal networks. The main signals involved in the instantaneous neural processing are neural impulses, and the units, which process impulses in a network, are individual neurons. We now put a question: In the context of higher brain functions, like perception, what is a meaningful task a neuron performs with the signals it receives? Another question: Does the inhibition exist for taming neuronal activity only, or it can be endowed with a more intelligent signal processing role? In this article, we propose an abstract concept of signal processing in a generic neuron, which is relevant to the features/events binding well known for large-scale neural circuits. Within this concept, action of inhibition obtains its natural signal processing meaning.

BACKGROUND

Low-Level Concepts of Signal Processing in a Neuron

The main part of any biological neuron is the excitable membrane. The membrane is able to generate electrical (neural) impulses, if proper stimulated, and to propagate those impulses over long distances without attenuation. The low-level concepts are concerned with electrochemical characteristics of initiating and propagating of the impulses. These concepts are expressed in the form of differential equations, which govern the time course of the transmembrane potential.

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Hodgkin and Huxley Equations

If V denotes the displacement of the transmembrane potential of the excitable membrane from its resting state, then its time course is defined by the transmembrane currents as follows:

$$\frac{dV}{dt} = -\frac{1}{C_M}\sum_{k=1}^{n} I_k, \tag{1}$$

where n is the number of different ionic currents considered, C_M is the capacity of the membrane unit surface and I_k, $k = 1,\ldots,n,$ denote ionic currents through that surface. In the Hodgkin and Huxley (H-H) model, (Hodgkin & Huxley, 1952), three currents were considered, namely, the potassium, sodium and leakage current. These currents depend on the V by the following way:

$$\begin{aligned} I_K &= g_K n^4 (V - V_K), \\ I_{Na} &= g_{Na} m^3 h (V - V_{Na}), \\ I_l &= g_l (V - V_l), \end{aligned} \tag{2}$$

where g_k, V_k, $k \in \{''K'', ''Na'', ''l''\}$ are time-independent. The so called gating parameters m, n, h depend on t in accordance to the following equations:

$$\begin{aligned} dn \,/\, dt &= \alpha_n (1-n) - \beta_n n, \\ dm \,/\, dt &= \alpha_m (1-m) - \beta_m m, \\ dh \,/\, dt &= \alpha_h (1-h) - \beta_h h. \end{aligned} \tag{3}$$

Here parameters α_k, β_k, $k \in \{''h'', ''m'', ''n''\}$, depend on V in a nonlinear manner, see (Hodgkin & Huxley, 1952) for the exact expressions. The system (1)–(3) has resting state with $V = 0$. The temporal

dynamics is usually introduced into (1)–(3) through a choice of proper initial conditions with a nonzero V value. This corresponds to experimental manipulation known as the voltage clamp method. After the voltage clamp is released, the temporal dynamics of V can be observed either experimentally, or by solving (1)–(3) numerically.

The remarkable feature of the H-H set of equations is that if the initially clamped value of V corresponds to depolarization and is high enough, then the dynamics itself builds up further depolarization up to a definite value, V_{peak}, and then returns to its resting state. This transient process is known for real neurons as the action potential, or spike, and it constitutes the essence of the neural impulse, when propagates along the membrane of a neural fiber, (Hodgkin, 1971). Both for real neurons, and for the set of Equations (1)–(3) neither the time course of the action potential, nor its peak value does depend on the initially clamped value of V. Moreover, the time course of the action potential obtained by solving (1)–(3) is in perfect correspondence with that observed experimentally for the giant nerve fiber of squid (see Hodgkin & Huxley, 1952, Figs 13, 14).

The ideas of H-H equations received further development in several directions. First, additional ionic currents found in other neurons and the dynamical properties of corresponding ionic channels are added to the (2) and (3) (Huguenard & McCormick, 1992). Second, spatially distributed (compartmental) equations are considered in order to fit with morphology of real neurons (De Schutter & Bower, 1994). Third, for simplification of mathematical analysis, a reduced sets of equations were offered, which has lower dimension than (1)–(3), and still is suitable for generating spikes (FitzHugh, 1961).

Leaky Integrate and Fire Model

In the Leaky Integrate and Fire (LIF) neuron model (Stein, 1967; Knight, 1972), the membrane voltage time course is governed by the following differential equation:

$$\frac{dV}{dt} = \frac{1}{C_M} I(t) - \frac{1}{R_M C_M} V, \qquad (4)$$

where the first term corresponds to stimulating current due to input impulses and the second one – to exponential decay due to leakage. The model is additionally characterized with a threshold voltage, V_{th}. If V surpasses the V_{th}, then the neuron emits an impulse and V is reset to standard value, usually 0. The model has numerous modifications (Burkitt, 2006). The LIF model appeared to be quite useful for studying statistics of activity in individual neurons and neuronal populations.

The low level models were designed for quantitative description of membrane voltage and currents interplay. Any low level model retains a possibility to fire an output impulse (spike). The decision to fire or not is made based on the membrane voltage time course. At the same time, the output impulses emitted from a neuron are identical, bearing the only label – the emitting moment. The same should be expected about the input impulses for a neuron embedded in a neuronal network[1]. If so, then it would be natural to formulate the firing criterion in terms of arriving moments of the input impulses.

DIRECT REDUCTION TO LOW-LEVEL CONCEPTS IS UNFEASIBLE

The understanding of mechanisms of higher brain functions expects a continuous reduction from higher activities to lower ones, eventually, to activities in individual neurons, expressed in terms of membrane potentials and ionic currents. While this approach is correct scientifically and desirable for applications, the complete range of the reduction is unavailable to a single researcher due to human brain limited capacity. An attempt to describe a task solving within a brain in terms of membrane potentials and ionic currents would be similarly hopeless as to describe in terms of Kirchhoff's point and loop equations a program execution in a computer. In the computer circuits design, many abstractions, like NAND-gate, NOR-gate and so on, are used. The gates can be constructed as electrical or optical cells, but the hardware description language (see Shahdad, Lipsett, Marschner, Sheehan, & Cohen, 1985) deals only with abstract logical essence of the gate concept while concrete physical mechanisms employed are studied within another branch of science.

In analogy with computer science, it seems useful to abstract from the rules by which a neuron changes its membrane potential and currents to rules by which the informational signals, which are neuronal impulses, are processed in the neuron. The required abstraction can be derived by analysis, based on low level mechanisms, of how a neuron receives and sends out impulses.

The two abstract concepts, namely, the "coincidence detector" and "temporal integrator" are offered in this course (Abeles, 1982; König, Engel, & Singer, 1996). Both do not involve inhibition. Also, a realistic neuron can display both coincidence detector and temporal integrator modes of activity depending on the stimulation applied (see Rudolph & Destexhe, 2003).

THE BINDING NEURON CONCEPT

The Binding Problem in Neuroscience

During visual perception, such features as form, color and stereopsis are represented in the brain by different neuronal assemblies. These features are combined into a coherent percept if presented to vision within a definite time window. If scattered over a wider window, the features are perceived and referred separately (Treisman & Gelade, 1980). The problem of identification of mechanisms enabling to combine different features into a single percept is known as features/events binding problem (Sougné, 2003). The binding mechanisms operate also in auditory, tactile and multimodal perception. It is believed that correct timing of neuronal firings in different brain areas is required for the binding to occur (Eckhorn, et al., 1988; Damasio, 1989a, 1989b; Engel, König, Kreiter, Gray, & Singer, 1991; Merzenich, Schreiner, Jenkins, & Wang, 1993; deCharms & Merzenich, 1996). In the above-cited papers, the binding is considered, which happens within large-scale neuronal assemblies. On the other hand, a primitive binding mechanism can be attributed to a single generic neuron.

Generic Neuron with Multi-Impulse Stimulation

The binding neuron concept was derived from the Hodgkin and Huxley model (1)–(3) by applying the stimuli, which are similar to those received by a natural neuron in natural conditions. In order to characterize those stimuli, one should take into account that a single input impulse exerts very small excitation unable to trigger the neuron. A neuron like pyramidal cell has up to 30000 input places on its surface – the synapses (Megias, et al., 2001). Normally, several hundreds of input impulses are required to trigger a spike (Andersen, Raastad, & Storm, 1990). Each input impulse causes a transient change in the membrane voltage. This transient may have different time course in different parts of neuron, but what matters is the time course in the spike triggering zone (Moore, Stockbridge, & Westerfield, 1983). The transient in the spike triggering zone is known as unitary excitatory postsynaptic potential, EPSP. Denote as $EPSP(t)$ the time course of EPSP due to input impulse arrived at time $t = 0$. Taking into account that input impulses arrive to neuron seemingly randomly dispersed in time (Abeles, 1982), the voltage transient due to arrival of N impulses at moments $t_1, t_2, ..., t_N$ is as follows:

$$CompEPSP(t) = \sum_{k=1}^{N} EPSP(t - t_k). \quad (5)$$

This is equivalent to receiving the stimulating current $I_s(t)$ of the following form:

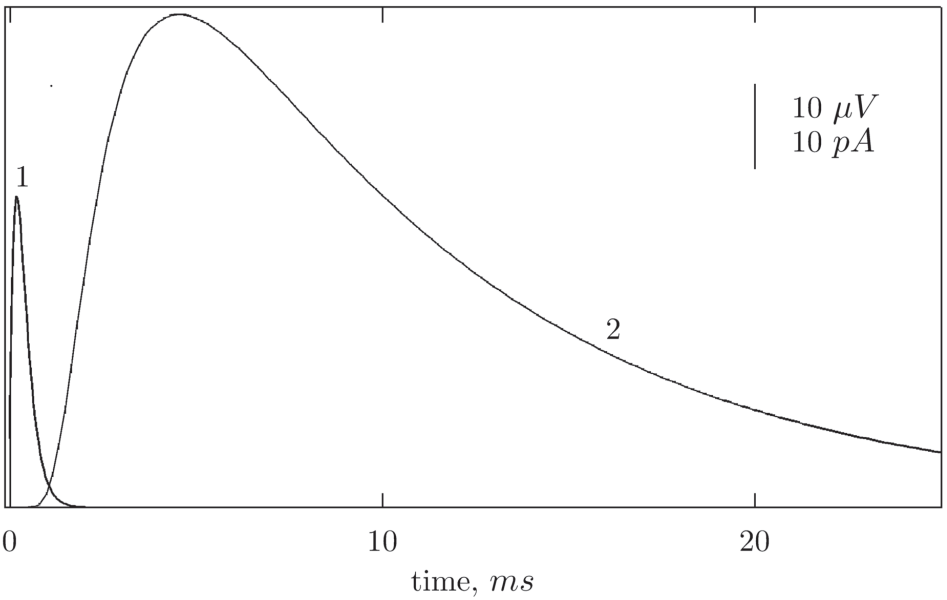
$$I_s(t) = C_M \frac{d}{dt} CompEPSP(t). \quad (6)$$

In order to have explicit expression for $I_s(t)$, one needs to know an explicit expression for the $EPSP(t)$. The latter can be estimated with a closer consideration of what happens during synaptic transmission. Each excitatory impulse produces a short-time inward current through membrane area under the corresponding synapse, excitatory postsynaptic current, ESC. The ESC time course is modeled with the so called α-function (Redman & Walmsley,1983) given as (see Figure 1):

$$ESC(t) = f_\alpha(t) = Q\alpha^2 t \exp(-\alpha t). \quad (7)$$

Here Q is the total positive charge injected into neuron due to synaptic transmission of arrived impulse. This charge migrates along the membrane decreasing its voltage[2]. Before this charge reaches the spike trig-

Figure 1. ESC(t), 1, and EPSP(t), 2, time courses. Notice the remarkable difference in the speed of two transients.



gering zone to produce the EPSP, it must pass through cylindrical structure known as dendrite. This allows one to apply the cable theory (Jack & Redman, 1971) and find the $EPSP(t)$ as:

$$EPSP(t) = \int_0^{t/\tau_M} f_\delta\,(t-\theta) f_\alpha(\theta)\, d\theta, \tag{8}$$

where

$$f_\delta(t) = \frac{1}{2\lambda C_{M1}\sqrt{\pi t}}\,\exp\left(-\frac{X^2}{4t} - t\right), \tag{9}$$

is the Hodgkin formula for the function of unit source in infinite cylindrical cable (Fatt & Katz, 1951). The time courses $ESC(t)$ and $EPSP(t)$ calculated by means of Equations (7)-(9) with parameter values known for cortical pyramidal neurons are presented in Figure 1. This completes definition of the stimulating current $I_s(t)$ in the spike triggering zone caused by N impulses with fixed arrival times $t_1, t_2, ..., t_N$. At first glance, $t_1, t_2, ..., t_N$ in natural conditions are distributed randomly. Different choices of $t_1, t_2, ..., t_N$ bring about different $I_s(t)$ which may or may not trigger the neuron (see Vidybida, 1996). Therefore, it is natural to ask: What is the probability to fire a spike with stimulus $I_s(t)$ if arrival times $t_1, t_2, ..., t_N$ of corresponding input impulses are taken by chance from a temporal window $[0;W]$? Denote this probability as fp. For calculating fp one can use the Monte Carlo method. Namely, chose randomly N numbers $t_1, t_2, ..., t_N$ from the interval $[0;W]$, substitute them into (5), find $I_s(t)$ as in (6) and add it to the Equation (1).

By solving numerically the obtained set of H-H equations one can decide if stimulation composed of N input impulses arriving at moments $t_1, t_2, ..., t_N$ is successful in generating spike, or not. The next trial should be performed with another set of N random numbers from $[0;W]$. After repeating this procedure many times, one can find the firing probability fp by dividing the number of successful trials on the total number of trials made. This whole procedure can be performed with various values of W, which gives the dependence $fp(W)$ of the firing probability on the window width W. In order to estimate the role of inhibitory hyperpolarization on the course of $fp(W)$, a term with additional constant potassium[3] conductance,

$-g_{iK}(V - V_K) / C_M$, is added to the right hand side of (1). Several values of g_{iK} are considered, which bring about different values of inhibitory potential (see Figure 2).

The dependencies obtained (Vidybida, 1996, 1998) are given in Figure 2, where the fp is presented as a function of temporal coherence instead of W. The temporal coherence between unitary EPSP within a compound stimulus is defined as $TC = 1 / W$.

The Concept

The step-like dependencies with the step position depending on the inhibitory hyperpolarization allows one to propound the following abstract description of signal processing in a generic neuron (the binding neuron concept):

BN-1: Excitatory synaptic currents (ESCs, Figure 1) are treated as elementary events, which a neuron is able to perceive.

BN-2: EPSP, which follows the ESC serves as short term memory mechanism for the perceived elementary event, because its duration is much longer than that of the ESC (Figure 1).

BN-3: A set of elementary events, which are coherent in time, can be treated as a compound event. In the neuron, the elementary events from the set are bound into an output spike. The output spike can be treated as abstract representation of the compound event (Figure 3).

BN-4: Inhibition serves as controller of this type of binding: The level of inhibitory potential controls the degree of temporal coherence between elementary events which is necessary for those events to be recognized in the neuron as coherent (bound) event (Figures 2 and 3).

Figure 2. Firing probability vs. temporal coherence between the unitary EPSPs within the compound stimulus of 1000 input impulses. The four curves correspond consecutively from the left to the right to the inhibition potentials 0.43, 3.08, 5.02, 6.30 mV.

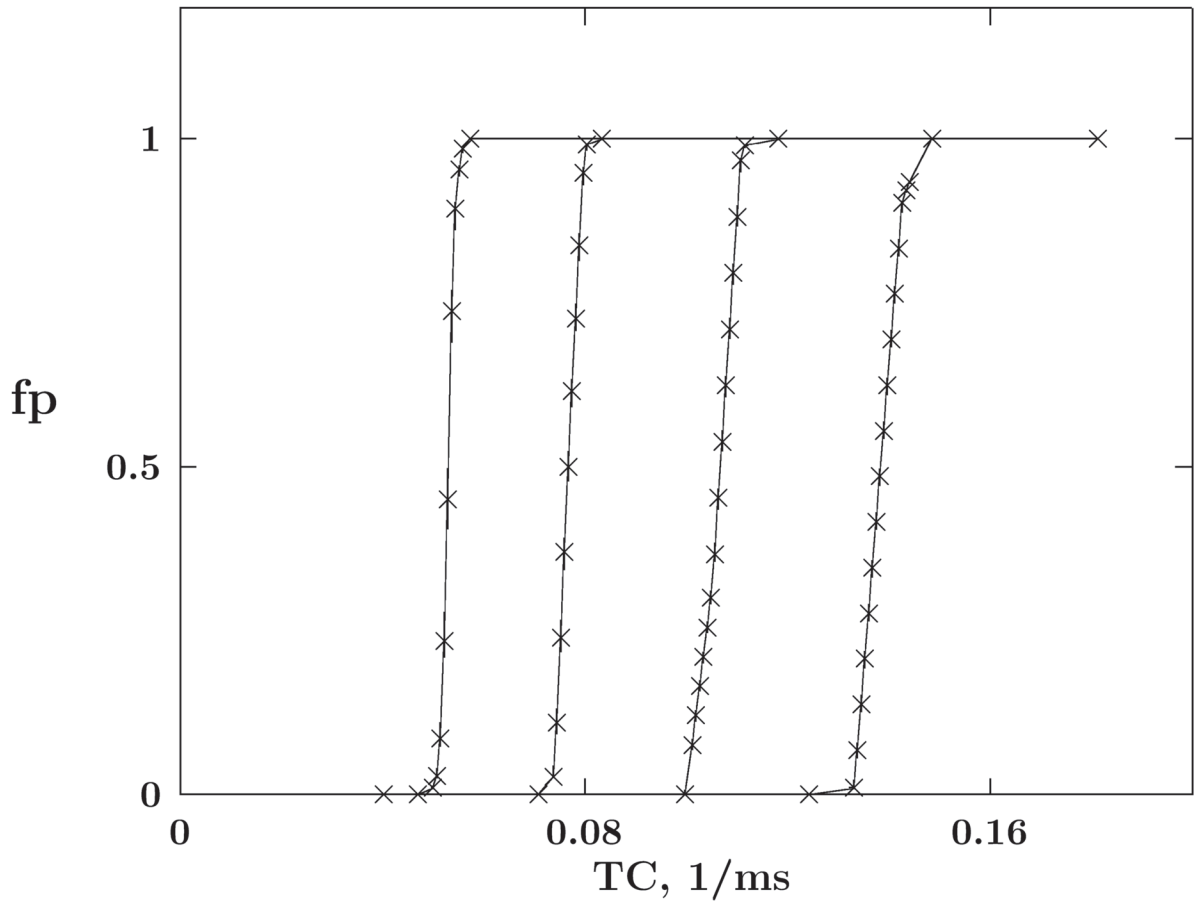
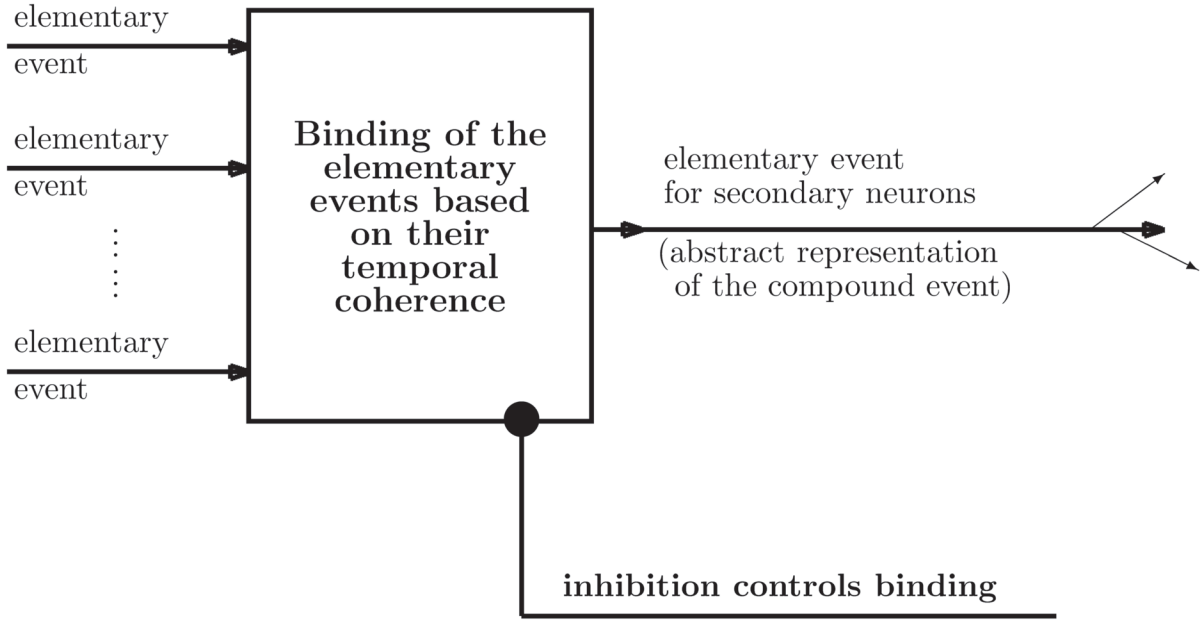


Figure 3. Signal processing in a neuron in accordance with the BN concept



Mathematical Implementation of the BN Concept

The BN concept described in BN-1 – BN-4, above, is derived from the dependencies in Figure 2. Since those dependencies are obtained based on the H-H equations, then the H-H equations could be one possible mathematical implementation. The LIF model could be another one since curves similar to those in Figure 2 can be obtained based on the LIF model with proper chosen mechanism of inhibition.

A model, which represents the BN concept in refined form, the BN model, could be realized as follows (Vidybida, 1998, 2003). Each input impulse is stored in the BN for a fixed time, τ, after which it disappears. The τ is similar to the tolerance interval discussed by MacKay (1962). The neuron fires an output impulse if the number of stored impulses, Σ, is equal or higher than the threshold value, N_{th}, and $\Sigma = 0$ just after firing. In this model, the presence of inhibition is expressed in the decreased τ value.

A formalized definition of the BN model can be given in the form of transfer function. The transfer function allows exact calculation of output in terms of input. In the case of neuron, input is a increasing sequence of discrete arriving moments of standard impulses:

$$T_{in} = \{l_1, l_2, l_3, ...\}.$$

The output is the sequence of discrete firing moments of BN:

$$T_{out} = \{f_1, f_2, ...\}.$$

It is clear that $T_{out} \subset T_{in}$. A transfer function in our case could be the function $\sigma(l)$, $l \in T_{in}$, which equals 1 if l is the firing moment, $l \in T_{out}$, and 0 otherwise. For BN with threshold N_{th} the required function can be defined as follows. It is clear that the first $N_{th} - 1$ input impulses are unable to trigger neuron, therefore

$$\sigma(l_1) = 0, ..., \sigma(l_{N_{th}-1}) = 0.$$

The next input impulse is able to trigger if and only if all first N_{th} arriving moments are confined within a time interval, which is no longer than τ:

$$\sigma(l_{N_{th}}) = 1 \text{ if and only if } l_{N_{th}} - l_1 \le \tau.$$

In order to determine $\sigma(l_{N_{th}+k})$, $k \geq 1$, one must take into account previous input moments, therefore we use notation $\sigma_{T_{in}}$ instead of σ. The values of $\sigma_{T_{in}}(l_{N_{th}+k})$ can be determined recursively:

$[\sigma_{T_{in}}(l_{N_{th}+k}) = 1]$
if and only if $[l_{N_{th}+k} - l_{k+1} \leq \tau$
and $\forall_{i\in\{k+1,\ldots,N_{th}+k-1\}}[\sigma_{T_{in}}(l_i) = 0]]$.

The computational disadvantage of the BN model as compared to the LIF one is that the state of BN must include not only the degree of excitation, which is Σ, but also the time to live of any impulse stored. The advantage is that traces of any impulse obtained disappear completely after finite time τ (see Figure 4). This fact allows one to obtain exact mathematical results as regards to firing statistics (see Vidybida & Kravchuk, 2010).

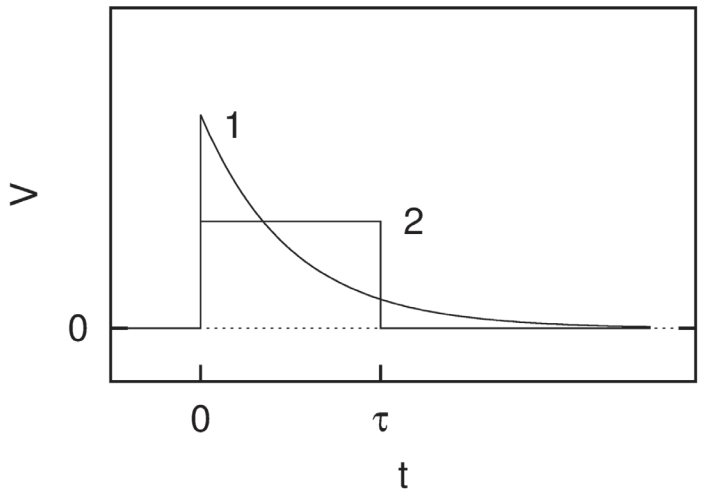
FUTURE RESEARCH DIRECTIONS

The BN concept offers a relative freedom in choosing mathematical model of a generic neuron. Indeed, the concept can be readily implemented with a model neuron, which satisfies the following two conditions: (1) the model neuron must fire after receiving some threshold input, (2) it must be forgetful in a sense that influence of any input impulse decreases end eventually disappears in time. In the above proposed BN model, the forgetfulness is realized due to the box-like function chosen for the $EPSP(t)$, in the H-H and LIF models – due to exponentially decaying $EPSP(t)$ (see Figures 1 and 4).

There are many functions in between suitable to realize forgetfulness and being in compliance with the BN concept, e. g. $\min(1,(t/\tau)^{-p})$ with $p > 0$, τ – const. Some of them could be more suitable then others for calculating some features of a neuron or neuronal network.

Relative simplicity of the BN model and its "discreteness," if considered with identical and unmodifiable synaptic weights, makes it attractive for hardware implementation. A step in this direction is made in Wang, Cohen, Stiefel, Hamilton, Tapson, and van Schaik (2013), where a network of 4K identical binding neurons with $\tau = 1$ ms, $N_{th} = 3$ is implemented on a Field-Programmable Gate Array (FPGA) chip. Further steps in the hardware implementation could be introducing modifiable synaptic weights and inhibitory connections in the network similarly to what is done in Vidybida (2003) at software level.

Figure 4. Response of the LIF, 1, and BN, 2 models to a single input impulse delivered at $t = 0$ (surrogates for the $EPSP(t)$)



At the level of network of BNs, it would be interesting to test how the binding idea could be realized for more complicated stimuli than a single bunch of input impulses used above. A step in this direction is made in Vidybida (2003).

There is a technical demand for mechanisms like features/events binding. For example, in the audio-visual tracking of moving objects, the binding in its very initial form is known as visual and/or audio-visual integration (see Talantzis, Pnevmatikakis, & Constantinides, 2012). It would be interesting to test what the binding neuron concept could offer to this practical area. A step in this direction is made in Wrigley and Brown (2005).

CONCLUSION

The signal processing function of a neuron can be grasped if one considers stimuli similar to those a neuron receives in natural conditions, namely, irregularly scattered in time sequences of impulses. For stimuli of this type, a neuron performs elementary events binding task – a bunch of impulses, which comes within narrow time window, triggers the neuron, and emitted impulse can be treated as abstract representation of that bunch. A window width, which is suitable for triggering, can be efficiently controlled by the level of inhibition. The binding ability could be the reason for neuron-like cells to survive the natural selection in those early times when multi-neuronal assemblies were still to be invented.

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KEY TERMS AND DEFINITIONS

Action Potential: In the excitable membrane, an abrupt short-time change of the membrane voltage produced due to the membrane excitability. Can propagate along neuronal fibers. Serves as interneuronal communication unit (neuronal impulse).

Axon: A long projection of a neuron through which spikes leave the neuron and course to other neurons or

muscles. At the end, has branching structure through which a single action potential produced in the neuron can be delivered to many synapses at different neurons. The strength of any action potential delivered through a branch is identical to that of initially generated spike due to active properties of excitable membrane all axons are made of.

Binding Problem: In neuroscience, the problem of how sensory elements in a scene organize into coherent perceived objects, or percepts. Has spatial aspect, when the elements to bind are scattered in space (mainly in visual perception) and temporal aspect, when the elements to bind are scattered in time (mainly in auditory and multimodal perception).

Membrane Voltage: See "Transmembrane Potential."

Neural Impulse: See "Action Potential."

Spike: See "Action Potential."

Synapse: Electrochemical construct at the end of neuronal fiber (axonal branch) of a neuron, attached to another neuron. The point, where interneuronal communication takes place.

Synaptic Current: Transmembrane current, generated under synapse when neuronal impulse arrives to that synapse.

Transmembrane Potential: The electric potential difference between internal and external sides of membrane.

ENDNOTES

1 In this statement, we expect that synaptic strength is standard and unmodifiable.

2 Without stimulation, the inner side of membrane has negative electric potential with respect to the outer side.

3 Concentration of potassium ions is higher inside the cell. Due to additional potassium conductance, potassium ions have additional possibility to go out through the membrane. This makes the membrane inner side more negative. Created this way additional negative potential is known as inhibitory potential/hyperpolarization.