FIRST-ORDER MARKOV PROPERTY OF THE AUDITORY SPIKING NEURON MODEL RESPONSE

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ABSTRACT

This paper explores properties of the spiking neuron model of auditory nerve fiber. As it results from the described reasoning, the model response in a form of the spike sequence is in fact a first-order Markov chain of certain non-overlapping sub-sequences, which, being taken separately, encode the incoming signal on the corresponding time intervals. This observation comes as a direct consequence of the finite precision of the spike registration process at the higher levels of neural signal processing. The result has important implications to the modelling of auditory apparatus and signal processing algorithmic interpretation of hearing physiology.

1. INTRODUCTION

Auditory neurons produce a very peculiar representation of the incoming audio signal. They respond with short electrical pulses to the acoustic stimulation. Traditionally it was perceived that the frequency of these pulses represent the frequency of the incoming stimulation at the lower part of the spectrum (less than 1 kHz) in accordance with the "frequency" theory. However, at the higher frequency range, much more than 1 kHz, the firing rate encodes the amplitude of the stimulus, which is captured by the "place" theory [1]. Neither of these theories can ultimately explain the neural "code" in the mid-frequency range. Besides, both of them deal with the steady spike generation in response to the stationary stimulation, which is rarely the case for "real life" signals. Another point of criticism is that in accordance with the mentioned theories, spike production by auditory neurons does not seem to benefit from the complex chemo-electrical cochlear mechanics, which is observed and proved to be important for hearing.

Indeed, the cumulative action of the middle and inner parts of the ear is equivalent to the action of the variable signal-dependent band-pass filter in accordance with the "active cochlea" model [2]. The so-called "suppressive" action of the active cochlea has been observed to play essential role in the sound perception [3-5] and has certain signal processing interpretation [6,7]. Thus, each sound-sensory cell, i.e. inner hair cell (IHC), is excited with the band-passed version of the original audio signal.

This excitation, in turn, results in the release of the neurotransmitter into synaptic cleft between IHC and the auditory neuron fiber. The neurotransmitter release process is also rather complex. It is successfully captured by the reservoir model of the IHC [8-10]. As it is shown in [11], it is possible to interpret this model as an automatic gain control (AGC) mechanism and, additionally, it can be linked to a class of modulation spectrum filtering techniques. Under the stimulation, coming from the IHC side, the auditory neurons produce a series of "spikes", i.e. action potentials, short electrical discharges, which travel along their axons to submit information about the sound source to the higher regions of the brain, where the further signal processing is performed.

The final result of this enormously complex process is the species ability to access auditory scene and relay information through sound. As it is evident from the comparison [12], human auditory system represents a universally fine tool for sound and speech processing. It outperforms by far all known artificial signal processing strategies, especially when it is being subjected to environment interferences. This observation suggests that better understanding of the way our auditory system encodes and processes sounds will lead to improved novel artificial sound processing strategies. It is rather safe to assume that all information about the sound source, remaining at the level of the auditory nerve, is contained in the specific pattern of the action potentials. The fact that these spikes are registered by the higher neurons with finite precision gives a ground for the information theoretical approach (e.g. see [13]) to the study of neuronal response patterns. Additionally it offers a possibility to transfer auditory cochlear and neuronal models into a digital domain.

Quantification of the information, transmitted through the neuronal channel, is of fundamental importance for many possible neuromorphic audio signal processing techniques. First of all, cochlear prosthetic devices would clearly benefit from a better knowledge of the way auditory neurons encode audio-signals. Audio coding may also benefit from the attempt to discriminate between parts of the incoming signal on the basis of their ability to change the spike pattern of the auditory neurons. Automated speech recognition is also to gain, especially in robustness to the environment interference, due to the reasons mentioned above.

The present paper is an attempt to contribute to the understanding of the neuronal "code" for audio signals. Particularly, it is shown here that the pulse train, generated by the spiking neuron model, is, in fact, a first-order Markov chain

consisting of sub-sequences of spikes as discrete "labels" for the incoming signal on the corresponding time intervals. As it is shown here, this property is a direct result of the finite precision of the spike-registration process by the higher level auditory neurons.

The current study of the properties of the simple spiking neuron model was originated and motivated in an attempt to understand the behaviour of auditory nerve neurons. Indeed, this model is known to successfully capture the essence of spike-generation process by the auditory neurons [2]. However, the obtained results are valid in any case, where the simple phenomenological spiking neuron model is applicable.

2. THE SPIKING NEURON MODEL

Generation of spikes by the spiking neuron model (see fig.1) [14-16] is described by the following set of equations:

$$\frac{dU(t)}{dt} = -\alpha U(t) + V[X(t) - U(t)]; \qquad (1)$$
$$Y(t) = [X(t) - U(t)];$$
$$[a] = \begin{cases} 1 & if \quad a \geq 0 \\ 0 & if \quad a < 0 \end{cases};$$

i.e. the dynamic firing threshold $U(t)$ of the neuron is being reduced up to the moment, when it becomes equal to the internal activity $X(t)$. At that moment the firing threshold is rapidly increased by the amount V and the spiking neuron emits an output action potential $Y(t)$.

input X →
U →
[...]
$[X - U]$ → spikes
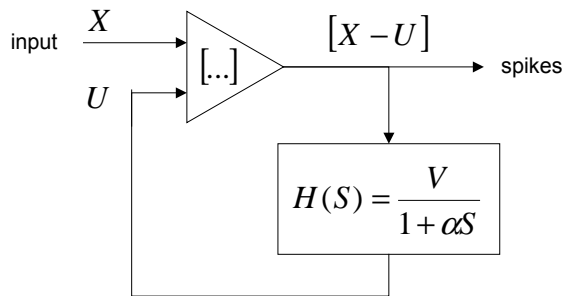$$H(S) = \frac{V}{1 + \alpha S}$$

Figure 1 - The neuronal spike generator schema

Let us assume that immediately before the spiking at "zero" time instant $t = T_0 = 0$ the neuron firing threshold is equal to ε. In accordance with the neuron properties (1), immediately after this spike it's firing threshold will be increased by V:

$$U_-(T_0) = \varepsilon \qquad U_+(T_0) = \varepsilon + V \cdot \qquad (2)$$

The values of ε and V are strictly positive parameters of the spiking neuron model.

Until the next spike ($t \in (T_0, T_1)$) the firing threshold decreases exponentially. In general case of spike sequence at the time instants $t = T_i, i = \overline{1...n}$ the firing threshold is reflected by the following expressions:

$$U_-(T_n) = \left(\varepsilon e^{\alpha T_0} + V \sum_{i=0}^{n-1} e^{\alpha T_i} \right) e^{-\alpha T_n}; \quad U_+(T_n) = \left(\varepsilon e^{\alpha T_0} + V \sum_{i=0}^{n} e^{\alpha T_i} \right) e^{-\alpha T_n}. \quad (3)$$

In the intervals $t \in (T_{n-1}, T_n)$ between the successive spikes the firing threshold $U(t)$ is expressed identically to $U_-(T_n)$, but with the appropriate change of the argument:

$$U(t) = U_+(T_{n-1}) e^{-\alpha(t - T_{n-1})} = U_-(t) = \left(\varepsilon e^{\alpha T_0} + V \sum_{i=0}^{n-1} e^{\alpha T_i} \right) e^{-\alpha t}. \qquad (4)$$

An example of the firing threshold evolution of the spiking neuron model in response to the applied signal is provided by the fig.2.
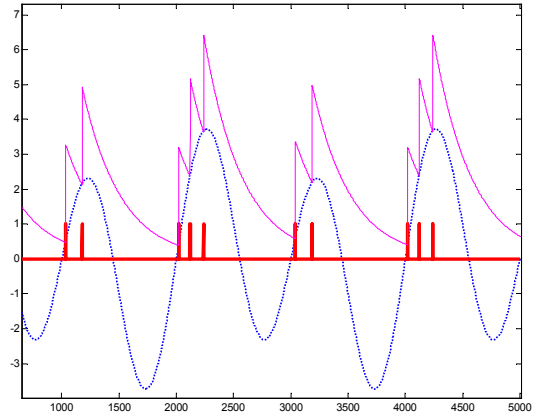

Figure 2 - Evolution of the spiking neuron model. Input signal – blue dots, output signal – red bold, internal activity – magenta line)

3. INDEPENDENCE OF FORTHCOMING SPIKE FROM THE NEURON'S INITIAL STATE

For the sake of simplicity let us assume, that the incoming signal $X(t) = X_n$ does not change on the interval $t \in [T_n - \Delta t/2, T_n + \Delta t/2]$. In practice this means that the incoming signal varies slowly in comparison with interval length Δt and may be represented by it's approximate value X_n.

The real neuron of the spiral ganglion (SG) is linked via synapses with neurons in cochlear nucleus (CN) that perform further stages of the incoming signal processing. The uncertainty of spike propagation and registration processes over this link is about $\Delta t \sim 0.5ms$ [16,17]. It means, that from the point of view of the receiving end there is no difference in which particular moment of the interval $t \in (T_n - \Delta t/2, T_n + \Delta t/2)$ the spike has occurred.

Conditions (3) and (4) reflect the influence of the neuron initial state ε on it's further activity. In accordance with these expressions the firing threshold is a function of parameters of the spiking neuron model (α, V), the initial condition ε and a sequence of the spikes preceding the current moment of time $\{T_i\}_1^{n-1} : i = \overline{1...n-1}$. The condition of independence of the spike at the time instant T_n from the initial condition $\varepsilon \in [0, E]$, for the fixed spike train $\{T_i\}_1^{n-1} : i = \overline{1...n-1}$ and the uncertainty of the spike registration Δt, is defined as follows:

$$T_n \geq T_0 + \frac{1}{\alpha} \ln \left(\frac{E}{2X_n sh(\alpha \Delta t/2)} \right). \qquad (5)$$

The reasoning, which leads to the inequality (5), is given below. From (4) it follows, that for any fixed $\varepsilon \in [0, E]$ and the constant spike sequence $\{T_i\}_1^{n-1} : i = \overline{1...n-1}$, the firing threshold $U(t) = Ce^{-\alpha t}$ is a monotonically decreasing function, where $C = \varepsilon e^{\alpha T_0} + V \sum\limits_{i=0}^{n-1} e^{\alpha T_i}$ is a constant. Further, in accordance with (1) the following inequality holds:

$$\left(X_n e^{\alpha\left(T_n - \frac{\Delta t}{2}\right)} - V\sum_{i=0}^{n-1} e^{\alpha T_i} \right) e^{-\alpha T_0} < \varepsilon < \left(X_n e^{\alpha\left(T_n + \frac{\Delta t}{2}\right)} - V\sum_{i=0}^{n-1} e^{\alpha T_i} \right) e^{-\alpha T_0}.$$

This inequality should hold for any initial condition $\varepsilon \in [0, E]$, which means that the right-hand side should be bigger than the biggest possible $\varepsilon = E$, and left-hand side should be smaller then the smallest possible $\varepsilon = 0$:

$$\left(X_n e^{\alpha\left(T_n + \frac{\Delta t}{2}\right)} - V\sum_{i=0}^{n-1} e^{\alpha T_i} \right) e^{-\alpha T_0} \geq E; \left(-X_n e^{\alpha\left(T_n - \frac{\Delta t}{2}\right)} + V\sum_{i=0}^{n-1} e^{\alpha T_i} \right) e^{-\alpha T_0} > 0.$$

Summation of both inequalities leads to the following expression:

$$X_n e^{\alpha(T_n - T_0)}\left(e^{\frac{\alpha \Delta t}{2}} - e^{-\frac{\alpha \Delta t}{2}} \right) \geq E. \tag{6}$$

The inequality (5), which defines the spike independence condition, directly follows from the above inequality.

4. CONSISTENCY OF INDEPENDENCE CONCLUSION

Lemma. If the impulse of the spiking neuron model at the time instant T_n does not depend upon initial condition ε, then all subsequent impulses $T_k, k > n$ are independent from this condition.

□

As it is evident from (1) for the action potential to appear the following condition should hold:

$$X_{n+1} \geq (X_n + V)e^{-\alpha(T_{n+1} - T_n)}. \tag{7}$$

Substitution of the condition on X_n, obtained from (6)

$$X_n \geq \frac{E}{2sh(\alpha \Delta t/2)} e^{-\alpha(T_n - T_0)} \tag{8}$$

into inequality (7) gives the following result:

$$X_{n+1} \geq \left(\frac{E}{2sh(\alpha \Delta t/2)} e^{-\alpha(T_n - T_0)} + V \right) e^{-\alpha(T_{n+1} - T_n)} > \frac{E}{2sh(\alpha \Delta t/2)} e^{-\alpha(T_{n+1} - T_0)}$$

This formula is a similar condition to (8), but it is formulated for the impulse in the time instant T_{n+1}. Subsequent recursive application of this result gives a statement, that for any $T_k, k > n$ the present lemma holds true.

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5. DEPENDENCY INTERVAL LENGTH

As a matter of fact, the logarithm in (5) reflects the time-difference between the two time instants T_n and T_0. The initial condition ε, in accordance with (2), reflects the total firing threshold immediately before the spike at the time instant T_0. This total firing threshold may reflect not only the "true" initial condition, but also a cumulative effect of all spikes, preceding the time instant T_0. The initial time instant T_0 should not necessarily coincide with the time scale zero

point. It is only remarkable for the fact, that this is the most ancient spike, which still affects the present spike generation at the time instant T_n. It is also the closest spike to a present one, which is in the past at least by the time difference

$$\tau_n(E, X_n) = \frac{1}{\alpha}\left\{ \ln\left(\frac{E}{X_n} \right) - \ln\left(2sh\left(\frac{\alpha \Delta t}{2} \right) \right) \right\}, \tag{9}$$

which we'll further denote as the minimum dependency interval τ_n for the spike at the time instance T_n.

Further, instead of the term T_0, reflecting the most ancient, but still significant impulse for the spike at the time T_n, the term T_{n-h_n} will be used. This change in notation is convenient since it removes an association between particular T_n and the length of the dependency interval τ_n.

Remarkably, the interval length does not depend upon the recharging magnitude constant V. Another particularly notable property of the dependency interval is a possibility to estimate it's length with a certain predefined confidence. Let us assume that the initial condition ε will not exceed the boundary E with a probability $P(\varepsilon \leq E)$, then with the same probability all history prior to the impulse T_0 will not affect the current impulse. Obviously, the formula (9) is meaningful, when

$$E > 2sh\left(\frac{\alpha \Delta t}{2} \right) X_n, \tag{10}$$

otherwise τ_n should be regarded as zero.

In reality the dependency interval should be somewhat bigger than τ_n, since it spans up to the impulse immediately preceding the time instant $-\tau_n$ (if zero of the time scale coincides with the present). Theoretically the maximum dependency interval might be infinite, but in this case there should not be any spikes before $-\tau_n$. However in practice one can disregard such unrealistic scenario (since it is a spiking rather than silent neuron, which is of interest) and consider the maximum dependency interval $(T_0 - T_{n-h_n})$ to be finite, but somewhat bigger than the minimum value.

6. SPIKE SEQUENCE AS A FIRST-ORDER MARKOV CHAIN

As it was shown above, for any spike at the certain time instance T_n it is possible to choose a finite spike history span $\{T_i\}_{n-h_n}^{n-1} : i = \overline{n - h_n ... n - 1}$, which will contain all possible factors that affect the current impulse. The current impulse T_n is not dependent on whatever has happened before T_{n-h_n}, this irrelevant history is cumulatively denoted as $\varepsilon_n \in [0, E]$. It is assumed that precision Δt and initial condition boundary E are fixed and known.

Then the full probability of the spike sequence $\{T\}_0^n = \{T_i\} : i = \overline{0...n}$ is expressed as:

$$P(\{T\}_0^n) = P(T_n \mid \{T\}_{n-h_n}^{n-1}) * ... * P(T_{k+1} \mid \{T\}_{k-h_{k+1}}^k) * \tag{11}$$
$$* P(T_k \mid \{T\}_{k-h_k}^{k-1}) * ... * P(T_0 \mid \varepsilon_0) * P(\varepsilon_0)$$

At the sequence beginning, when $m - h_m \leq 0$ there exists a dependency upon the "true initial" value ε_0. Further along the sequence, when $m - h_m > 0$, there is only a need to estimate the probabilities of the form $P(T_m \mid \{T\}_{m-h_m}^{m-1})$. The se-

quence in (11) is a variable-order Markov sequence since history length h_m is bounded and after certain finite sequence is smaller than the current index m. But this relevant history length is varying through time. Dependency intervals $\{T\}_{m-h_m}^{m-1}$ and $\{T\}_{m+1-h_{m+1}}^{m}$ of successive impulses are overlapped in general case.

Let us choose an arbitrary spike in the sequence at the time instance T_k. As the dependency interval is always finite, there must be the most early spike $T_m, m > k$, such that it's position is independent upon anything happening before T_k.
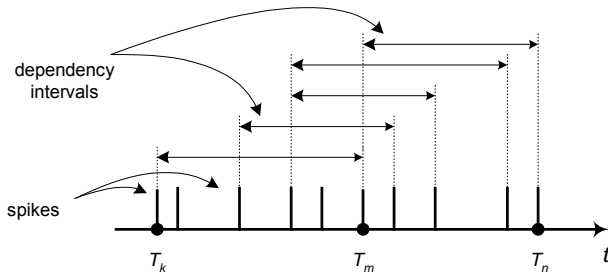

Figure 3 – Spikes and their maximal dependency intervals

Let us further choose the earliest spike at the moment $T_n, n > m$, so that it's position is only dependent upon history including and after the moment T_m (see fig. 3 for illustration).

On the basis of the proved lemma one may easily conclude, that dependency intervals of all spikes $T_j : m \le j < n$ lay inside time interval between T_k and T_{j-1}. All spikes $T_l : l > n$ will obviously be independent upon the history before T_m.

The dependency interval of the compound event is a superposition of the dependency intervals of it's elementary events. Subsequently, one may write the following statement for the fragments $\{T\}_k^{m-1}$ and $\{T\}_m^{n-1}$ of the original spike sequence:

$$P\left(\{T\}_m^{n-1} \mid \{T\}_0^{m-1}\right) = P\left(\{T\}_m^{n-1} \mid \{T\}_k^{m-1}\right).$$

Recursive application of the above reasoning leads to the conclusion that it is possible to rewrite formula (11) in the following form:

$$P(\{T\}_0^n) = P(\{T\}_{m+1}^n \mid \{T\}_{k+1}^m) * \ldots \qquad , \quad (12)$$
$$* P(\{T\}_a^{a+b-1} \mid \{T\}_0^{a-1}) * P(\{T\}_0^{a-1} \mid \varepsilon_0) * P(\varepsilon_0)$$

where indexes $a, b, \ldots, k, m, n$ define the appropriate fragmentation of the original spike train into sub-sequences, which form the first-order Markov chain. A complete set of all possible sub-sequences defines an alphabet of the Markov source.

Each of the sub-sequences is in fact a vector Λ of discrete integer values of the form

$$\lambda_n = \left\lfloor (T_n - T_{n-1})/\Delta t \right\rfloor,$$

because of the finite precision of the spike registration. Here the term $\lfloor\ \rfloor$ denotes a floor operation. In accordance with the rule of spike generation (1) these vectors represent an irregularly under-sampled representation of the corresponding input signal frame. The rule of sample selection, as it obviously follows from (1), (3) and (4), links the inter-spike

intervals (i.e. inter-sample intervals) and amplitudes of the incoming signal at the moment of the spike (sample):

$$X_n = (X_{n-1} + V)e^{-\alpha(T_n - T_{n-1})}.$$

The combination of the two above equations allows to express the vector components through the amplitudes of the input signal at the moment of spikes:

$$\lambda_n = \left\lfloor \frac{\ln(X_{n-1} + V) - \ln(X_n)}{\alpha \Delta t} \right\rfloor.$$

7. PROPERIES OF THE AUDITORY SPIKING NEURON AS A MARKOV SOURSE

The tasks of quantification of the information transfer through the neural connection and assessment of the degree of surprise to encounter a particular sequence of spikes demand estimation of the spike-train probabilities.

In order to have a principal possibility to estimate the probability of the particular spike sequence, i.e. the inverse of the degree of surprise, in accordance with (12) one needs an estimate of the transition matrix, which characterizes this particular first-order Markov source:

$$A = \left| a_{ij} \right| = \left| P(\Lambda_i \mid \Lambda_j) \right|$$

and a knowledge of the appropriate factorisation of the spike sequence of the observed neuron.

The real CN neuron, receiving the output of the SG neuron, sees only inter-spike intervals as the source of information about the incoming stimulation. As it was established above, this sequence can be reduced to the first-order Markov chain to the extent of validity of the spiking neuron model. But the appropriate segmentation needs to be somehow communicated from the SG neuron to the information receiving end in the CN.

Let us assume that the SG neuron under consideration emits impulses for a quite long time for initial conditions to become irrelevant. In this situation there is no any special "anchor" point to start decomposition of the spike train into the Markov chain. As a matter of fact, there exist multiple ways to decompose spike train with the formula (12). The difference is introduced by the specific choice of the starting point T_k of the chain. Further tracking of the possible Markov chains results in the observation that they tend to converge to the single possible chain if there exists such situation, when $\tau_n < T_n - T_{n-1}$, i.e. if a single-value vector occurs. In accordance with the formulae (9) and (10) this situation becomes possible if the current value of the incoming signal becomes large in comparison with the expected maximal initial condition E.

It is a remarkable coincidence, that AGC of the chemical synapse between IHC and the afferent neural fiber in the cochlea emphasizes transient processes in the incoming signal [11]. In hearing physiology this phenomenon is known as IHC adaptation. The immediate neurotransmitter release rate in response to just-applied stimulation is much higher than it's equilibrium rate for the same stimulus intensity. The particularly strong and short in duration emphasis of the incoming signal is observed in the synapses with high-spontaneous spiking rate fibers. The present analysis shows that, besides of having other useful properties [11], the adap-

tation mechanism possibly serves as a tool to synchronize the receiving neurons with the certain "true" spike train decomposition.

8.   CONCLUSION

The analysis of the spiking neuron model results in the conclusion that it is possible to represent its spike train as a first-order Markov chain, consisting of the non-overlapping sub-sequences of spikes. Superposition of these elementary sub-sequences constitutes to the entire sequence. This result suggests a possible encoding method of the input stimulation by the auditory neuron – each elementary subsequence is a vector of integers, describing an irregularly undersampled representation of the corresponding incoming signal frame. The particular form of each vector is dependent only upon the current frame of the input signal and the immediately preceding vector.

There exists an important synergy between the properties of "hair cell – auditory nerve" synapse and the proposed coding scheme. Indeed, the adaptive response of the IHC tends to produce a condition for a single-value representation-vector during the transient regions of the incoming signal and, thus, to synchronize various possible decompositions of the spike train with an "ideal" one.

The fact, that the spiking neuron represents a true first-order Markov source, implies that there is no need to gather a higher order statistics to estimate probabilities of the particular spike train. To do this one needs only a square matrix of conditional probabilities and access to an optimal spike-train segmentation.

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