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A multi-timescale adaptive threshold model for the SAI tactile afferent to predict response to mechanical vibration

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Abstract

The Leaky Integrate and Fire (LIF) model of a neuron is one of the best known models for a spiking neuron. A current limitation of the LIF model is that it may not accurately reproduce the dynamics of an action potential. There have recently been some studies suggesting that a LIF coupled with a multi-timescale adaptive threshold (MAT) may increase LIF's accuracy in predicting spikes in cortical neurons. We propose a mechanotransduction process coupled with a LIF model with multi-timescale adaptive threshold to model slowly adapting type I (SAI) mechanoreceptor in monkey's glabrous skin. In order to test the performance of the model, the spike timings predicted by this MAT model are compared with neural data. We also test a fixed threshold variant of the model by comparing its outcome with the neural data. Initial results indicate that the MAT model predicts spike timings better than a fixed threshold LIF model only.

I. Introduction

Modeling of tactile mechanoreceptors such as the SAI holds important implications for the next generation neural prosthetics. Several researchers have modeled the responses of tactile afferents in response to static and vibratory indentations. Freeman and Johnson's model of the SAI [1] was one of the earliest models used to simulate the mechanoreceptive properties of the SAI afferent. Slavik and Bell [2] showed that adding hyper-excitability and an absolute refractory period to the Freeman and Johnson's model increased the match between the neural data and model data but that the two processes worked against each other. Looft [3] came up with a threshold related to position-velocity-acceleration function to improve the performance of the Freeman and Johnson's model. It was later shown by Bensmaia [4] that Looft's model would be incompatible with observed responses of rapidly adapting (RA) afferents to step indentation. Some recent models of the SAI afferent include a finite element model employing a sigmoidal mechanotransduction process coupled with a LIF [5], a current related to derivatives of force mechanotransduction process coupled with a LIF [6] and a temporal LIF model driven by four inputs, indentation depth, velocity, acceleration and jerk combined with a spatial model [7]. Because of the type of mechanotransduction process used in some of the models, the model may not predict correct spike timings for all indentation types. In some other cases, the number of free parameters in the system may be quite high, creating the potential for difficulty in authenticating their fitting. Since the multi-timescale adaptive threshold model is driven by two equations, one for membrane potential and one for voltage threshold, it retains some of the complexity of a higher order system such as a neuron as opposed to LIF only but at the same time the two equations interact in a piecewise iteration process so as to keep the free parameters of the system low, eleven in this study, in number.

II. THEORY

Neuron models can be broadly classified under two categories, biophysical or phenomenological [8]. Biophysical models such as the Hodgkin-Huxley (H-H) model of the squid axon [9] tend to be conductance based and consist of a set of equations describing the kinetics of the ionic channels. On the other hand, phenomenological models such as the LIF model are based upon experimental results and use simple mathematical formulations to depict the working of a neuron. Some notable phenomenological models include Fitzhugh-Nagumo model [10], Izhikevich model of a cortical neuron [11] and Brette and Gerstner's Adaptive Exponential Integrate and Fire model [12].

Abbott and Kepler [13] reduced the H-H model to a set of two first order ordinary differential equations. In the same research, they provided some of the missing links between the H-H model and some of the phenomenological models such as LIF and FitzHugh-Nagumo. An important takeaway message from this reduction and what Slavik and Bell [2] had done was to recognize the importance of having an absolute refractory period in the LIF. To improve upon his previous threshold function [3], Looft made the threshold, in the Freeman Johnson's model, variable [14]. Results indicated that a better match between neural and model data was achievable with a variable threshold. Later on Kobayashi's multi-adaptive threshold (MAT) model [15] for a neuron predicted 81.6% of spike times [16]. Kobayashi's model and Looft's model were similar in the sense that they had multiple time constants for the adaptive threshold. They were different in the sense that Looft used the Freeman Johnson's conductance based representation of LIF. Another difference was that the membrane potential in Kobayashi's model did not fully reset to zero whereas Looft's membrane potential reset to zero after an action potential.

In order to test the MAT concept in SAI, we decided to couple a mechanotransduction process with a resetting multi-adaptive LIF with two time constants. We think that adding a smaller and a larger time constant would perhaps account for the fast and slow ionic processes that happen during an action potential and could perhaps increase the model's ability to predict a spike as compared with a fixed threshold LIF model.

III. METHODS

A. Model

Our model presented herein of a single SAI afferent has two parts. The first part of the model represents the mechanotransduction of the sinusoidal mechanical stimulus to a transducer current. It has been shown in adult inner hair cells [17] that a sigmoidal function can represent the transduction from basilar membrane vibration to a transducer current. We use the following function for the transduction process:

$$I = \frac{I_{max}}{\left(1 + \exp\left[\frac{x_1 - x}{\alpha}\right]\right)} \quad (1)$$

where x is a half sinusoid composed of positive mechanical indentation only and I_{max} , x_1 and α are the free parameters for the transduction process in our model and their values are shown in Table 1.

The LIF process is represented by the following equation:

$$\tau_m \frac{dV}{dt} = -V + RI \quad (2)$$

where τ_m is the membrane time constant, V is the membrane potential, R is the membrane resistance and I is the transduction current. τ_m and R are the free parameters for the LIF process in our model and their values are shown in Table 1.

We used the following two equations used for calculation of membrane potential and adaptive threshold:

$$V_{n+1} = V_n \exp\left(-\frac{\Delta t}{\tau_m}\right) + RI(1 - \exp\left(-\frac{\Delta t}{\tau_m}\right)) \quad (3)$$

$$Vth_{n+1} = Vth_{resting} + A_1 \Delta V \exp\left(-\frac{t-t_{ap}}{\tau_1}\right) + A_2 \Delta V \exp\left(-\frac{t-t_{ap}}{\tau_2}\right) \quad (4)$$

where V is the membrane voltage, $Vth_{resting}$ is the resting value for threshold Vth , ΔV is the amount by which Vth gets elevated after each action potential, Δt is the time step for iteration which was fixed at .01 ms, t_{ap} is the time of the last action potential, τ_1 and τ_2 are the two time constants for the MAT process and A_1 and A_2 are their weights respectively. The absolute refractory period after an action potential is fixed at 200 ms. $Vth_{resting}$, ΔV , τ_1 , A_1 , τ_2 and A_2 are the free parameters for the MAT process and their values are shown in Table 1.

B. Numerical Experiments

The model was run in response to a 10 Hz, 30 Hz and 50 Hz mechanical sinusoidal stimuli for both fixed threshold and adaptive threshold cases. The fixed threshold case utilizes equations (1) and (3) and a fixed threshold of 70 mV. The model has 6 degrees of freedom for a fixed threshold case consisting of I_{max} , x_1 , α , τ_m , R and $Vth_{resting}$. For a MAT case the model has an additional 5 degrees of freedom consisting of ΔV , τ_1 , τ_2 , A_1 and A_2 . The values used for the free parameters of the transduction process were taken from the final fit from [5]. R 's value was taken from [15]. τ_m , $Vth_{resting}$ and ΔV were chosen arbitrarily to maximize model's performance for 10 Hz. The MAT time constants were taken from the final fit for Looft's model [14]. Figure 1 shows the state flow diagram for an adaptive threshold. The fixed threshold case is represented by a similar process with the difference that V is not elevated by ΔV .

A coincidence factor [18], [19], [20] method was used to evaluate the performance of the model in predicting spike timings for both the fixed threshold and multi-timescale adaptive threshold cases. The Coincidence Factor is given by:

$$\Gamma = \frac{N_{coinc} - \langle N_{coinc} \rangle}{N_1 + N_2} \times \frac{2}{1 - 2v\delta} \quad (5)$$

where N_1 and N_2 , respectively, represent the numbers of spikes in the reference train and the data to be compared, N_{coinc} is the number of coincident spikes with an allowable range of $\delta = 5$ ms. $\langle N_{coinc} \rangle$ is the expected number of coincidences between the reference train and the random Poisson spikes of the given rate $v = N_1/T$ (where T is the duration of the experiment), $\langle N_{coinc} \rangle = 2v\delta N_1$. The coefficient takes a value close to zero for mutually

independent spike trains. A value of 1 predicts optimal performance by the model. Table 2 lists the coefficient factors for fixed threshold and adaptive threshold cases for the three different frequencies of 10 Hz, 30 Hz and 50 Hz.

IV. Results

Figure 2 show the position, current (I), membrane potential V, threshold voltage V_{th} , neural spike timings and model spike timings plotted vs. time for a 10 Hz input stimulation for a MAT variant of the system. Figure 3 show position, I, V, neural spike timings and model spike timings for a fixed threshold at 70 mV for 10 Hz sinusoid.

V. Discussion

We tested the MAT model to predict spike timings for a SAI afferent in response to a mechanical sinusoidal stimulus. Our purpose was to do a qualitative comparison of the MAT model versus a fixed threshold model and to use the coincidence factor to quantitatively compare the results of the two models. Table 2 indicates that the coincidence factor for the MAT was slightly superior to the fixed threshold for any given frequency. An average improvement of the MAT system over the fixed threshold was 17%. In order to limit the degrees of freedom of the model, we tried to use tested values of the free parameters. Since these imported values may not be unique in the studies they were used in, there is a high possibility that we could improve the functioning of our model by fine tuning these parameters. We also reset the membrane potential to zero after an action potential as in Looft [14] as opposed to Kobayashi et al. [15] in which V gets reduced by a fixed amount after every action potential. If the quantity by which the membrane potential is reduced after an action potential is introduced as another free parameter in the MAT model, it may improve spike prediction of the model. We may also add another time constant into the adaptive threshold model thus making it a MAT3 model [15] and tune those constants to perhaps better approximate the time constants of the various ionic currents during and after an action potential. Standage and Trappenberg [21] have shown in order for LIF to better approximate a conductance based model such as an H-H model there should either be a variable threshold or a dynamic time scale parameter. We feel that the dynamic time scale parameter is something that should be further looked into since it might compensate for the frequency dependence of the model. Furthermore, Machery et al. [8] have shown a dependence of threshold on frequency for an auditory nerve model. We think quite a similar process exists in the SAI afferent where either the membrane time constant or the voltage threshold or both need to be a function of the input frequency, besides incorporating the MAT time constants for the model, to match the actual and model data at all frequencies.

VI. Conclusion

We have tested a multi-timescale adaptive threshold (MAT) model for a SAI afferent and compared its results with fixed threshold model. Initial results suggest that the coincidence factors for MAT are slightly superior to the fixed threshold SAI model. We need to further study the frequency dependence of the model and fine tune the MAT time constants for better approximation between the model and neural data.

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Fig 1.
Process Flow Diagram for MAT

Fig 2.
Plot of position, current (I), membrane potential (V), threshold voltage (V_{th}), spike timings for neural data and model. A 1 on the y-axis for the spike plots indicates the occurrence of an action potential

Fig 3. Plot of position, current (I), membrane potential (V), spike timings for the neural data and model. A 1 on the y-axis for the spike plots indicates the occurrence of an action potential

Table 1

Free Parameters

Symbol	Quantity	Units
$I_{\max}$	1.46e-5	mA
x_1	513.72	μm
α	272.257	μm
τ_m	50	ms
R	50	$\text{M}\Omega$
$V_{\text{th_resting}}$	70	mV
ΔV	10	mV
τ_1	3.56	ms
τ_2	38	ms
A_1	1.95	
A_2	1.37	

Table 2Coincidence Factor Γ

Mechanical Frequency	Fixed Threshold Model vs. Data	MAT Model vs. Data
10 Hz	0.4065	0.5306
30 Hz	0.474	0.514
50 Hz	0.5185	0.5833