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EFFECT OF CELLULAR MEMBRANE RESISTIVITY INHOMOGENEITY ON THE THERMAL NOISE-LIMIT

Gyula Vincze, Andras Szasz
St. Istvan University, Dept. Biotechnics, Hungary
biotech@gek.szie.hu

ABSTRACT

Our objective is to generalize the Weaver-Astumian (WA) and Kaune (KA) models of thermal noise limit to the case of cellular membrane resistivity asymmetry. The asymmetry of resistivity causes different effects in the two models. In the KA model, asymmetry decreases the characteristic field strength of the thermal limit over and increases it below the breaking frequency ($\omega_0 = \tau_m^{-1}$), while asymmetry decreases the spectral field strength of the thermal noise limit at all frequencies. We show that asymmetry does not change the character of the models, showing the absence of thermal noise limit at high and low frequencies in WA and KA models, respectively.

Key words

membrane inhomogeneity, noise-limit, Weaver-Astumian-model, Kaune-model, Twiss's-theorem

Academic Discipline And Sub-Disciplines

Biophysics

TYPE (METHOD/APPROACH)

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INTRODUCTION

There are long-time debates about the thermal noise limit in the cellular membrane [1], [2], [3], [4]. As we presented in one of our earlier works [5], the Weaver-Astumian (WA) model [1] and the Kaune-modification (KA) [3] could be described in an integrative manner by the method of symmetric components [6]. The method was further developed and significantly simplified [7].

Membrane homogeneity is a rough simplification of the membrane reality, which has multiple clusters of transmembrane proteins (membrane rafts [8]) and could be changed by various diseases [9]. In addition, membrane resistivity differs robustly in the cancerous state from that of the healthy membrane condition [10]. Membrane rafts are novel targets of cancer therapies [11]. Membrane rafts have many specialized proteins involved in sensory mechanisms [12] as well as cell-cell connections, which could change the conductivity of the spot [13], leading to drastic changes in the thermal noise limit [14].

Our objective is to generalize these models, keeping their physical meaning, but questioning the effects of inhomogeneity of the membranes, which is caused by rafts that are present on them.

The symmetrical component networks of a symmetrical membrane

In constructing the simple model, we first investigate a two-segment situation, in which the segments are identical in their physical parameters. The model circuit of this looks as shown in fig.1. [3].

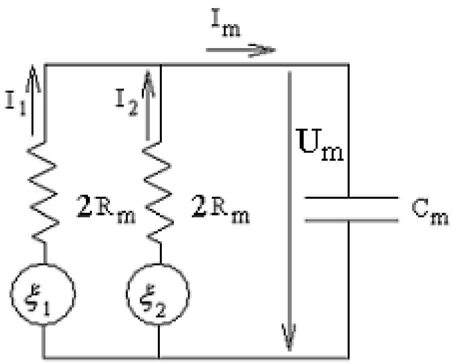

Figure 1. Equivalent circuit of membrane approximated by two segments, where R_m is the resistivity, C_m the capacity of the membrane and ξ_1, ξ_2 are the noise potentials originating from the individual segments.

For the Fourier transforms of noise potential, the Kirchhoff's equations can be written

$$\xi_1 = \left(2R_m + \frac{1}{j\omega C_m}\right) I_1 + \frac{1}{j\omega C_m} I_2, \qquad (1)$$

$$\xi_2 = \frac{1}{j\omega C_m} I_1 + \left(2R_m + \frac{1}{j\omega C_m}\right) I_2$$

and may also be expressed in the following matrix form:

$$\bar{\xi} = \begin{bmatrix} \xi_1 \\ \xi_2 \end{bmatrix} = \begin{bmatrix} 2R_m + \frac{1}{j\omega C_m} & \frac{1}{j\omega C_m} \\ \frac{1}{j\omega C_m} & 2R_m + \frac{1}{j\omega C_m} \end{bmatrix} \begin{bmatrix} I_1 \\ I_2 \end{bmatrix} = \bar{\bar{Z}}\bar{I} \qquad (2)$$

Let us calculate the spectral energy distribution from the Nyquist-Twiss law [15].

$$\bar{\xi}\bar{\xi}^{*T} = \begin{bmatrix} \xi_1\xi_1^* & \xi_1\xi_2^* \\ \xi_2\xi_1^* & \xi_2\xi_2^* \end{bmatrix} = 2kT\left(\bar{\bar{Z}} + \bar{\bar{Z}}^{*T}\right) = \begin{bmatrix} 8kTR_m & 0 \\ 0 & 8kTR_m \end{bmatrix} \qquad (3)$$

Therefore, the noise potentials of each segment are independent.

Let us perform the decomposition into symmetrical components in accordance with Kirchhoff equations (1) in a descriptive way. It is easy to see that the equations

$$\begin{aligned} \xi_s^0 &:= \frac{\xi_1 + \xi_2}{\sqrt{2}} = 2R_m \frac{1 + j\omega\tau_m}{j\omega\tau_m} \frac{I_1 + I_2}{\sqrt{2}} = Z_0^s I_0^s \\ \xi_s^1 &:= \frac{\xi_1 - \xi_2}{\sqrt{2}} = 2R_m \frac{I_1 - I_2}{\sqrt{2}} = Z_1^s I_0^s \end{aligned} \qquad (4)$$

follow from (1), and these are the symmetrical components.

The equivalent circuit of symmetrical component networks is set forth in the following figure.

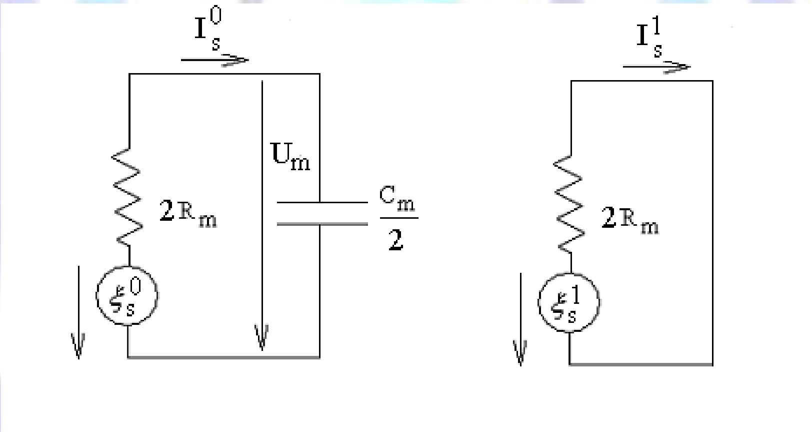

Figure 2. Symmetrical component networks of the membrane

From Nyquist's law, we may calculate the spectral power density of the symmetrical components of noise potentials.

$$\begin{aligned} \xi_s^0 \xi_s^{0*} &= 8kTR_m \\ \xi_s^1 \xi_s^{1*} &= 8kTR_m \end{aligned} \qquad (5)$$

We may see that the symmetrical component transformation did not change the spectral power densities.

Connection of the WA and KA models with symmetric components

Accordant to the WA model, for the calculation of the effective field strength, we shall specify the double value of the spectral power density of the capacitor of a zero sequence equivalent circuit. In accordance with Figure 2.

$$\left|E_{netWA}\right|^2 = \frac{\frac{C_m}{2} U_m U_m^*}{A_m d_m \varepsilon} = \frac{1}{2d_m^2}\left(I_0^s \frac{1}{j\omega \frac{C_m}{2}}\right)\left(I_0^s \frac{1}{j\omega \frac{C_m}{2}}\right)^* = \tag{6}$$

$$= \frac{1}{2d_m^2}\left(\frac{\xi_s^0}{Z_s^0} \frac{1}{j\omega \frac{C_m}{2}}\right)\left(\frac{\xi_s^0}{Z_s^0} \frac{1}{j\omega \frac{C_m}{2}}\right)^* = \frac{1}{2d_m^2}\frac{\xi_s^0 \xi_s^0}{1+\omega^2\tau_m^2} =$$

$$= \frac{1}{2d_m^2}\frac{8kTR_m}{1+\omega^2\tau_m^2} = \frac{4kT}{\sigma_m d_m A_m}\frac{1}{1+\omega^2\tau_m^2}$$

where we applied the relationships (4) and (5).

Let us specify the Kaune field strength from the dissipated power generated on the resistances of the equivalent circuit.

In the equivalent circuit of zero sequence

$$\left|E^0{}_{netKaune}\right|^2 = \frac{2R_m I_0^s I_0^{s*}}{A_m d_m \sigma_m} = \tag{7}$$

$$= \frac{2R_m}{A_m \sigma_m d_m}\left(\frac{\xi_s^0}{Z_s^0}\right)\left(\frac{\xi_s^0}{Z_s^0}\right)^* = \frac{2R_m}{A_m \sigma_m d_m}\frac{\xi_s^0 \xi_s^0 \omega^2\tau_m^2}{4R_m^2\left(1+\omega^2\tau_m^2\right)} = \frac{4kT}{\sigma_m d_m A_m}\frac{\omega^2\tau_m^2}{\left(1+\omega^2\tau_m^2\right)}$$

$$= \frac{1}{2d_m^2}\frac{8kTR_m}{1+\omega^2\tau_m^2} = \frac{4kT}{\sigma_m d_m A_m}\frac{1}{1+\omega^2\tau_m^2}$$

which conforms to the result of Kaune where we applied the relationships (4) and (5).

We get the field strength in the first sequence equivalent circuit from the relationships (4) and (5).

$$\left|E^1{}_{netKaune}\right|^2 = \frac{2R_m I_s^1 I_s^{1*}}{A_m d_m \sigma_m} = \frac{2R_m}{A_m \sigma_m d_m}\left(\frac{\xi_s^0}{Z_s^1}\right)\left(\frac{\xi_s^0}{Z_s^1}\right)^* = \frac{2R_m}{A_m \sigma_m d_m}\frac{\xi_s^0 \xi_s^0}{4R_m^2} = \frac{4kT}{\sigma_m d_m}\ldots \tag{8}$$

We shall observe that these results seem not to be dependent on the number of membrane segments.

In reality, the number of symmetrical components is identical to the number of membrane segments.

This means that the white noise of form (7) appears in each component.

Thermal noise models of the asymmetric membrane

A criticisable point of the Kaune treatment is that it sets out from membrane segments of the same properties, and it is not clear in what way it is possible to extend the theory to a membrane consisting of different segments. The method described below can be applied in this case as well.

We are dealing with a membrane consisting of segments of different electrical properties (for example, because of an illness).

Next, for the sake of simplicity and demonstration we are going to examine a two-segment membrane.

The equivalent circuit of membrane can be seen in the following picture.

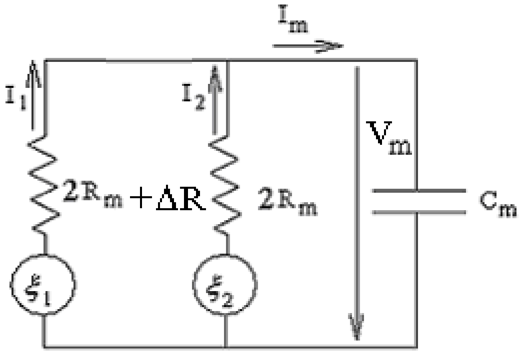

Figure 3. Equivalent circuit of membrane approximated by two segments and having resistance failure

Let us formulate the Kirchhoff equations for the Fourier transforms of noise quantities:

$$\xi_1 = I_1(2R_m + \frac{1}{j\omega C_m}) + I_2\frac{1}{j\omega C_m} + I_1\Delta R,$$
$$\xi_2 = I_1\frac{1}{j\omega C_m} + I_2(2R_m + \frac{1}{j\omega C_m}) \quad (9)$$

Let us introduce for these the symmetrical components as described above:

$$\xi_0^s = I_0^s\left[2R_m(1+\frac{1}{j\omega\tau_m}) + \frac{\Delta R}{2}\right] + I_1^s\frac{\Delta R}{2}$$
$$\xi_1^s = I_0^s\frac{\Delta R}{2} + I_1^s\left[2R_m + \frac{\Delta R}{2}\right] \quad (10)$$

The equivalent circuit from Figure 4 can be attached to the equations.

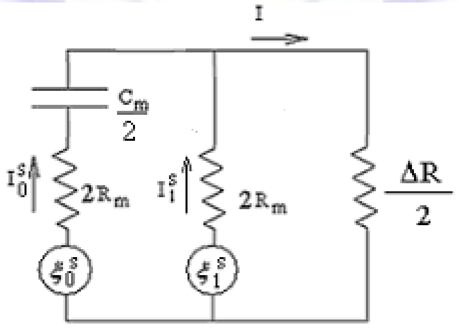

Figure 4. Equivalent circuit of faulty membrane represented by symmetrical component networks

The above equations can be written in matrix form as follows:

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$$\begin{bmatrix}\xi_0^s\\ \xi_1^s\end{bmatrix}=\begin{bmatrix}2R_m(1+\frac{1}{j\omega\tau_m}+\frac{\Delta R}{4R_m}) & \frac{\Delta R}{2}\\ \frac{\Delta R}{2} & 2R_m(1+\frac{\Delta R}{4R_m})\end{bmatrix}\begin{bmatrix}I_0^s\\ I_1^s\end{bmatrix}=\overline{\overline{Z}}\begin{bmatrix}I_0^s\\ I_1^s\end{bmatrix} \tag{11}$$

From the impedance matrix we may specify the spectral power density of noise potential by using the Twiss theorem.

$$\begin{bmatrix}\xi_0^s\xi_0^{s*} & \xi_0^s\xi_1^{s*}\\ \xi_1^s\xi_0^{s*} & \xi_1^s\xi_1^{s*}\end{bmatrix}=2kT\begin{bmatrix}4R_m(1+\frac{\Delta R}{4R_m}) & \Delta R\\ \Delta R & 4R_m(1+\frac{\Delta R}{4R_m})\end{bmatrix} \tag{12}$$

Now, we see that the noise potentials are correlated!

Let us formulate the assumption of Kaune [3] as follows: the effective field strength dissipates the same energy in the cellular membrane as the zero sequence current on the resistance of zero sequence circuit, namely $E_{net}^2=\frac{I_0^{s2}\,2R_m}{\sigma_m A_m d_m}$.

For this we have to specify the zero sequence current from (11). Then we get that

$$I_0^s=\frac{\xi_0^s}{2R_m(1+\frac{1}{j\omega\tau_m}+\frac{\Delta R}{4R_m})}-\frac{\xi_1^s}{4R_m^2(1+\frac{1}{j\omega\tau_m}+\frac{\Delta R}{4R_m})(1+\frac{\Delta R}{4R_m})}\frac{\Delta R}{2} \tag{13}$$

We get the result from (12) (13) and from the above assumption of Kaune by taking into account the order of magnitude:

$$\left|\overline{E_{netKau}^2}\right|=\frac{4kT}{\sigma_m A_m d_m}\frac{(1+\alpha)^2\omega^2\tau_m^2}{1+(1+\alpha)^2\omega^2\tau_m^2}(1-\frac{\alpha^2}{(1+\alpha)^2}), \tag{14}$$

$$\alpha=\frac{\Delta R}{4R_m}$$

Applying the WA model, we get the following result:

$$\left|\overline{E_{netWA}^2}\right|=\frac{4kT}{\sigma_m A_m d_m}\frac{1}{1+(1+\alpha)^2\omega^2\tau_m^2}(1-\frac{\alpha^2}{(1+\alpha)^2}) \tag{15}$$

Consequently, the resistance failure of the membrane decreases the effective field strength.

It could be shown by analogy with the above, that when a membrane having N segments where the resistivity of one of those is higher by ΔR, $\alpha=\Delta R/N^2R_m$. Consequently, the effect of asymmetry by increasing the number of segments by N of segments decreases.

The next two figures show the $\sqrt{\left|E_{net}^2\right| / \frac{4kT}{\sigma_m A_m d_m}}$ normalized spectral value of these field strengths as a function of normalized frequency and in two different areas. The ratio of resistances is $\alpha = \Delta R / 4R_m = 0.3$ on the figures.

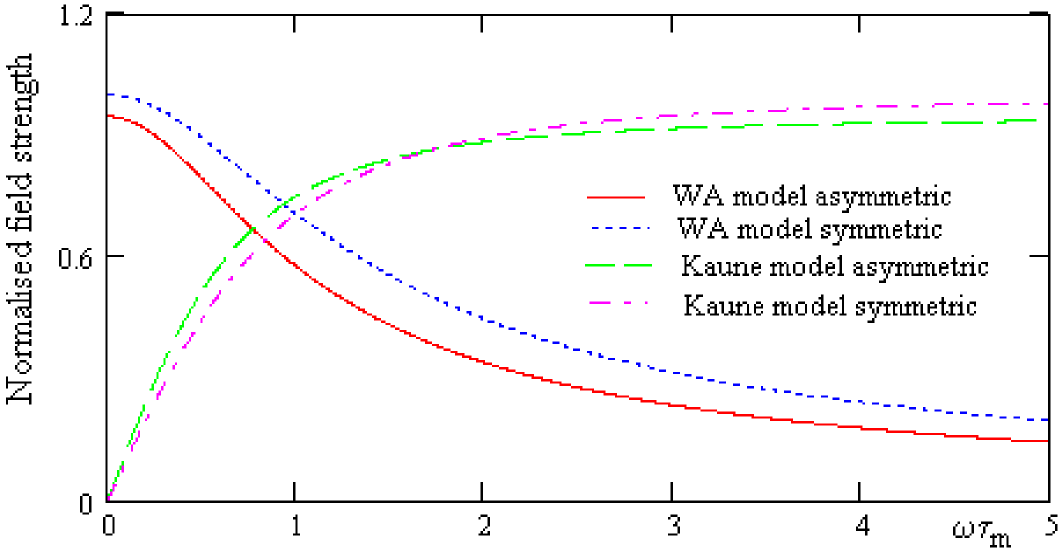

Figure 5. Normalized field strength as a function of normalized frequency

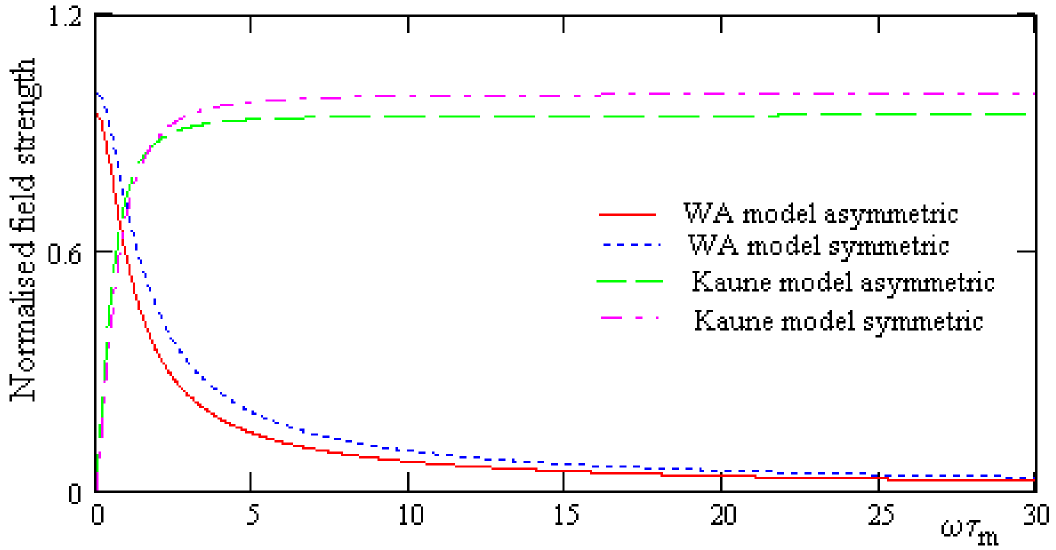

Figure 6. Normalized field strength as a function of normalized frequency in a larger area

DISCUSSION

We have shown that both KA and WA models can be generalized to cases where membrane resistivity is asymmetric.

In the case of faulty membrane resistance, not only the zero but also the first symmetrical components influence the course of the effective field strength. Asymmetry causes different effects in the two models.

The change in field strength of the noise limit in the KA model grows under the $\omega_0 = \tau_m^{-1}$ break-point frequency, while the above does the opposite. However, in the WA model, asymmetry decreases the field strength of the noise limit at every frequency. With a growing number of segments, the effect of membrane asymmetry of resistivity gradually decreases.

Asymmetry of resistivity does not change the character of the described models, having no noise limit at low and high frequencies in the KA and WA models, respectively.

Therefore, membrane resistance asymmetry does not cause substantial change. We do not have to change the models because of membrane failures, as the modification effect is slight.

Additional note

The symmetric component transformation is unitary; therefore, the instantaneous powers of noise are equal in the several equivalent circuits introduced above, i.e.

$$U_1 I_1 + U_2 I_2 = U_0^s I_0^s + U_1^s I_1^s \tag{16}$$

Due to this, two possible definitions of field-strength characterize the noise limit. These are only apparently different, because the simplest characterization of stochastic processes can be made by their power-density spectrum.

According to Kaune's original definition [3], the field-strength characterising the noise limit is constructed by the conductive current through the membrane, which has the same value as the displacement current (capacitive current) on the membrane (a detailed analysis see below). Consequently, using the circuit-picture,

$$E_{Kau} := \frac{I_{cm} R_m}{d_m} = \frac{(I_1 + I_2) R_m}{d_m} \tag{17}$$

However, only the power spectrum has meaning:

$$E_{Kau} E_{Kau}^* := \frac{(I_1 + I_2)(I_1 + I_2)^* R_m^2}{d_m^2} = \frac{\left(\sqrt{2} I_0^s\right)\left(\sqrt{2} I_0^s\right)^* R_m^2}{d_m^2} = \tag{18}$$
$$= \frac{I_0^s I_0^{s*} (2R_m)}{A_m d_m \sigma_m}$$

From this we conclude with our definition: the field-strength characterising the noise-limit is determined by the dissipated power in the unit volume of membrane in a zero-order substitutive network.

We will show that it is possible to define two concepts: There are conceptual differences in the effective field strength of the cell membrane by the WA, and Kaune models. On the basis of the cellular membrane model (Figure 7.), we suppose that the lipid double layer is a glossy, dielectric material with ε_m permittivity and finite, non-zero σ_m conductivity. As a consequence of thermal motion, a random electromotive force (emf) develops in the membrane. The field strength belonging to this emf is denoted by $\overline{E}_\xi$. This is the so-called Jonhson's field strength. According to the Langevin hypothesis, the net electric field strength $\overline{E}$ in the membrane can be resolved into two components: (i) the $\overline{E}_\xi$ field strength, which is a temporally uncorrelated randomly fluctuating quantity having zero-mean and (ii) and a dissipative field strength, which is proportional to the conducting current density $\overline{j}_d$ of the membrane. The conduction current is statistically independent of the Jonhson's field strength. This assures the fulfilment of the second law of thermodynamics in accordance with Langevin's statement. The conduction current generates, in the ion layer to be found on both sides of lipid layer, the Σ random surface charge density represented in figure 7. The surface charge density generates the displacement current density $\overline{j}_d$, which closes the current circuit, thus assuring the conservation of electric charge.

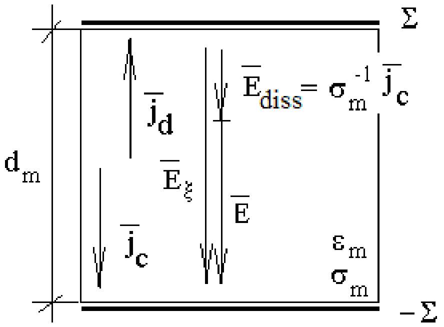

Figure 7. For the calculation of the effective field strength of the cell membrane

From an energetic point of view, we may have two possibilities to choose the effective field strength. One of them is that we consider that field strength as effective which belongs to the electric energy density is storage in membrane. That is

$$E_{netWA} = \sqrt{\frac{2w_e}{\varepsilon}} = E \tag{19}$$

This selection means that the dielectric polarization is considered relevant, for example, we could assume that polarization might lead to a degree at which the polarized charges are separated and can contribute to membrane conduction with some biological consequences. Another option is that we consider the field strength as effective and belonging to the field strength as part of to the electric energy dissipation density per unit time of the membrane, namely

$$E_{netKaune} = \sqrt{\frac{j_c^2}{\sigma_m^2}} = \frac{j_c}{\sigma_m} = E_{diss} \tag{20}$$

In this case, we could suppose that the thermal effect of dissipation generated by noise (for example thermal breakdown) might causes the biological effect. Next, we are going to specify the consequences of these. We can set up the equations according to Figure 7:

$$\begin{gathered} j_c = j_d = \varepsilon_m \frac{dE}{dt}, \\ E_\xi = \sigma_m^{-1} j_c + E \end{gathered} \tag{21}$$

If we suppose that the distribution of field strengths and current densities is homogenous in the membrane, we get

$$\begin{gathered} U_m + R_m I_m = \xi_m, \\ R_m = \sigma_m^{-1}\frac{d_m}{A_m}, \quad U_m = d_m E, \quad \xi_m = d_m E_\xi \end{gathered} \tag{22}$$

Where U_m is the potential, R_m is the resistance, A_m is the surface, d_m is the thickness and ξ_m is the random voltage, that is the so-called Johnson emf generated in the membrane. The equivalent circuit of Figure 8. belongs to the above equations, and here we marked the introduced effective field strengths.

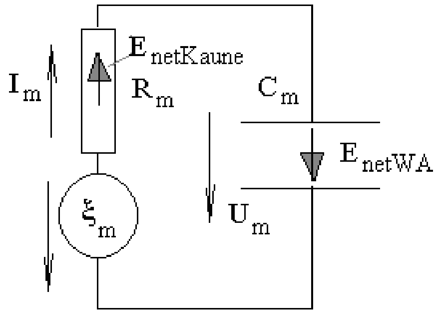

Figure 8. Equivalent circuit of the cell membrane

From the equations (21) and (22) we get the differential equation of the network, namely

$$\tau_m \frac{dU_m}{dt} + U_m = \xi_m, \qquad (23)$$

$$\tau_m = R_m C_m, C_m = \varepsilon_m \frac{A_m}{d_m},$$

where τ_m is the time constant and C_m is the capacity of the membrane. By multiplying the equation by U_m and calculating the average, we get the equation,

$$\frac{d}{dt}\overline{\left(\frac{1}{2}C_m U_m^2\right)} + R_m^{-1}\overline{U_m^2} = R_m^{-1}\overline{\xi_m U_m} = 0, \rightarrow \frac{d}{dt}\overline{\left(\frac{1}{2}C_m U_m^2\right)} = -\frac{2}{\tau_m}\frac{1}{2}C_m \overline{U_m^2} \qquad (24)$$

from which it follows that the electric energy generated by the fluctuation of membrane potential is transformed into heat by the membrane resistance . The characteristic time constant of the transformation is $\frac{\tau_m}{2}$.

If we knew $\xi_m(j\omega)$, the Fourier transform of ξ_m, then we would have the following solution to equation (23):

$$U_m(j\omega) = \frac{\xi_m(j\omega)}{1 + j\omega\tau_m} \qquad (25)$$

But, instead of $\xi_m(j\omega)$ we know the $S(f) = \frac{\xi_m(j\omega)\xi^*(j\omega)}{2\pi}$ power spectral density, where $S(f)df$ gives the portion of the intensity $\overline{\xi_m^2(t)}$ of $\xi_m(t)$ that is due to frequencies belonging to the interval $(f, f+df)$. Accordant to the Nyquist theorem:

$$S(f) = 4kTR_m \qquad (26)$$

Thus, the power spectral density of the membrane potential:

$$U_m(j\omega)U_m^*(j\omega) = \frac{\xi_m(j\omega)\xi_m^*(j\omega)}{1+\omega^2\tau_m^2} = \frac{4kTR_m}{2\pi}\cdot\frac{1}{1+\omega^2\tau_m^2} \tag{27}$$

Also the effective field strength accordant to the WA theory:

$$\overline{E_{netWA}^2} = \frac{\overline{U_m^2(t)}}{d_m^2} = \int_0^\infty \frac{\xi_m(j\omega)\xi_m^*(j\omega)}{1+\omega^2\tau_m^2}d\omega = \int_0^\infty \frac{4kT}{\sigma_m A_m d_m}\cdot\frac{1}{1+\omega^2\tau_m^2}df \tag{28}$$

The Fourier transform of the dissipative field strength from equations (20) and (21) has the form of

$$E_{netKaun}(j\omega) = \frac{\varepsilon_m}{\sigma_m}\frac{j\omega U_m(j\omega)}{d_m} = \frac{1}{d_m}\frac{j\omega\tau_m\xi_m(j\omega)}{1+j\omega\tau_m} \tag{29}$$

from which we get the effective field strength accordant to the Kaune theory

$$\overline{E_{netKaune}^2} = \int_0^\infty \frac{1}{d_m^2}\frac{\omega^2\tau_m^2\xi_m(j\omega)\xi_m^*(j\omega)}{1+\omega^2\tau_m^2}d\omega = \int_0^\infty \frac{4kT}{\sigma_m A_m d_m}\cdot\frac{\omega^2\tau_m^2}{1+\omega^2\tau_m^2}df \tag{30}$$

The basic character of the models does not change.

CONCLUSION

The appearance of membrane rafts in the models of thermal limit does not have a drastic influence on the homogeneous membrane models of thermal limit.

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Author' biography with Photo

Curriculum Vitae **Andras SZASZ**

PERSONAL

1947. November 04. Born in Budapest, Hungary

STUDIES

1967-72	Studies at Eötvös University (Physics) [MS graduation, thesis: Positron annihilation]
1974	Doctor's degree at Eötvös University (Physics)
1983	Candidate of Mathematical and Physical Sciences of Russian Academy of Sciences, (Surface physics)
1983	Candidate of Physical Sciences of Hungarian Academy of Sciences (Physics)
1996	Habilitation at St. Istvan University (Hungary) (Biophysics)

ACADEMIC APPOINTMENTS

1972-1974:	Assistant professor in Eotvos University Budapest, Hungary
1974-1982:	Associate professor in Eotvos University Budapest, Hungary
1982-1985:	Head of Metalab and Laboratory of Surface Physics in Eotvos University
1985-1986:	Head of Dept. Solid State Physic, Eotvos University Budapest, Hungary
1986-1987:	Research fellow Scottish Surface Centre, Strathclyde University, Glasgow, UK
1988-2004:	Appointed visiting professor to Material Engineering Department of Strathclyde University, Glasgow, UK
1996-cont.	Professor at St. Istvan University, Gödöllö, Hungary (biophysics)
2012-cont.	Appointed visiting professor, Pazmany Catholic University, Hungary (bioelectrodynamics)
2013-cont.	Appointed visiting professor at Chiba University, Japan (fractal physiology)

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PRESENT ADMINISTRATIVE POSITIONS

2000-cont. Head of Biotechnics Department in St. Istvan University, Faculty of Engineering. Hungary

2001-cont. CSO of OncoTherm (www.oncotherm.de) (both the Hungarian and German Branches)

SCIENCE AWARD

2000 Dennis Gabor Award (Hungarian Academy of Science)

PUBLICATIONS

Author and co-author of about 700 publications (articles, conference contributions/abstracts), co-author of eight books, and co-author of 40+ patents