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VARIABLE MECHANISMS OF ACTION OF LITHIUM DURING GENERATING OF MEMBRANE POTENTIAL OSCILLATIONS ACROSS THE EXCITABLE MEMBRANE OF THE NITTELA CELL**

ABSTRACT: This study presents results on variable mechanisms of lithium transport processes during generating of membrane potential oscillations across the very excitable membrane of the Nittela cell. Generating of several classes of oscillations, single and local impulses of the membrane potential, were presented in dependence on effects of a high LiCl concentration (10 mM), with which the cell membrane is very excited. Results on membrane potential oscillations are presented, and then some of oscillogram parameters were displayed. The assertion is that oscillations of the membrane potential are caused by total oscillatory transport processes: Li+, K+, Na+ and Cl− across the very excitable cell membrane. The paper presents the hypothesis on mechanisms of oscillatory transport processes of ions (Li, Na, K and Cl) expressed over different classes of oscillations, single and local impulses of the membrane potential across the excitable membrane of the Nittela cell.

KEY WORDS: excitable membrane, lithium, membrane potential, Nittela cell, oscillation parameters, oscillatory transport

INTRODUCTION

General information on lithium – Lithium is alkaline earth metal, which occurs in nature in the form of different minerals or ions in minerals or sea water (140-270 ppb, parts per billion) (Crichton, 2008). Lithium is found in trace amounts in biological systems lithium. Furthermore, lithium in low concentrations (69-5760 ppb) is found in plants, planktons and inverte-
brates. Almost all tissues and tissue fluids of vertebrates contain lithium (21-763 ppb). Marine organisms have tendency to accumulate lithium in greater concentrations (Chasard-Bouchaud et al., 1984). Its role within biological systems and under physiological conditions has not been yet sufficiently clarified. Recent nutritional studies on mammals show that the presence of lithium in the rate of 1 mg per day affects health of organisms, which suggests that lithium could be classified as an essential biomicroelement. It was observed that a low-dose lithium uptake promotes longevity in humans and metazoans (Zarse et al., 2011). In medicine, lithium in the form of Li-carbonate or Li-citrate, is used to treat bipolar disorder (Ghasemi et al., 2008, 2009, 2010, Baldessarini et al., 2006). In industry, lithium is used in the manufacture of ceramics and glass resistant to high temperatures, and in the production of lubricants resistant to high temperatures, as well as, in the production of Li-ion batteries (Ebensperger et al., 2005).

**Lithium-oscillations of the membrane potential** – The method of recording biopotentials by means of microelectrodes is being used to study a variable mechanism of action of lithium during generating of membrane potential oscillations, and indirectly during the inducement of the oscillatory lithium transport across the excitable membrane of the Nittela cell (Vorbiev et al, 1967, 1968). A rhythmic fluctuation of the membrane potential was recorded by the minimum improvement of this method (Radonović et al., 1968). However, only in 1976, some bioelectric responses to the membrane of the Nittela cell (change in ψm, membrane oscillations and single impulses) induced by lithium concentrations were registered for the first time (Radonović, 1976). Somewhat later, typical oscillations ψm were registered (Radonović and Penčić, 1970), and then oscillations ψm caused by monovalent cations, among which Li+ had also been present, were registered (Radonović et al., 1977). The Nitella and Chara (freshwater green algae of the family Characeae) were used as the object of studies on membrane potential oscillations induced by lithium. The greatest number of experiments with actions of lithium was performed on the Nitella mucronata cells. These cells are large (diameter: 0.6-1.0 mm, length: 40-80 mm) and they are suitable for bioelectrochemical and electrophysiological studies. Today, the stated objects are considered the conventional model object for studies of complex membrane-transport processes (Vukosnović et al., 1998, Radonović, 2001, Radonović et al., 2006).

Results obtained in scarce previous studies are not sufficient to develop a complete and complex idea of the oscillatory transport of Li⁺ across the very excitable membrane of the Nitella cell. Some new issues related to oscillatory membrane processes arose. It was assumed that Li⁺ was their inevitable inducer, but not the only (Damjanović and Radonović, 1971, Radonović and Vučinić, 1976, 1985, Radonović, 1985a). New issues are primarily related to various oscillations of transport processes caused by effects of shocking levels of lithium ions (Radonović et al., 1977, 2006).

The special attention in this study was paid to variable mechanisms of lithium transport processes during generating oscillations ψm across the very excitable membrane of the Nitella cell.
MATERIAL AND METHODS

**Plant objects** – The experiments were performed on cells of freshwater alga *Nitella mucronata*. These cells are large (diameter: 0.6-1.0 mm, length: 40-80 mm) and they are suitable for bioelectrochemical and electrophysiological studies. Growing conditions, object preparations, treatment prior and during measuring of $\psi_m$ were described in previously published papers (Radenović and Pencić, 1970, Radenović, 1974, Radenović and Vučinić, 1976, Radenović et al., 1977). It is generally accepted that these cells represent a classical model system for diverse studying on membrane-transport processes (Radenović, 1982, 1985a, 1985b, 2001, Vukšanović et al., 1998, Radenović et al., 2005, 2006).

**Method** – The measurement of rhythmic and membrane bioelectric signals: single impulses, sequences of impulses and different forms of membrane potential oscillation ($\psi_m$, mV) was performed after the method with a microelectrode technique, which was previously described in principle and details in studies carried out by Radenović and Pencić, 1970, Radenović, 1974, Radenović and Vučinić, 1976, Radenović et al., 1977, (Fig. 1).

![Fig. 1](image_url) – Schematic diagram of the method of measurement of the membrane potential across the *Nitella* cell applying the microelectrode technique: ME$_1$ – microelectrode in the vacuole, ME$_2$ – microelectrode in the cell wall, RE – reference electrode, A$_1$ and A$_2$ – amplifiers, REC – recorders.
RESULTS

The initial measurement of the equilibrium resting membrane potential ($\psi_m$, mV) is generally accepted as a rule, for bioelectric (bioelectrochemical and electrophysiological) measurements across membranes of the *Nitella* cell. If its value ranges from -80 mV to -150mV the experiment on the membrane of the *Nitella* cell can be continued. It should be known that the value of the uniform resting membrane potential in the *Nitella* cell depends on a physiological state of the cell, growing conditions, age, as well as, on the season (Radenović, 1974).

There is a possibility to observe different classes of membrane potential oscillations, single and local impulses within numerous bioelectric studies (Radenović, 1985b). In order to recognise the oscillatory response easily the following is given:

- Local impulse can occur in the initial part of the oscillation, but it can be clearly pronounced and easily registered.
- Single impulse can be pronounced more often and more regularly and can simply be registered.
- Sequences of single impulses occur often and they are simply registered. In literature, they are referred to as membrane potential oscillations.
- It is shown that membranes of the *Nitelle* cell are capable, under effects of selected stimuli, to generate local and single impulses and repetitive membrane potential oscillations (Radenović and Pencić, 1970, Radenović and Vučinić, 1976, Radenović et al., 1977).

This paper presents four examples of Li-oscillations of the membrane potential.

1. **Instantaneous generation of lithium-oscillations in the direction of membrane potential depolarisation**

   Generation of lithium-oscillations in the direction of depolarisation of the membrane potential is given in the form of six different classes (Fig. 2.1-2.6). Their generation is explained by the effects of the concentration gradient of lithium (10 mM), sodium (1 mM), and potassium (0.1 mM). Furthermore, the electrochemical potential gradient and the electric potential gradient also affect the generation of lithium oscillations. They induce the formation of a strong electric field that pulls out the ions (Li, Na and K) and in such a way, their transport is provided. The intensity and dynamics of the overall transport processes of the ions (Li, Na, and K) are significantly affected by the nature of movements of active molecules (proteins, lipids and pigments): rotational, flip-flop and lateral. When the membrane is very excited, the mentioned types of movements of active molecules and the effects of stated gradients establish the interdependence of processes that affect six different classes of oscillations. Therefore, the interdependence of processes of competitiveness of ions (Li, Na, and K) in the overall transport processes, the dominance of certain types of movements of active molecules and the very excitable membrane, determine parameters and form of six classes of membrane potential oscillations.
Fig. 2.1-2.6. – Instantaneous generation of lithium-oscillations in the direction of membrane potential depolarisation triggered off by the exchange of the standard solution for the LiCl solution of the shocking concentration of 10 mM.

Symbols: standard solution (SR: 0.1 mM KCl + 1.0 mM NaCl), $\psi_1$ – equilibrium membrane potential prior to oscillating, $\psi_2$ – equilibrium membrane potential generated by effects of Li after oscillating, $\psi_{os}$ – class of membrane potential oscillations established by effects of shocking LiCl concentration, arrows – indicate the moment when SR was replaced with LiCl solution of the shocking concentration. This Fig. shows six different classes of membrane potential oscillations.

The stated classes of Li-oscillations of the membrane potential are characterised by non-standard parameters (Tab. 1).
Tab. 1. – Non-standard parameters of lithium-oscillations in the direction of membrane potential depolarisation

<table>
<thead>
<tr>
<th>Figures designations</th>
<th>Ψ₁</th>
<th>Ψ₂</th>
<th>Number of impulses</th>
<th>Duration of oscillation</th>
<th>Type of oscillation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fig. 2.1.</td>
<td>-155</td>
<td>-110</td>
<td>10</td>
<td>shorter than standard</td>
<td>symmetric damped</td>
</tr>
<tr>
<td>Fig. 2.2.</td>
<td>-160</td>
<td>-60</td>
<td>10</td>
<td>shorter than standard</td>
<td>unsymmetric damped</td>
</tr>
<tr>
<td>Fig. 2.2.</td>
<td>-135</td>
<td>-55</td>
<td>18</td>
<td>within limits of standard</td>
<td>symmetric / unsymmetric damped</td>
</tr>
<tr>
<td>Fig. 2.4.</td>
<td>-120</td>
<td>-40</td>
<td>28</td>
<td>longer than standard</td>
<td>unsymmetric damped</td>
</tr>
<tr>
<td>Fig. 2.5.</td>
<td>-150</td>
<td>-30</td>
<td>16</td>
<td>somewhat shorter than standard</td>
<td>irregularly – symmetric damped</td>
</tr>
<tr>
<td>Fig. 2.6.</td>
<td>-90</td>
<td>-30</td>
<td>14</td>
<td>somewhat longer than standard</td>
<td>differently damped</td>
</tr>
</tbody>
</table>

2. Delayed generation of lithium-oscillations in the direction of membrane potential depolarisation

Delayed generation of lithium-oscillations in the direction of membrane potential depolarisation is presented in the form of three different classes (Fig. 3.1-3.3). They are affected by concentration gradients of competitive ions (Li, Na, and K) in transport processes. The certain classes of membrane potential oscillations ($\psi_m$, mV), (Fig. 3.1-3.3) appear when dominance of particular types of movements of active molecules (protein, lipids and pigments) occur. A gradual generation of the equilibrium membrane potential ($\psi_1$) in the direction of its repolarisation (Fig. 3.3) precedes the occurrence of membrane potential oscillations. It is believed that Na⁺ causes such generation of $\psi_1$. However, $\psi_{os}$ oscillations are different from all three classes of membrane potential oscillations ($\psi_m$, mV), (Fig. 3.1-3.3).

These classes of lithium-oscillations of the membrane potential (Fig. 3.1-3.3) can be analysed through non-standard parameters (Tab. 2).

Tab. 2. – Non-standard parameters of delayed generation of lithium-oscillations

<table>
<thead>
<tr>
<th>Figures designations</th>
<th>Ψ₁</th>
<th>Ψ₂</th>
<th>Number of impulses</th>
<th>Duration of oscillation, (min)</th>
<th>Type of oscillation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fig. 3.1.</td>
<td>-95</td>
<td>-60</td>
<td>16</td>
<td>8</td>
<td>irregularly – unsymmetric damped</td>
</tr>
<tr>
<td>Fig. 3.2.</td>
<td>-120</td>
<td>-55</td>
<td>20</td>
<td>15</td>
<td>unsymmetric damped</td>
</tr>
<tr>
<td>Fig. 3.3.</td>
<td>-100</td>
<td>-60</td>
<td>8</td>
<td>10</td>
<td>irregularly – unsymmetric damped</td>
</tr>
</tbody>
</table>
Fig. 3.1-3.3. – Delayed generation of lithium-oscillations in the direction of membrane potential depolarisation triggered off by the exchange of SR for the LiCl solution of shocking concentration (10 mM). Symbols are the same as in Fig. 2.1-2.6. This Fig. shows three different classes of membrane potential oscillations.
3. Instantaneous generation of lithium-oscillations in the direction of membrane potential repolarisation

Generation of lithium-oscillations in the direction of membrane potential repolarisation rarely occurs and it is presented in Fig. 4. Basically, the explanation of this class of membrane potential oscillations is identical as in Fig. 2.1-2.6 and Fig. 3.1-3.3. Different physical and chemical conditions occurring in the very excitable membrane lead, not so infrequently, to interdependence of various processes that move, some one way and some in the opposite direction. Such a state of interdependent processes refers to both, transport processes of ions (Li, Na, and K) and frequent changes in types of movements of active molecules, first of all proteins. Bearing in mind herein stated, it is possible to understand “anomalies” occurring during generation of $\psi_2$, and in the case of specific oscillation $\psi_{os}$ presented in Fig. 4.

Lithium-oscillations in the direction of membrane potential repolarisation (Fig. 4) have the following non-standard parameters: $\psi_1 = -120$ mV, $\psi_2 = -130$ mV, number of impulses = 5, duration of lithium-oscillation = 7 min and the type of lithium-oscillation is irregular, unsymmetric and undamped.

4. Instantaneous generation of lithium with the unaltered level of membrane potential prior to and after oscillating

Generation of lithium with the unaltered level of membrane potential prior to and after oscillating extremely rarely occurs and it is presented in Fig. 5.

Lithium-oscillations with the unaltered level of membrane potential prior to and after oscillating (Fig. 5) was triggered off by the exchange of SR for the LiCl solution of a shocking concentration and has the following non-standard parameters: $\psi_1 = -100$ mV, $\psi_2 = -100$ mV, number of impulses = 8, duration of lithium-oscillation = 4 min and the type of lithium-oscillation is less regular, unsymmetric and damped.
DISCUSSION

Discussion on general information on lithium – A molecular mechanisms of effects of lithium are still insufficiently clarified (Klein and Melton, 1996). According to its ionic radius $\text{Li}^{+}$ is the most similar to $\text{Mg}$ ion, which suggests its possible competition with the activities of $\text{Mg}$ ion. It is considered that $\text{Li}$ ion can affect inactivation of enzyme GSK3$\beta$, which can cause resetting of the circadian clock in the brain (Yin et al., 2006). Recently it has been suggested that lithium could interfere with NO regulatory pathway, which has a key role in the nervous system (Ghasemi et al, 2008.). It was also shown that lithium could interfere with inositol phosphatases, i.e. could inhibit inositol monophosphatase (Eina et al., 1998.). Besides, it is considered that the $\text{Li}$ ion interferes with the transmembrane transport of monovalent and bivalent cations of nerve cells due to its similarity with them ($\text{Na}$, $\text{K}$ and $\text{Mg}$, Tab. 3) (Lassalles et al., 1981).

Tab. 3. – Physical and chemical characteristics of $\text{Li}$, $\text{K}$, $\text{Na}$ and $\text{Mg}$

<table>
<thead>
<tr>
<th>Characteristics</th>
<th>$\text{Li}$</th>
<th>$\text{K}$</th>
<th>$\text{Na}$</th>
<th>$\text{Mg}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Atomic radius ($\text{Å}$)</td>
<td>1.33</td>
<td>2.03</td>
<td>1.57</td>
<td>1.36</td>
</tr>
<tr>
<td>Ionic radius ($\text{Å}$)</td>
<td>0.60</td>
<td>1.33</td>
<td>0.95</td>
<td>0.65</td>
</tr>
<tr>
<td>Hydrated radius ($\text{Å}$)</td>
<td>3.40</td>
<td>2.32</td>
<td>2.76</td>
<td>4.67</td>
</tr>
<tr>
<td>Polarizing power ($z/r^2$)</td>
<td>2.80</td>
<td>0.56</td>
<td>1.12</td>
<td>2.05</td>
</tr>
<tr>
<td>Electronegativity</td>
<td>1.0</td>
<td>0.80</td>
<td>0.9</td>
<td>1.0</td>
</tr>
</tbody>
</table>

Discussion on studies presented in this paper. – Results obtained on oscillatory bioelectric signal (local impulses, isolated single impulses, sequence of local and single impulses and typical oscillation of the membrane...
potential), presented in this paper, are only a smaller part of our long-term studies on total membrane potential oscillations, and indirectly on oscillatory transport of ions (K, Na, Ca, Li, and Cl) across excitable cell membrane (Radnović, 1982, 1985a, Vučinić et al., 1987, Vuletić et al., 1985, 1987). This is especially true for lithium-oscillations of the membrane potential, which are very specific and as such give the possibility to analyse a number of questions to which answers are not yet known in detail.

Some parameters of lithium-oscillations of the membrane potential have already been studied (Radnović et al., 1977, Radnović, 1982, 1985a, 1985b). However, they should be mentioned considering that there is a possibility to establish the analogy between oscillations in physics and biology (Vukšanović et al., 1998, Koljs et al., 1993). These parameters are: basic level of the membrane potential oscillation, impulse spike potential (the level up to which a membrane is depolarised during generating single or successive impulses and the complete oscillation), amplitude of single or successive impulses generated during the membrane potential oscillation, the relationship of the amplitude of one impulse with the amplitude of the following or previous impulse in the selected membrane potential oscillation, impulse interval (the duration between two successive impulses) and other standard parameters given in Tab. 4 (Radnović et al., 1977).

Tab. 4. – Standard parameters of membrane potential oscillations induced by effects of standard concentrations of Li, Na and K on the membrane of the Nitella cell

<table>
<thead>
<tr>
<th>Ions</th>
<th>Oscillation duration (min)</th>
<th>Number of impulses</th>
<th>Impulse amplitude (mV)</th>
<th>Frequency (imp/min)</th>
<th>Damping factor</th>
</tr>
</thead>
<tbody>
<tr>
<td>Li⁺</td>
<td>11.7</td>
<td>13</td>
<td>39±14</td>
<td>1.44±0.6</td>
<td>1.195</td>
</tr>
<tr>
<td>K⁺</td>
<td>1.9</td>
<td>6</td>
<td>39±19</td>
<td>3.62±1.4</td>
<td>2.153</td>
</tr>
<tr>
<td>Na⁺</td>
<td>24.1</td>
<td>24</td>
<td>54±16</td>
<td>1.04±0.5</td>
<td>1.081</td>
</tr>
</tbody>
</table>

In addition, attention should be paid to issues such as the kinetics of single impulses and the kinetics of the complete oscillation of the membrane potential. The important issues are the character of occurrence and behaviour of rhythms of bioelectric signals (Damjanović and Radnović, 1971, Radnović and Vučinić, 1976, Vučinić et al., 1987), but also effects of concentrations of selected ions on generating membrane potential oscillations (Vuletić et al., 1985, 1987). The above-mentioned issues and parameters characterising membrane potential oscillations are directly dependent on transport processes occurring across the very excitable cell membrane (Radnović, 1998).

As it is known, systems with one or two degrees of freedom are the basis for studying the mechanism of the membrane potential. Furthermore, different types of movements of lipids, proteins, pigments and other complex-bound structures contribute to the mechanism of the total transport processes across the very excitable cell membrane (Radnović, 1998). These types of movements within the very excitable membrane can be as follows: lateral movement
rotational movement (typical for proteins specialised for the ion transport) and so-called flip-flop movement (typical for lipids and proteins that regulate the ion transport from one side of excitable cell membrane to other).

When the degree of excitability of the cell membrane is higher, then the variable types of movements of active molecules (lipids, proteins and other molecules) are more significant in their intensity, dynamics and diversity, which affects the total ion transport processes (Koljš et al., 1993, Radenović, 1998), especially lithium transport processes (Radenović, 1976, Radenović et al., 1977, 2005, 2006).

As it is known, the transport of ions (including lithium) across the very excitable cell membrane is characterised by passive and active ion transport processes. Diffusion is considered to be a dominant bearer of passive transport processes in the very excitable membrane. It is expressed as a simple, limited, and facilitated diffusion. It is clear that there are at least three promoters of the passive ion transport: concentration gradient, electrochemical potential gradient, and electric potential gradient.

Obtained results, presented in this paper, indicate that lithium-oscillations in the direction of membrane potential depolarisation occurs under particular conditions (Fig. 2.1-2.6, Tab. 1). Moreover, delayed generation of lithium-oscillations in the direction of membrane potential depolarisation occurs (Fig. 3.1-3.3.; Tab. 2). Generation of lithium-oscillations in the direction of membrane potential repolarisation also occurs (Fig. 4). It is interesting to mention that generation of lithium with the unaltered level of the membrane potential also occurs prior to and after oscillating (Fig. 5).

CONCLUSION

Based on the gained results and the discussion, as well as, our overall information on oscillatory processes induced by Li, K, Na, NH₄ and Ca, we present the following hypothesis:

- Lithium-oscillations (local and single impulses and other classes of oscillations) of the membrane potential occur when the cell membrane is very excited. Such a membrane, as a rule, is accompanied by the activities of ions K⁺, Na⁺, Li⁺ and Cl⁻, which are not constant under such conditions in subcellular components (vacuole, cytoplasm, and cell wall).

- The usual ion transport processes are disturbed under effects of lithium: first, diffusion (concentration gradient is altered), electrodiffusion (electrochemical potential gradient is changed), biocurrents (electric potential gradient is altered), and fluid flow (hydrostatic pressure gradient is modified). The mentioned dynamic states determine the degree of excitability of the very excitable cell membrane. Hence, when the cell membrane is very excited, then local, single and complete membrane potential oscillations inevitably occur. These oscillations occur in the form of certain classes, but also in the form of different irregularities (chaos). At the same time and under such conditions,
oscillating of active proteins starts in the cell membrane, and they rhythmically, regularly, irregularly (state of chaos) induce the transport of ions, Na, K and Li, across the very excitable membrane, which takes an oscillatory regime. In such a state, transport processes of ions, K, Na and Li, adopt a co-operative character, which induce conformational changes of active ion channels that stretch and contract within the oscillatory regime, and thereby rhythmically modify transport ability of the excitable cell membrane for ions of K, Na and Li.

- Under such conditions, oscillatory changes occur in cell supplying, and thereby in supplying the very excitable membrane with energy: electric, osmotic and chemical.
- Moreover, the bonds between membrane transport processes and metabolism are disturbed, i.e. weakened. This is particularly related to weakening of the self-regulation of the matter within each cell.

REFERENCES


ПРОМЕНЉИВИ МЕХАНИЗМИ ДЕЛОВАЊА ЛИТИЈУМА ПРИ НАСТАЈАЊУ ОСЦИЛАЦИЈА МЕМБРАНСКОГ ПОТЕНЦИЈАЛА НА ПОБУЂЕНОЈ ЋЕЛИЈСКОЈ МЕМБРАНИ NITELLE

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Резиме

У овом раду су изложени резултати проучавања променљивог механизма транспортних процеса литијума, при настајању осцилација мембранског потенцијала, на екстремно побуђеној мембрани ћелије Nitelle. Показано је настајање неколико класа осцилација, појединачних и локалних импулса мембранског потенцијала, у зависности од деловања шокантне концентрације (10 mM) LiCl, са којом се ћелијска мембрана екстремно побуђује. Дају се резултати осциловања мембранског потенцијала, а затим се излазу неки од параметара осцилограма. Тврди се да је осциловање мембранског потенцијала условљено укупним осцилаторним транспортним процесима: Li\(^+\), K\(^+\), Na\(^+\) и Cl\(^-\) кроз екстремно побуђену ћелијску мембрану. Изложена је хипотеза о механизмима осцилаторних транспортних процеса јона (Li, Na, K и Cl) изражена преко различитих класа осцилација, појединачних и локалних импулса мембранског потенцијала кроз екстремно побуђену мембрану ћелије Nitelle.

КЉУЧНЕ РЕЧИ: литијум, мембрански потенцијал, осцилаторни транспорт, параметри осциловања, побуђена мембрана, ћелија Nitelle