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On possible role of DNA electrodynamics in chromatin regulation

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1. Introduction

In spite of extensive research, gene regulation is still not fully understood. Although all major transcription factors, gene promoter sequences and regulatory elements have been thoroughly characterized, our ability to predict transcription levels of genes is very limited. Even Genomatix (Patel et al., 2012), the leader in gene promoter analysis for the last 16 years, still has limited ability to predict the transcription of genes based on their regulatory sequences and the presence of transcription factors. It is hypothesized by us and others that this uncertainty regarding gene transcription is caused not by the complexity of gene regulation but by an incomplete understanding of the mechanisms of gene regulation. In other words, gene promoters may contain yet

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undeciphered signals which are regulated neither by transcription factors nor by any other chemical means but via another principle discussed below.

Comparative genomics also suggests that additional yet unknown regulatory mechanisms are in place. "The most surprising discovery about the human genome was that the majority of the functional sequence does not encode proteins," (Lander, 2011) reflected Eric Lander on the sequencing of the human genome (Lander and International Human Genome Sequencing Consortium, 2001). Specifically, in addition to 1.5% protein coding sequences in the genome, there are 6% of sequences which, though they do not code for proteins, are also conserved and therefore would have an important biological function (Lander, 2011). Now, 16 years after the initial sequencing of the human genome, the functions of the majority of functional untranscribed sequences are still unknown. This strongly suggests that there are yet unknown mechanisms by which untranscribed sequences exert their function. We suggest here that this unknown mechanism of gene regulation is electrical in nature.

There is much electrical activity in the cell. Neurons are well studied for their electric properties. But even non-neural cells are full of electrical activity. All membranes are strongly charged: the cell membrane, the nuclear membrane and the membranes of organelles. There are many strongly charged macromolecules: DNA, histones and many of the cell's proteins. When charged molecules move, they produce an electromagnetic field and affect surrounding charged molecules. Spinning of charged molecules also produces a magnetic field. In addition to the conductance of the cell's milieu, electricity is conducted by DNA and microtubules (Friesen et al., 2015; Havelka et al., 2014a) and this happens without leaking, not unlike conductance in insulated wires. Much of the movement within the cell is assisted by electromagnetic forces (Havelka et al., 2014b; Preto et al., 2012, 2015; Zhao and Zhan, 2012). In this way, the cell may be understood as a factory powered by electricity. In this respect, we find it most promising to focus on DNA conductivity, since it may be directly involved in gene regulation.

2. Electric conductivity of DNA

It is well established that DNA is a semiconductor. Charge transfer takes place in the DNA core via the overlapping π-electron system of stacked base pairs (Odom et al., 2000). Both positive and negative charges, which are electron holes and excess electrons, respectively, could be transported through the DNA chain (Fujitsuka and Majima, 2012). Depending on the DNA sequence, charge transfer occurs via multistep hopping or coherent superexchange (tunneling) mechanisms (Giese et al., 2001).

The conductivity of DNA is sequence-dependent (Krokhin et al., 2009). Purine stretches transfer electron holes better due to the lower ionization potentials (Bruot et al., 2015). Periodic purine stretches, such as poly-GC, are the best among conducting sequences (Wells et al., 2009). Cytosine methylation decreases DNA conductivity (Qi et al., 2015).

Initial in vitro studies of DNA charge transport were performed using photosensitizers, fluorescence quenching, scanning tunneling microscopy and metal-ion-modified DNA molecules (Fujitsuka and Majima, 2012; Kratochvílová et al., 2008; Shao et al., 2005; Toward, 2010). These methods elucidated charge transfer mechanisms occurring in DNA and their kinetic properties, including electron transfer times. Usually, in vitro studies are conducted with relatively short DNA duplexes or hairpins: up to 200 base pairs spanning about 70 nm. The details of charge transfer over longer distances are yet to be clarified. Charge transfer is robust in DNA wrapped around nucleosomes (Arnold et al., 2016). Packaging of DNA around the nucleosome does not inhibit charge transfer (Núñez et al., 2002). It has been experimentally demonstrated that the cellular machinery uses the loss of DNA conductivity to monitor the DNA integrity of specific genes (Grodick et al., 2015).

3. Resonance response to EMF

There is a body of research substantiating specific positive effects of low-power electromagnetic radiation on biological function, reviewed in (Cifra et al., 2011). These include light, microwave and other parts of electromagnetic spectrum. There is also a substantial body of experimental evidence where developmental patterning of the embryo was controlled experimentally in model biological systems via electricity, reviewed in (Levin et al., 2017).

There are electromagnetic (EM) waves that cause wide spectrum response without an obvious resonance effect (such as light in the red and infrared regions of the spectrum), but there are also a few frequencies at which the resonance effect was observed. Typically, a resonance effect in any system, not necessarily biological, is characterized by a specific response and a narrow frequency action peak in response to a low incident fluence of waves. In physics and engineering, good resonators with a narrow frequency action peak, such as radio receivers, are characterized by high Q-factor (quality factor). Such resonance effects have been reported for low fluence 42.2 GHz microwave irradiation, which improves the viability of cells, with a narrow frequency action peak (Angeluts et al., 2014).

4. Possible EM resonators

As discussed in Ref. (Cifra et al., 2011), many cell structures, such as membranes of the cell, the nucleus and organelles, are polarized and could serve as generators and receivers of EMF. Many proteins, such as hemoglobin and cytochrome oxidase C, can serve as chromophores for capturing visible and infrared light with high specificity.

Chromatin is highly polarized: DNA is strongly negative due to phosphate groups and histone proteins of the nucleosome are strongly positive due to lysine and arginine residues. Chromatin is very dynamic: cell cycle stages, transcription, protein synthesis and replication involve well coordinated and vast chromatin reorganization. Since chromatin is strongly polarized and dynamic, strong electrodynamic phenomena must occur (Zhao and Zhan, 2012) and these phenomena should be important for chromatin's function. Although the molecular side of chromatin function is well researched, its electrodynamic side is not sufficiently characterized.

Since DNA is structured with high periodicity and conducts electricity, it has been hypothesized that EM resonances play a role in genome function and gene regulation (Bischof, 1995; Gariaev et al., 2001). Since DNA conductivity and structure is dependent on its sequence, these resonances may be sequence-dependent. Therefore, it has been hypothesized that sequence-dependent resonances in DNA may be a part of natural gene regulation. If so, the genomic code could be functionally tied up with EM fields and this could be utilized by nature for the purposes of gene regulation.

5. Possible EM resonating structures in DNA

For DNA to engage in functionally important resonance, it should be able to support lasting oscillations. Which DNA structures could be electronic oscillators?

DNA is organized into several structures on different levels. Because of its simplicity and order, the double helix is the best understood among DNA structures. The double helical DNA is

wrapped on nucleosomes, forming the “beads on a string structure”. The nucleosomal structure of DNA is very dynamic, and its movements are involved in the regulation of gene expression. The individual nucleosomes either stay in one place or roll along the DNA. The nucleosomes are further packed into di- and tetranucleosomes and further into irregular polynucleosomal structures (Li et al., 2015; Maeshima et al., 2016; Ou et al., 2017).

6. Oscillators

In technology, a basic electronic oscillator consists of a capacitor and an induction coil, Fig. 1 **A**. Such oscillators are used in radios, computers and nearly every electronic device. Among possible candidates for resonating structures in DNA, we suggest that adjacent pairs of nucleosomes could possibly work as natural electronic oscillators, Fig. 1 **B**.

In this model, oscillation occurs by alternation of charges between the two nucleosomes. The united π-orbital electron cloud of the base stack of the DNA oscillates back and forth between the two nucleosomes. In this model, each nucleosome works both as a capacitor and as an induction coil. The inductance here is provided by DNA coils around nucleosomes. The electric capacitance of the nucleosome is enhanced due to its polar nature: the negative charge accumulated in the DNA core is retained by the attraction of the positive charge of the histones. The positive charge accumulated in the DNA core is retained by the attraction of the negative charge of the DNA backbone.

Note that such an oscillation mode may occur in healthy physiological conditions via partial shifting of the united electron cloud and should not require ionization of individual DNA bases, which causes mutations.

7. A polynucleosomal oscillator

Since the nucleosome has only 1.7 turns of the coil, the inductance of DNA wrapped around it is limited, limiting the oscillator efficiency (quality factor). Yet, if many di-nucleosomes are oscillating in a coordinated synergistic fashion, the efficiency of this collective oscillator should be higher.

Initially, a number of polynucleosomal structures have been observed in reconstituted chromatin, including the variants of two-start zigzag and solenoid (Ausió, 2015; Schalch et al., 2005; Song et al., 2014). Yet, recent studies in live cells suggest that among polynucleosomal structures, the most abundant are the di- and tetra-nucleosomes and the orderliness of the structures fades as the structure's size increases (Li et al., 2015; Maeshima et al., 2016; Ou et al., 2017). Specifically, it is observed that unlike reconstituted chromatin on a periodic DNA template, in live cells, bigger structures are likely to be non-periodic because the linker lengths between the nucleosomes are irregular (Li et al., 2015; Maeshima et al., 2016; Ou et al., 2017). Therefore, a tetranucleosome emerges as the largest regular DNA structure that is abundant in live cells, and bigger structures are either irregular or rare in the cell. Here we suggest a possible synergistic arrangement of the dinucleosomal oscillators in a tetranucleosome, Fig. 2. Although the stacked nucleosomes would repel each other due to induced charge during oscillations, they would still be attached to each other due to their acidic patches.

The model shown implies synchronized oscillation of all nucleosomes. In addition, we can consider the possibility of asynchronous oscillations of different nucleosomes. The number of possible oscillation modes grew as we allowed for a phase delay of the oscillations along the DNA chain. Also the number of models increased as we allowed harmonics (such as the plus-neutral-minus-neutral sequence of nucleosomes). Some of the models seemed to sustain oscillations better than others due to synergy between opposite charges and between electromagnets formed by the adjacent nucleosomes (not shown). Further modeling and experimentation is required to test whether some of these models might occur in nature.

8. Powering the oscillations

Which mechanisms could power electric oscillations in chromatin? In traditional technologies, electronic oscillations are generated by periodically powering the oscillator at its natural frequency. In every cycle, a bit of energy is fed to the oscillator at the right time. This is achieved by positive feedback loops - the voltage in the oscillator triggers a synergistic electric spike. Similarly, the electric oscillations in chromatin may be powered by chemical processes which would periodically spike some energy into the DNA chain.

As a source of energy for oscillations, chromatin-associated ATPases, including chromatin remodelers, would be good candidates. Chromatin remodelers SWI/SNF,ISWI, CHD, INO80 belong to the SNF2-family (Bao and Shen, 2007). They can bind either the nucleosomal part of DNA or linker DNA connecting nucleosomes, remodel chromatin, move nucleosomes and enable access of regulation factors to DNA (Liu et al., 2017). Importantly, ATPase domains of chromatin remodelers are located in the proximity of the DNA chain. This proximity may enable the transfer of electronic oscillations produced by ATP hydrolysis to the base stack. In addition, movement of the ISW2 chromatin remodelling complex over DNA (Narlikar et al., 2013) may induce periodic oscillations of the electron cloud in the base stack.

Another possible source of energy for electronic oscillations in DNA is the transcription complex. It is powered by breaking nucleotide triphosphates and produces extra energy at every step of RNA polymerization. This energy may be utilized by the cell to induce electron cloud oscillations in the base stack.

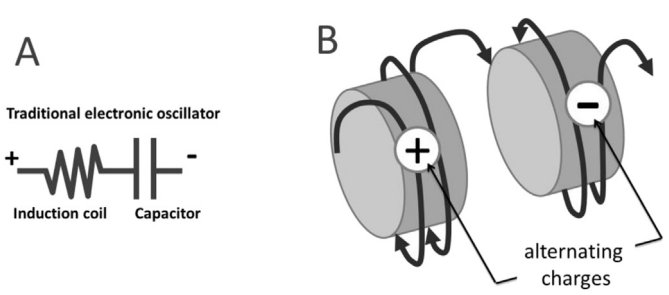

Fig. 1. Oscillator models. A. A traditional electronic oscillator (resonant circuit, LC circuit). **B.** The proposed hypothetical dinucleosomal oscillator.

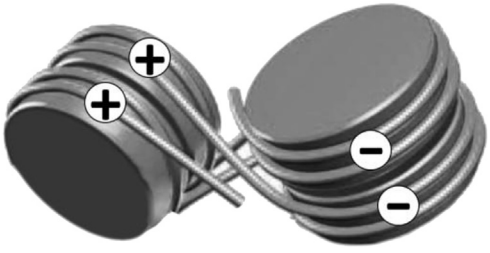

Fig. 2. The suggested model of charge oscillations in a tetranucleosome. One of the two phases of the oscillation cycle is shown. In the other phase, the charges are reversed, not shown. The shape of the two-start solenoid is adapted from (Song et al., 2014) with permission; the charge labels are added.

Proteins containing Fe-S clusters, which inject or extract electrons from the base stack (Fuss et al., 2015; Grodick et al., 2014), may also play a part. Although they are not known to induce oscillations, they might be used by the cell to break through the hydrophobic insulation of the base stack to deliver alternating current to the base stack.

Another possible source of electric oscillations may be a hypothetical centrosomal dynamo proposed in Ref. (Zhao, 2015). In this model, a pulsed current is produced by spinning of electrically charged centrioles during the mitosis phase of cell division. The spinning could be powered by motor proteins such as dyneins and kinesins that utilize ATP. The centrosomal dynamo model is supported by the recent discoveries of higher order organizational features of the centrosome by subdiffraction imaging (Lawo et al., 2012), live visualization of electromagnetic pumping induced spontaneous growth of microtubules (Sahu et al., 2014) and origination of electric fields during mitosis (Jelínek et al., 2009).

For the oscillations to be generated and sustained in live subcellular structures, the conditions of the Frohlich model (Frohlich, 1988; Fröhlich, 1968) could be applied. These conditions, which include pumping of energy through the system and a high level of coherence in the system, could be applicable to the proposed nucleosomal charge oscillation model. The energy pumping through the system could be supplied by the above mentioned mechanisms and the coherence could be achieved by resonance between multiple polynucleosomal structures.

9. Frequency

Although the molecular structure of a nucleosome is known, estimation of the frequency of a di- and poly-nucleosomal oscillators is not trivial because their size is at the borderline between the micro- and macro scales. It is likely they would combine the properties of the micro scale governed by quantum physics and of the macro scale governed by traditional electrodynamics. The macro scale calculations utilizing traditional electrodynamic rules (see Supplement 1) estimate the natural frequency of the dinucleosomal oscillator in the range of 360 THz, although the source values of inductance and capacitance of the DNA coil are rough estimates and the method of computation ignores the quantum properties of the structure. For example, if inductance and the capacitance of the nucleosome is found to be enhanced by the nucleosome core, the estimate could easily drop to a few GHz.

10. Potential approaches to testing the model

It should be possible to use computational molecular modeling to estimate the capacitance and inductance of di- and polynucleosomal models, and from that to estimate the natural frequency of such oscillators.

Although very little experimental data is published on DNA or chromatin oscillations, the electromagnetic oscillations have been detected in microtubules and other cellular components, reviewed in Ref. (Cifra, 2015). Possibly, the natural frequency of nucleosomes could be measured in reconstituted chromatin using cyclic voltammetry (Anne and Demaille, 2006) and other electrochemical methods. The natural frequency of polynucleosomes should depend on compaction and thus be affected by the DNA sequence, magnesium and sodium concentrations and the presence of Histone H1 or intercalating dyes.

Also a reverse approach can be used: applying electromagnetic field (EMF) and alternating currents at the polynucleosomal natural frequency to cells and polynucleosomes should affect their compaction. This could be visualized using fluorescent microscopy or mapped using genome-wide chromatin accessibility assays (such as ATAC-seq and DNAse-seq).

11. Potential implications

The importance of electronic resonance between DNA structures arises from the possibility of remote information transmission without chemical messengers. Science is already aware of information transfer via electricity in the body - the transmission of information via neurons. It is also possible that information is transferred between resonating DNA structures in the nucleus. This information transfer could be sequence-dependent and thus could represent a novel mechanism of genome self-regulation. Further, understanding of the mechanisms of such communication between parts of the genome could uncover the function of the conserved noncoding DNA sequences. In addition, the ability of chromatin to send and receive information in a sequence-dependent manner could be of importance in the information exchange between cells and between the cell and the organism as a whole. Such extracellular electromagnetic information transfer could be mediated by neural electricity, electric transfer via extracellular microtubules and other carriers.

Author contributions

NK, IG and MMR suggested that charge transfer in DNA may be a physical means which mediates the information transfer from the DNA sequence to a transmittable non-chemical signal; MMR, VG and OP proposed that nucleosomal structures could be natural electric oscillators and resonators, and came up with models for the polynucleosomal charge oscillators. YZ proposed the centrosomal dynamo model, AM and AT did the calculations.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.pbiomolbio.2017.12.006.

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