

HISTORY OF MEDICINE AND DEVELOPMENT

The scientific heritage of Professor Aron Gutman (Commemorating the 10th anniversary of Aron Gutman's death)

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Summary. Aron Gutman started his scientific research when he was a student of the Department of Physics and Mathematics, Vilnius University. At that time, he developed the theory of nonhomogenous vector relations between magnetic moments of electrons in an atom and applied it for explanation of energy spectrum of real atoms. Since 1960, he worked in Kaunas Medical Institute, and his main field of scientific interests was theoretical biophysics and electrophysiology of living tissues and cells. The earlier biophysical works of A. Gutman dealt with problems of the bioelectrical fields that underlie electroencephalogram, electrocorticogram, and electrocardiogram. The most important achievement was a theory of individual potential or postsynaptic field potential of synapses from individual axon (EEG quantum) and its role in shaping of electroencephalogram. In the later works (from 1971), he looked into properties and function of the individual nerve cells. He had created and developed the theory of nonlinear (bistable) dendrites and analyzed functional implications of such dendrites. In the last works, A. Gutman tried to relate the functioning of the nervous system at the cellular and system levels. He made efforts to find connection between the properties of individual neurones and principles (laws) of functioning of the nervous system. He had managed to relate dendritic bistability of neurones and Gelfand-Tsetlin principle of the functioning of the central nervous system (also known as the principle of minimal afferentiation). He explained some regularities in motor control by the dendritic bistability of motoneurones.

Short biography

Aron Gutman was a famous Lithuanian Jewish scientist, Professor of Biophysics, the principal researcher of the Laboratory of Neurophysiology at the Institute of Biomedical Research of Kaunas Medical University.

Aron Gutman was born in 1936 in Zhitomir, Ukraine. In 1945, Gutman's family moved to Lithuania, and it has been living there since. In 1958, Aron graduated from the Faculty of Physics of Vilnius University. In 1959, he started to work in the Laboratory of the Scientific Investigations of Kaunas Medical Institute. Aron Gutman carried out scientific research concerning biopotentials of the brain, and at the same time, he taught at the Department of Physics, Mathematics,

and Biophysics of Kaunas Medical Institute. In 1962, he defended his PhD thesis in the field of quantum physics entitled "Nonhomogenous vector relations in the atomic spectra." In 1965, he was appointed to the position of Head of the Department of Physics, Mathematics, and Biophysics and promoted to Associate Professor in 1969. In 1974, he defended his thesis of Habilitated Doctor in field of biophysics and electrophysiology entitled "Extra- and intra-cellular electrical fields of the dendrites of neocortex" and became Habilitated Doctor of Biophysics, the first one in Lithuania. In 1990, Aron Gutman was advanced to the professorship in biophysics.

Aron Gutman is an author and coauthor of more than 200 scientific publications, including two books



Professor Aron Gutman

and a series of chapters in biophysics textbooks. He is well known among the biophysicists and neuroscientists across the world. Professor Gutman's papers were published in prestigious international scientific journals, and his works have been frequently cited by scientists in Lithuania and abroad. Aron Gutman was an excellent teacher and mentor. He trained a number of neuroscientists who are successfully working in Lithuanian as well as European and American Universities. His knowledge and erudition were surprisingly deep, such that researchers from other fields outside of biophysics frequently asked for Aron's advice on various complicated scientific matters.

A. Gutman was a member of the Society for Neuroscience and the International Academy of Social and Natural Sciences. He was a referee of Human Frontier Science Program Organization. In 1999, he was granted a Lithuanian State Stipend for outstanding researchers. The Kapitsa medal was awarded to him for his achievements in physics.

In addition to his scientific activity, Aron Gutman actively participated in the social and political life of Lithuania. He was a member of the Lithuanian Movement for Independence, Sąjūdis, which was the main force in restoration of independence of Lithuania in 1991. He propagated a peaceful way of solving conflicts, and he publicly condemned violence of Soviet troops in Lithuania in January 1991. For many

years, Aron Gutman was an active member of the Lithuanian Jewish community. He was also working at the International Council for the Investigation of the Crimes by Occupational Regimes.

Scientific research

Below we present more detailed description of A. Gutman's scientific research pointing out the scientific problem, field of science, period, when A. Gutman was engaged in solving the corresponding problem, and principal publications related to the problem.

1. Inhomogeneous vector relations (atomic quantum mechanics), 1957–1963

Together with his supervisor Y. Levinson, A. Gutman had formulated a general theory of inhomogeneous vector relations for magnetic momenta of atomic electrons and applied it to the $l^m l'$ configuration. He discovered a new vector relation SL_0 and the corresponding energy spectra of real atoms. A. Gutman suggested using the principle of inhomogeneous vector relations to explain x-ray spectra. The theory was later applied at the Vilnius University by the group of Prof. J. Jucys. Principal publications are (1, 2).

2. Description of δ -activity in the electrocorticogram (electrophysiology of the cortex), 1963–1969.

In the electrical activity of the cortex (electrocorticogram), one distinguishes a number of oscillations with a different frequency. Among these, low frequency (~ 1 Hz) oscillations are termed the δ -activity. A. Gutman together with K. Grinevičius and others proposed the adequate phenomenological description of the δ -activity. They proved that the δ -activity reflects an electrical bistability of the cortex. The bistability of the cortical pyramidal neurones that could be related to the electrical bistability of the cortex was observed experimentally (3, 4). The results of this work were used to explain the nature of high frequency (~ 100 Hz) oscillations in the electrocorticogram. They were useful in the analysis of the evoked potentials and changes in electrocorticogram under narcosis. Principal publications are (5–11).

3. Development of the theory of extracellular current field (biophysical bases of electrophysiology), 1967–1980.

A. Gutman supplemented the theory of extracellular current field by simple quantitative and semiquantitative estimation methods. He succeeded in deriving formulae, whose parameters were directly related to known morphological and electrophysiological quantities. This made it possible to an-

swer why the impulse activity of the cortex cells only weakly is reflected in the electrocorticogram; to explain theoretically the magnitude of the observed potentials of the electrocorticogram; to explain the pattern of the electric potential change deep in the cortex; to improve the theory of electrostimulation and to invalidate the ephaptic theory according to which the neurons were thought interact strongly via their extracellular current fields. Later he had used the results of this work to introduce the notion of a quantum of the encephalogram (EEG) and to analyze the electrotonic (ohmic) properties of the neurons. Principal publications are (12–20).

4. Description of anisotropic syncytial media of the myocardium (biophysical bases of heart electrophysiology), 1970–1988. Dr. F. Bukauskas, the biophysicist from Institute for Biomedical Research, Kaunas University of Medicine, and his coworkers investigated the spreading of the electric excitation in the heart muscle. To explain the properties of this spreading, a model of anisotropic syncytium that treats the myocardium as network of the muscle cells connected with each other by the anisotropic intercellular contacts was used. A. Gutman described such syncytial medium using an anisotropic equation of the intracellular field. This greatly simplified the theory and its matching to the experimental data. His students continued the work in this field at the Laboratory of Heart Electrophysiology, Institute for Biomedical Research, Kaunas University of Medicine. Principal publications are (21–25).

5. Quantum of electroencephalogram (biophysical bases of brain electrophysiology), 1969–1989. The introduction of a notion of quantum of encephalogram (an elementary impulse of the electrical brain activity) and foundation of the corresponding theory is one of A. Gutman's greatest scientific achievements. The theory of the quantum of the EEG enabled to interpret the EEG as an impulse process and to explain general features of the frequency spectrum of EEG. The theory had elucidated the nature of high frequency oscillations studied by Prof. A. Mickis and his students. A. Gutman had estimated the magnitude of EEG quantum by using the theory of the extracellular current field, which he described in his book "Biophysics of the extracellular brain currents" (13). He proved that the magnitude of the EEG quantum is large enough to detect it experimentally. The biophysicists of the Institute for Biomedical Research, Kaunas University of Medicine, registered the quantum in the frog tectum and in the somatosensory cortex of rabbits (26). They achieved

this independently from famous American neurophysiologists Mendel and Henneman, who discovered this impulse at the same time by accident (27). The registration of the quantum of EEG became one of the standard methods of investigation of synaptic transmission in the central nervous system (CNS). This method is still used in the Laboratory of Neurophysiology, the Institute for Biomedical Research, Kaunas University of Medicine, to study the properties of the synaptic transmission from frog retina to tectum (28–30). Principal publications are (31–34).

6. Theory of electric properties of the skull and scalp (biophysical bases of human encephalography), 1972–1989. The electric potentials of the surface of the head (electroencephalogram, EEG) are a reflection of the electric potentials of the cortex (electrocorticogram) disturbed by the scalp and the bones of the skull. Therefore, it is important to understand how the cover tissues of the brain transform the electrocorticogram into EEG. A. Gutman proposed a simplified solution to this problem by treating the brain cover tissues as thin double layers. This enabled him to use equations for a 2D spherical cable in order to describe the above transformation and to obtain analytical mathematical expressions with a clear physical meaning. Dr. A. Šimoliūnas (Vilnius Institute of Mathematics and Informatics) developed numerical algorithms based on this theory, which were applied to solve the reverse problem of electroencephalography – to restore the electrocorticogram from EEG. The theory was applied to examine possibilities of the electrostimulation of the brain as well as in search of the correlation between the position of the electrodes on the scalp and the physiological significance of the electric potentials registered. Dr. A. Šimoliūnas was further developing this theory for a number of years. Principal publications are (35–42).

7. Dendritic bistability (theoretical neuro-electrophysiology), from 1969. Dendrites are neuronal processes that branch in a tree-like manner. They can be a few mm long and a few μm thick. For more than 100 years, when the first pictures of silver-stained neurons had been obtained, the neurophysiologists have been interested in general function of dendrites. For a long time it was believed that dendrites are simple linear summators, and their main function is to add up synaptic signals arriving from other neurons. In 1971, having analyzed experimental data on neurons electrical properties, A. Gutman proposed the hypothesis of bistable (or N-) dendrites, which postulated nonlinear electrical properties of the dendritic membrane (43). Based

on the hypothesis of bistable dendrites, A. Gutman predicted electrophysiological phenomena that were later observed experimentally (44–47). Results of experimental investigations on electrical properties of motoneurons confirmed that at least the dendrites of the motoneurons are bistable (48–52). The information processing can take place in the bistable dendrites. For example, the elementary logical operations can be performed in a single dendritic branchlet (53–57). Such neurons can implement the general Gelfand-Tsetlin's minimal afferentiation principle of functioning of the CNS (58). Based on the theory of bistable dendrites, A. Gutman explained the principles behind the functioning of the motor nervous system (unpublished results). A. Gutman and coworkers theoretically analyzed the propagation of the synaptic signals along the bistable dendrites (59, 60). They suggested the new interpretation of the slow negative potential of the cortex surface that is based on stable depolarization of the apical dendrites of the pyramidal neurons rather than on depolarization of glia cells caused by increased extracellular concentration of potassium ions. The theory of dendrite bistability is further developed by A. Gutman's students (61, 62). New experiments are proposed, and the theory is applied to propose novel hypotheses on motor control (63).

8. Electrotonic reconstruction of neurones (biophysical bases of neuroelectrophysiology), from 1980. In order to understand the function of neurons, it is

important to know how fast potential deviations evoked by synaptic inputs fall off with distance from the source along the dendrite. Passive propagation of the potential in the dendrites is termed electrotonic one. Neurophysiologists have been engaged in the problem of the electrotonic reconstruction of neurons for a long time (64–66). Yet, no reliable way to solve it exists (67, 68). Presently, the most widely used method of electrotonic reconstruction of neurons is computer simulation of the cell response to a short current impulse. A. number of various model parameters have to be fitted to the experimental data. A. Gutman and his coworker and former PhD student G. Svirskis suggested a new method of the electrotonic reconstruction of neurones that exploits the response of a neuron to an extracellular current field (DC current field) (69). This method allowed reducing the number of fitted parameters (70) and to detect heterogeneity of membrane properties (69). The method was applied to the turtle spinal motoneurons and interneurons, and their electrotonic reconstructions were obtained. A. Gutman and collaborators had investigated how the irregularity and inhomogeneity in cross-section of dendrites influence their electrotonic properties (71). They proposed and developed an adiabatic method for solving the cable equation, which could help to estimate the electrotonic parameters of neurones and dendritic cables (72). A. Gutman's students continue to work in this field (73).

Profesorius Arono Gutmano mokslinis palikimas (Arono Gutmano 10-osioms mirties metinėms paminėti)

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Raktažodžiai: nervų sistema, elektroencefalograma, elektrokardiograma, neuronas, dendritai.

Santrauka Savo mokslinę veiklą Aronas Gutmanas pradėjo dar būdamas Vilniaus universiteto Fizikos-matematikos fakulteto studentu. Tuo metu jis plėtojo nehomogeninių vektorinių ryšių tarp atomo elektronų magnetinių momentų teoriją ir taikė ją realių atomų energetinių spektrų paaiškinimui. Nuo 1960 m. jis dirbo Kauno medicinos institute. Pagrindinė jo mokslinių interesų sritis buvo teorinė biofizika ir gyvųjų audinių bei ląstelių elektrofiziologija. Ankstyvieji Arono Gutmano biofizikos darbai skirti bioelektrinių laukų (elektroencefalogramos, elektrokortikogramos ir elektrokardiogramos) kilmės problemoms. Svarbiausias pasiekimas buvo individualaus aksono sinapsių aktyvumo sukeltą posinapsinio potencialo (EEG kvanto) teorija, aiškinanti elektroencefalogramos struktūrą. Vėliau (nuo 1971 m.) jis gilinosi į atskiros nervų ląstelės funkciją bei savybes. Jis sukūrė bei plėtojo netiesinių (bistabilių) dendritų teoriją ir analizavo tokių dendritų funkcines savybes.

Paskutiniuose savo darbuose Aronas Gutmanas mėgino susieti nervų sistemos funkcionavimą ląsteliniame ir sisteminiame lygmenyse. Jis stengėsi išaiškinti ryšį tarp individualaus neurono savybių ir nervų sistemos funkcionavimo dėsnių. Siedamas neuronų dendritų bistabilumą su Gelfand-Tsetlin'o centrinės nervų sistemos veikimo principu (kitai vadinamu minimalios aferentacijos principu), Aronas Gutmanas paaiškino kai kuriuos judesių kontrolės mechanizmo savitumus motoneuronų dendritų bistabilumu.

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References

- Gutman AM, Levinson IB. Nonhomogeneous vector coupling in atomic spectra. *Soviet Astronomy* 1960;4:83
- Gutman AM, Levinson IB. Inhomogeneous vector couplings in atomic spectra. *Astron Papers* 1967;8:20-5.
- Silvabarrat C, Champagnat J. A potassium current controls burst termination in rat neocortical neurons after GABA withdrawal. *Neuroscience Letters* 1995;189:105-8.
- Schwindt P, Crill W. Equivalence of amplified current flowing from dendrite to soma measured by alteration of repetitive firing and by voltage clamp in layer five pyramidal neurons. *J Neurophysiol* 1996;76:3731-9.
- Griniavichius KA, Gutman AM, Jokubauskas II, Mickis AM. Odnomernoe raspredelenie EKG zritelnoj kory krolika (Unidimensional distribution of the rabbit visual cortex electrocorticogram.) *Zh Vyssh Nerv Deiat Im I P Pavlova* 1966;16:726-8.
- Maslauskas A, Grinevičius K, Gutman A, Miliauskas R. Duration of positive potential of electrocorticogram (ECoG) under influence of barbiturates. In: *The Nature of Sleep*. Stuttgart; 1973. p. 35-9.
- Grinevičius K, Miliukas V, Gutman A, Miliauskas R. Dva podprocessa v elektrokortikogramme zritelnoj kory krolika y aktivnost nejronov. (Two subprocesses in the rabbit visual cortex electrocorticogram and neuronal activity.) *Zh Vyssh Nerv Deiat Im I P Pavlova* 1969;19:178-80.
- Grinevičius KA, Gutman AM. Struktura elektrokortikogrammy krolika. (Structure of the electrocorticogram in rabbits.) *Zh Vyssh Nerv Deiat Im I P Pavlova* 1966;16:1123-5.
- Grinevičius KA, Gutman AM. Razlichie v svoystvakh dvukh podprocessov v elektrokortikogramme krolika. (Differences in the properties of two subprocesses in the rabbit electrocorticogram.) *Zh Vyssh Nerv Deiat Im I P Pavlova* 1968;18:329-33
- Venslauskas MI, Grinevičius KA, Gutman AM. Statisticheskaja model elektroencefalogrammy. (A statistical model of the electroencephalogram.) *Zh Vyssh Nerv Deiat Im I P Pavlova* 1964;14:726-31.
- Gutman A, Miliukas V. Delta-volna kak summa vnekletochnykh potencialov piramidnykh nejronov. Teoreticheskaja ocenka amplitudy. (Delta waves as the sum of pyramidal neuron extracellular potentials. Theoretical evaluation of the amplitude.) *Zh Vyssh Nerv Deiat Im I P Pavlova* 1969;19:671-9.
- Gutman AM, Morgenshtern VI. Vozmozhnyj mehanizm geneza magnitoencefalogrammy. (Possible mechanism of generation of the magnetoencephalogram.) *Biofizika* 1977;22:529-33.
- Gutman A.M. Biofizika vnekletochnykh tokov mozga. (Biophysics of the extracellular brain currents.) Moskva: Nauka; 1980.
- Gutman AM. Teorija dipolia vnekletochno go polia. (Dipole theory of the extracellular field.) *Biofizika* 1968;13:679-84.
- Gutman A M. Ocenka velichiny elektrokortikograficheskikh potencialov (Estimation of the value of electrocorticographic potentials.) *Biofizika* 1969;14:891-6.
- Gutman AM. K interpretacii profilj potencialov. (Interpretation of potential profiles.) *Biofizika* 1970;15:888-93.
- Gutman AM. Dva dopolnenija k raschetu dipolnogo momenta vnekletochno go polia: utochnenie formuly dipolia i ocenka dipolia serdca cheloveka. (Two supplements to the calculation of the dipole moment of an extracellular field: improvement of dipole formula and estimation of human heart dipole.) *Biofizika* 1972;17:173-4.
- Gutman AM. Teorija vlijanija postojannogo vnekletochno go polia na nejrony. (Theory of the effect of a constant extracellular field on neurons.) *Biofizika* 1972;17:278-83.
- Veseliūnienė MA, Gutman AM, Liesienė VA. Vlijanie nembutala na tormoznuju volnu antidromno vyzvannogo potenciala motornoj kory koski. (Effect of nembutal upon the inhibitory wave of antidromically evoked potential in the motor cortex of the cat.) *Farmakol Toksikol* 1971;34:520-2.
- Veseliūnienė MA, Gutman AM. Poslojnoe issledovanie d-aktivnosti zritelnoj kory krolika. (Laminar study of the delta activity of rabbit visual cortex.) *Fiziol Zh SSSR Im I M Sechenova* 1976;62:825-30.
- Bukauskas F, Bytautas A, Gutman A, Veteikis R. Simulation of passive electric properties in two- and three-dimensional anisotropic syncytial media. In: *Nonlinear science in intercellular communication*. Manchester; 1991. p. 203-17.
- Bukauskas F, Gutman A, Kišūnas K, Veteikis R. Electrical cell coupling in rabbit sinoatrial node and atrium: experimental and theoretical evaluation. Cardiac rate and rhythm. Physiological, morphological and developmental aspects. Hague; 1982: 195-216.
- Bukauskas FF, Veteikis RP, Gutman AM, Mutskus KS. Mezkhkletchnaja sviaz v sinusnom uzle serdca krolika. (Intercellular coupling in the sinus node of the rabbit heart.) *Biofizika* 1977;22:108-12.
- Bukauskas FF, Veteikis RP, Gutman AM. Model passivnogo trekhmernogo anizotropnogo sincitija kak nepreryvnoj sredy. (Model of a passive 3-dimensional anisotropic syncytium as a continuous medium.) *Biofizika* 1975;20:1083-6.
- Bukauskas FF, Veteikis RP, Gutman AM. Elektricheskaja sviaz mezhdū voloknami miokarda i genez elektrokardiogrammy. (Electrical connections between myocardial fibers and genesis of the electrocardiogram.) *Biofizika* 1975;20:118-20.
- Gruodis J, Gutman A, Kuras A, Mildažis V, Miliukas V, Mickienė V, et al. Kvant EEG (poniatie, ocenka velichiny, registracija). (EEG quantum (definition, measurement, registration).) *Dokl Akad Nauk SSSR* 1972;204:1246-9.

27. Mendel LM, Henneman E. Terminals of single IA fibers: location, density, and distribution within a pool of 300 homonymous motoneurons. *J Neurophysiol* 1971;34:171-87.
28. Kuras A, Gutmanienė N. Preparation of carbon-fibre micro-electrode for extracellular recording of synaptic potentials. *J Neurosci Methods* 1995;62:207-12.
29. Kuras A, Gutmanienė N. Multi-channel metallic electrode for threshold stimulation of frog's retina. *J Neurosci Methods* 1997;75:99-102.
30. Kuras A, Gutmanienė N. Technique for producing a carbon-fibre microelectrode with fine recording tip. *J Neurosci Methods* 2000;96:99-102.
31. Bistrabas RJ, Gutman AM, Kuras AV, Mickis AM, Chusainovienė NP. Vlijanie jonov kadmija na sinapticheskuju peredachu v tektume legushki. (The effect of cadmium ions on synaptic transmission in the tectum of the frog.) *Neirofiziologija* 1989;21:756-65.
32. Gruodis J, Gutman A, Kuras A. Registracija kvanta EEG i ee primeneniye. (Recording the EEG quantum and its application.) In: Funkcional'noe znachenie elektricheskikh processov golovno mozga. Moskva: Nauka; 1977. p. 269-74.
33. Gutman A, Kuras A. Issledovanie retino-tektal'nykh sinapsov liagushki s pomoshchju metoda registracii sumarnogo vnekletochnogo PSP sinapsov odnogo aksona. (Study of frog retino-tectal synapses using a method of recording the summary extracellular PSP of the synapses of a single neuron.) *Neirofiziologija* 1976;8:434-7.
34. Gutman AM, Kuras AV, Chusainovienė NP. Svoystva vnekletochnogo monosinapticheskogo potentsiala odinochnogo afferenta v svete teorii dendritov s N-obraznoj volt-ampernoj kharakteristikoj. (Properties of extracellular monosynaptic potential of a single afferent in the light of the theory of dendrites with N-shaped volt-ampere characteristics.) *Biofizika* 1989; 34:124-9.
35. Gutman A, Šimoliūnas A. Teorija potentsiala EEG v modeli tonkikh obolochek mozga. 5. Tangencialno orientirovannye dipoli v glubine i na poverkhnosti mozga. (EEG potential theory in a model with thin brain integuments. V. Tangentially oriented dipoles in the depth and on the surface of the brain.) *Biofizika* 1976;21:1126-9.
36. Gutman A, Šimoliūnas A. Teorija potentsiala EEG v modeli tonkikh obolochek mozga. 4. Radialnye dipoli i ikh dvojnye sloi v glubine i na poverkhnosti mozga. (Theory of the EEG potential in models of the leptomeninges of the brain. IV. Radial dipoles and their double layers in the depths and on the surface of the brain.) *Biofizika* 1976;21:898-904.
37. Gutman A, Šimoliūnas A. Teorija potentsiala EEG v modeli tonkikh obolochek mozga. 3. Istochnik – tangencialnyj dvojnoj sloj (EEG potential theory in a model with thin brain integuments. III. Source-tangential double layer in the cortex.) *Biofizika* 1976;21:551-5.
38. Gutman A, Šimoliūnas A. Teorija potentsiala EEG v modeli tonkikh obolochek mozga. 2. Model mnogoslajnogo ploskogo kabelia. (Theory of EEG potentials in a model of thin brain integuments. II. Model of a multilayer flat cable.) *Biofizika* 1976;21:349-51.
39. Gutman A, Šimoliūnas A. Teorija potentsiala EEG v modeli tonkikh obolochek mozga. 1. Model mnogoslajnogo sfericheskogo kabelia. (EEG potential theory in a model with thin brain integuments. I. Multilayer spherical cable model.) *Biofizika* 1976;21:129-33.
40. Gutman A, Šimoliūnas A. Sravnenie reshenij priamoj i obratnoj zadach elektroencefalografii v modeliakh izolirovanogo shara i tonkikh obolochek mozga. (Comparison of solutions to linear and reciprocal problems of electroencephalography in models of an isolated sphere and the leptomeninges of the brain.) *Biofizika* 1980;25:700-2.
41. Gutman A, Šimoliūnas A. Teorija polia tokov, navedennykh sistemoy elektrodov, raspolzhenykh na skalpe. (The theory of current fields induced by scalp electrodes.) *Biofizika* 1990; 35:128-31.
42. Gutman A, Telksnys L, Šimoliūnas A. Teorija potentsiala EEG v modeli tonkikh obolochek mozga. (Theory of EEG potential in a model of the thin membranes of the brain.) *Biofizika* 1979;24:299-306.
43. Gutman AM. Ieshchio ob effektivnosti dendritnykh sinapsov. (Effectiveness of dendritic synapses.) *Biofizika* 1971;16:128-34.
44. Johnston D, Hablitz JJ, Wilson, WA. Voltage clamp discloses slow inward current in hippocampal burst-firing neurones. *Nature* 1980;286:391-3.
45. Llinas R, Sugimori M. Electrophysiological properties of *in vitro* Purkinje cell dendrites in mammalian cerebellar slices. *J Physiol (London)* 1980;305:197-214.
46. Schwindt PC, Crill WE. A persistent negative resistance in cat lumbar motoneurons. *Brain Res* 1977;120:173-8.
47. Schwindt PC, Crill WE. Properties of a persistent inward current in normal and TEA-injected motoneurons. *J Neurophysiol* 1980;43:1700-24.
48. Hounsgaard J, Hultborn H, Jespersen B, Kiehn O. Bistability of α -motoneurons in the decerebrate cat and in the acute spinal cat after intravenous 5-hydroxytryptophan. *J Physiol (London)* 1988;405:345-67.
49. Hsiao C, Christopher AN, Trueblood PR, Chandler SH. Ionic basis for serotonin-induced bistable membrane properties in guinea pig trigeminal motoneurons. *J Neurophysiol* 1998;79: 2847-56.
50. Kiehn O, Eken T. Functional role of plateau potentials in vertebrate motor neurons. *Curr Opin in Neurobiol* 1998;8:746-52.
51. Lee RH, Heckman CJ. Bistability in spinal motoneurons in vivo: systematic variations in rhythmic firing patterns. *J Neurophysiol* 1998;80:572-82.
52. Morisset V, Nagy F. Terminals of single IA fibers: location, density, and distribution within a pool of 300 homonymous motoneurons. *European J Neurosci* 1998;10:3642-52.
53. Baginskaskas A, Gutman A. Advances in neuron physiology: are they important for neurocomputer science? In: Neurocomputers and attention. Vol. I: Neurobiology, synchronisation and chaos. Holden AV, Kryukov VI, editors. Manchester: Manchester Univ. Press, 1991;1:19-31.
54. Garliauskas A, Gutman A, Šimoliūnas A. Some logic functions realized on stationary nonlinear dendrite. 1. Excitatory synapses. *Informatica* 1991;2:403-13.
55. Garliauskas A, Gutman A, Šimoliūnas A. Some logic functions realized on stationary nonlinear dendrite. 2. Inhibitory synapses. *Informatica* 1992;3:385-92.
56. Garliauskas A, Gutman A, Šimoliūnas A. Some logic functions realized on stationary nonlinear dendrite. 1. Interaction of excitatory and inhibitory synapses. *Informatica* 1992;3:469-73.
57. Gutman A. Dendritny nervnykh kletok. Teorija, elektrofiziologija, funkcija. (Nerve cell dendrites. Theory, electrophysiology, function.) Vilnius: Moksas; 1984.
58. Gutman A. Gelfand-Tsetlin principle of minimal afferentiation and bistability of dendrites. *Int J Neural Syst*

- 1994;5(2): 83-6.
59. Baginskas A, Gutman A. Forma i amplituda vozbuzhdajushchikh postsinapticheskikh potencialov na modeli nejrona s N-obraznoj voltampernoj kharakteristikoj dendritnoj membrany. (Shape and amplitude of stimulating postsynaptic potentials in a neuronal model with an N-shaped volt-ampere characteristic of the dendritic membrane.) Biofizika 1989;34: 863-7.
 60. Baginskas A, Gutman A. Zavisimost vozbuzhdajushchikh postsinapticheskikh tokov ot fiksirovannogo potenciala somy na modeli nejrona s nelinejnymi dendritami. (Relation between the excitatory synaptic currents and clamped somatic potential in the model of neuron with nonlinear dendrites.) Biofizika 1990;35:483-8.
 61. Alaburda A, Alaburda M, Baginskas A, Gutman A, Svirskis G. Uslovie bistabilnosti cilindricheskogo dendrita s peremennoj krutiznoj otricateknogo naklona N-obraznoj voltampernoj kharakteristiki membrany. (Criteria of bistability of the cylindrical dendrite with the variable negative slope of the N-shaped current-voltage membrane characteristic.) Biofizika 2001;46: 337-40.
 62. Alaburda A, Baginskas A, Gutman A. Vetviashchiasia struktura bistabil'nogo dendrita. Dendritnaja realizacija strogoj dizjunkcii. (The branching structure of the bistable dendrite.) Biofizika 2000;45:338-43.
 63. Vasiljeva ON, Baginskas A. Dvigatel'noje obuchenie pri minimalnom uchastii zritelnoj afferentacii. (Motor learning with the minimal involvement of visual afferentation.) Zh Vyssh Nerv Deiat Im I P Pavlova 2003;53:681-96.
 64. Rall W. Branching dendritic trees and motoneuron membrane resistivity. Expl Neurol 1959;1:491-527.
 65. Iasek R, Redman S. An analysis of the cable properties of spinal motoneurons using brief intracellular current pulse. J Physiol (Lond) 1973;234:613-36.
 66. Mainen ZF, Carnevale NT, Zador AM, Claiborne BJ, Brown TH. Electrotonic architecture of hippocampal CA1 pyramidal neurons based on three-dimensional reconstructions. J Neurophysiol 1996;76:1904-23.
 67. Major G, Evans JD, Jack JJB. Solutions for transients in arbitrarily branching cables: I. Voltage recording with a somatic shunt. Biophys J 1993;65:423-43.
 68. Spruston N, Jaffe DB, Johnston D. Dendritic attenuation of synaptic potentials and currents: the role of passive membrane properties. Trends Neurosci 1994;17:16-166.
 69. Svirskis G, Gutman A, Housgaard J. Detection of a membrane shunt by DC field polarization during intracellular and whole cell recording. J Neurophysiol 1997;77:579-86.
 70. Svirskis G, Baginskas A, Housgaard J, Gutman A. Electrotonic measurements by electric field-induced polarization in neurons: theory and experimental estimation. Biophys J 1997;73:3004-15.
 71. Alaburda A, Gutman A. Teorija kabelia s nepravil'nym secheniem. (Theory of a cable with an irregular cross section.) Biofizika 1996;41:723-8.
 72. Alaburda A, Baginskas A, Gutman A, Svirskis G. Adiabaticeskoe reshenie uravnenija omicheskogo kabelia. 1. Obshchaja teorija, odnorodnoe cilindricheskoe volokno. 2. Odnorodnaja kletka, vozmozhnosti dlia elektrotonicheskikh izmerenij. (Adiabatic solution of the ohmic cable equation. General theory, homogeneous cylindrical fiber.) Biofizika 1999;44:714-9.
 73. Baginskas A, Raastad M. An estimator for the electrotonic size of neurons independent of charge equalization time constants. J Comput Neurosci 2002;12:27-38.

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