

# DENDRITIC SPACE AS A CODER OF THE TEMPORAL OUTPUT

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### 1: Hierarchical temporal memory - Wikipedia

*Definition of the neuron D geometry of dendritic arborizations --Basics in bioelectricity --Cable theory and dendrites --Voltage transfer over dendrites --Current transfer over dendrites --Electrical structure of an artificial dendritic path --Electrical structure of a bifurcation --Geography of the dendritic space --Electrical structures of.*

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**Abstract** The advent of large scale neural computational platforms has highlighted the lack of algorithms for synthesis of neural structures to perform predefined cognitive tasks. The Neural Engineering Framework NEF offers one such synthesis, but it is most effective for a spike rate representation of neural information, and it requires a large number of neurons to implement simple functions. We describe a neural network synthesis method that generates synaptic connectivity for neurons which process time-encoded neural signals, and which makes very sparse use of neurons. The method allows the user to specify “arbitrarily” neuronal characteristics such as axonal and dendritic delays, and synaptic transfer functions, and then solves for the optimal input-output relationship using computed dendritic weights. The method may be used for batch or online learning and has an extremely fast optimization process. We demonstrate its use in generating a network to recognize speech which is sparsely encoded as spike times. These platforms range from analog VLSI systems in which neurons are directly simulated by using CMOS transistors as ion channels and synapses, to highly parallel custom silicon microprocessor arrays Boahen, ; Khan et al. Some of these platforms are now capable of modeling populations of over a million neurons, at rates which are significantly faster than biological real time. The advent of these systems has revealed a lack of concomitant progress in algorithmic development, and particularly in the synthesis of spiking neural networks. The NEF was first described in , and generally builds large systems from subnetworks with a standard three-layer neural structure, in which the first layer are inputs; the second layer is a very large hidden layer of non-linear interneurons, which may have recurrent connections; and the third layer is the output layer, which consists of neurons with linear input-output characteristics. The connections between the input and hidden layers are randomly weighted, and fixed they are not altered during training. The connections between the hidden and output layers are trained in a single pass, by mathematical computation rather than incremental learning. We will describe this structure in more detail in the following section. Most recently, Eliasmith and colleagues have used the method to synthesize subnetworks in a 2. This illustrates that the NEF is a meta-level framework for building cognitive systems, in which the LSHDI networks that are referred to in this report form only the building blocks. The NEF is an effective synthesis method, with three important caveats: This method also allows for adaptive learning, so that if the underlying function of the network changes, the weights can adapt to the new function. The relative merits of rate-encoding and time- or place-encoding of neural information is a subject of frequent and ongoing debate. There are strong arguments and evidence that the mammalian neural system uses spatio-temporal coding in at least some of its systems Van Rullen and Thorpe, ; Masuda and Aihara, , and that this may have significant benefits in reducing energy use Levy and Baxter, A synthesis method which can produce networks for temporally encoded spike information will have significant benefits in terms of modeling these biological systems, and in reducing the quantity of spikes used for any given information transmission. In this report we describe a new neural synthesis algorithm which uses the LSHDI principle to produce neurons that can implement spatio-temporal spike pattern recognition and processing; that is to say, these neurons are synthesized to respond to a particular spatio-temporal pattern of input spikes from single or multiple sources, with a particular pattern of output spikes. It is thus a method which intrinsically processes spike-time-encoded information. The synthesis method makes use of multiple

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synapses to create the required higher dimensionality, allowing for extreme parsimony in neurons. In most cases, the networks consist only of input neurons and output neurons, with the conventional hidden layer being replaced by synaptic connections. These simple networks can be cascaded to perform more complex functions. The starting point of the synthesis method is to have an ensemble of input channels emitting neuron spike trains; these are the input neurons. The desired output spike trains are emitted by the output neurons, and our method is used to generate the synaptic connectivity that produces the correct input-output relationship. Training may be carried out by pseudoinverse method or any similar convex optimization, so may be online, adaptable, and biologically plausible. The point of departure between this new method and our prior work Tapsan and van Schaik, is that the prior work OPIUM was suitable for solving conventional LSHDI problems but made no particular contribution to the special case of spike-timing dependent signals. The work described here is specifically aimed to provide a synthesis method for systems in which perhaps only a single spike, or none at all, is received in each channel during an observation interval. Methods which work on rate-based spike signals are generally dysfunctional in this regime, but it is considered to be widely used in mammalian neural signaling. This work also offers a synthesis method for networks to perform cortical sensory integration as postulated by Hopfield and Brody, This required that short, sparse spatio-temporal patterns be integrated to produce recognition of a learned input. There are a number of published network methodologies which process spatio-temporal spike patterns. These include reservoir computing techniques such as liquid state machines Maass et al. In particular, Maass and colleagues have analyzed the requirements for universal computation in terms of networks of these types, and have identified requirements such as network stability, input separability and fading memory as being necessary conditions Maass and Sontag, We will refer to this work in more detail in section Methods. The Tempotron consists of a leaky integrate-and-fire neuron with a number of synaptic inputs. The synaptic weights are trained by gradient descent so that the neuron exceeds its threshold for particular input patterns of spikes. This principle may well be implementable in most spatio-temporal pattern recognition networks, including that which is reported on here. A feature of the Tempotron is that the weights are learned incrementally, rather than synthesized. This report focuses on a synthesis method for networks; that is to say, one in which the network or synaptic weights are calculated analytically, rather than learned. The advantage of synthetic methods are in speed of development, and also in robustness of outcomes, as learning methods tend to be intrinsically stochastic and solutions are not necessarily repeatable. Nonetheless, it has been shown that learning methods such as spike-timing dependent plasticity STDP can produce extremely sensitive spatio-temporal pattern recognition Masquelier et al. There are also hybrid methods in which combinations of synthesis and evolution have been used to find the parameters for network weights and neurons Russell et al. Should a memory function be desired, the hidden layer may have recurrent connections. The hidden layer is usually much larger than the input layer values of  $10 \sim 50$  times are used by various practitioners; Huang and colleagues have tested networks in which the number is incrementally increased – Huang et al. The connections from the input layer to the hidden layer are randomly generated, and are not changed during training. Finally, the output layer neurons have a linear response to their inputs.

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## 2: Synthesis of neural networks for spatio-temporal spike pattern recognition and processing

*The authors explain how the whole dendritic arborization contributes to the generation of various output discharges and elucidate the mechanisms of the transfer function of all dendritic sites.*

Cohen, Saeed Afshar, Klaus M. The Neural Engineering Framework NEF offers one such synthesis, but it is most effective for a spike rate representation of neural information, and it requires a large number of neurons to implement simple functions. We describe a neural network synthesis method that generates synaptic connectivity for neurons which process time-encoded neural signals, and which makes very sparse use of neurons. The method allows the user to specify "arbitrarily" neuronal characteristics such as axonal and dendritic delays, and synaptic transfer functions, and then solves for the optimal input-output relationship using computed dendritic weights. The method may be used for batch or online learning and has an extremely fast optimization process. We demonstrate its use in generating a network to recognize speech which is sparsely encoded as spike times.

Introduction There has been significant research over the past two decades to develop hardware platforms which are optimized for spiking neural computation. These platforms range from analog VLSI systems in which neurons are directly simulated by using CMOS transistors as ion channels and synapses, to highly parallel custom silicon microprocessor arrays Boahen, ; Khan et al. Some of these platforms are now capable of modeling populations of over a million neurons, at rates which are significantly faster than biological real time. The advent of these systems has revealed a lack of concomitant progress in algorithmic development, and particularly in the synthesis of spiking neural networks. The NEF was first described in , and generally builds large systems from subnetworks with a standard three-layer neural structure, in which the first layer are inputs; the second layer is a very large hidden layer of non-linear interneurons, which may have recurrent connections; and the third layer is the output layer, which consists of neurons with linear input-output characteristics. The connections between the input and hidden layers are randomly weighted, and fixed they are not altered during training. The connections between the hidden and output layers are trained in a single pass, by mathematical computation rather than incremental learning. We will describe this structure in more detail in the following section. Most recently, Eliasmith and colleagues have used the method to synthesize subnetworks in a 2. This illustrates that the NEF is a meta-level framework for building cognitive systems, in which the LSHDI networks that are referred to in this report form only the building blocks. The NEF is an effective synthesis method, with three important caveats: This method also allows for adaptive learning, so that if the underlying function of the network changes, the weights can adapt to the new function. The relative merits of rate-encoding and time- or place-encoding of neural information is a subject of frequent and ongoing debate. There are strong arguments and evidence that the mammalian neural system uses spatio-temporal coding in at least some of its systems Van Rullen and Thorpe, ; Masuda and Aihara, , and that this may have significant benefits in reducing energy use Levy and Baxter, A synthesis method which can produce networks for temporally encoded spike information will have significant benefits in terms of modeling these biological systems, and in reducing the quantity of spikes used for any given information transmission. In this report we describe a new neural synthesis algorithm which uses the LSHDI principle to produce neurons that can implement spatio-temporal spike pattern recognition and processing; that is to say, these neurons are synthesized to respond to a particular spatio-temporal pattern of input spikes from single or multiple sources, with a particular pattern of output spikes. It is thus a method which intrinsically processes spike-time-encoded information. The synthesis method makes use of multiple synapses to create the required higher dimensionality, allowing for extreme parsimony in neurons. In most cases, the networks consist only of input neurons and output neurons, with the conventional hidden layer being replaced by synaptic connections. These simple networks can be cascaded to perform more complex functions. The starting point of the synthesis method is to have an ensemble of input channels emitting neuron spike trains; these are the input neurons. The desired output spike trains are emitted by the output neurons, and our

method is used to generate the synaptic connectivity that produces the correct input-output relationship. Training may be carried out by pseudoinverse method or any similar convex optimization, so may be online, adaptable, and biologically plausible. The point of departure between this new method and our prior work Tapsos and van Schaik, is that the prior work OPIUM was suitable for solving conventional LSHDI problems but made no particular contribution to the special case of spike-timing dependent signals. The work described here is specifically aimed to provide a synthesis method for systems in which perhaps only a single spike, or none at all, is received in each channel during an observation interval. Methods which work on rate-based spike signals are generally dysfunctional in this regime, but it is considered to be widely used in mammalian neural signaling. This work also offers a synthesis method for networks to perform cortical sensory integration as postulated by Hopfield and Brody, This required that short, sparse spatio-temporal patterns be integrated to produce recognition of a learned input. There are a number of published network methodologies which process spatio-temporal spike patterns. These include reservoir computing techniques such as liquid state machines Maass et al. In particular, Maass and colleagues have analyzed the requirements for universal computation in terms of networks of these types, and have identified requirements such as network stability, input separability and fading memory as being necessary conditions Maass and Sontag, We will refer to this work in more detail in section Methods. The Tempotron consists of a leaky integrate-and-fire neuron with a number of synaptic inputs. The synaptic weights are trained by gradient descent so that the neuron exceeds its threshold for particular input patterns of spikes. This principle may well be implementable in most spatio-temporal pattern recognition networks, including that which is reported on here. A feature of the Tempotron is that the weights are learned incrementally, rather than synthesized. This report focuses on a synthesis method for networks; that is to say, one in which the network or synaptic weights are calculated analytically, rather than learned. The advantage of synthetic methods are in speed of development, and also in robustness of outcomes, as learning methods tend to be intrinsically stochastic and solutions are not necessarily repeatable. Nonetheless, it has been shown that learning methods such as spike-timing dependent plasticity STDP can produce extremely sensitive spatio-temporal pattern recognition Masquelier et al. There are also hybrid methods in which combinations of synthesis and evolution have been used to find the parameters for network weights and neurons Russell et al. Should a memory function be desired, the hidden layer may have recurrent connections. The hidden layer is usually much larger than the input layer values of  $10^2$ – $50$  times are used by various practitioners; Huang and colleagues have tested networks in which the number is incrementally increased Huang et al. The connections from the input layer to the hidden layer are randomly generated, and are not changed during training. Finally, the output layer neurons have a linear response to their inputs. The input variables are projected to a higher dimension in this case, from 3D to 6D by means of random fixed weights and a non-linear transformation which in the case of NEF may be a leaky integrate-and-fire neuron, as inferred here. The outputs from the higher dimensional space are weighted and summed by linear output neurons, allowing for solution of the output weights by linear regression or classification. The key to the success of LSHDI networks is that they make use of the non-linear transformation that lies at the core of kernel methods such as kernel ridge regression and SVMs. This is a process by which data points or classes which are not linearly separable in their current space, are projected non-linearly into a higher dimensional space this assumes a classification task. If the projection is successful, the data are linearly separable in the higher dimensional space. In the case of regression or function approximation tasks, the problem of finding a non-linear relationship in the original space is transformed into the much simpler problem of finding a linear relationship in the higher dimensional space, i. A number of researchers have shown that random non-linear projections into the higher dimensional space work remarkably well Rahimi and Recht, ; Saxe et al. The NEF and ELM methods create randomly initialized static weights to connect the input layer to the hidden layer, and then use non-linear neurons in the hidden layer which in the case of NEF are usually leaky integrate-and-fire neurons, with a high degree of variability in their population. This paper is recommended to the reader both for its admirable readability, and the clarity with which it

explains the use of random projection as a viable alternative to learning in networks. As shown by Rahimi and Recht, random non-linear kernels can achieve the same results as random weighting of inputs to non-linear neurons. The linear output layer allows for easy solution of the hidden-to-output layer weights; in NEF this is computed in a single step by pseudoinversion, using SVD. In principle, any least-squares optimal regression method would work, including, for example, linear regression. We note that for a single-layer linear regression solution such as this, the problem of getting trapped in a local minimum when using gradient descent optimization should not occur, as the mapping is affine and hence this is a convex optimization problem. The LSHDI method has the advantages of being simple, accurate, fast to train, and almost parameter-free—the only real decisions are the number of interlayer neurons and the selection of a non-linearity, and neither of these decisions is likely to be particularly sensitive. A number of studies have shown that ELM implementations remain stable and have increasing accuracy as the number of interlayer neurons is increased Huang et al. It is intrinsically event-based and discrete rather than continuous, so networks based on smoothly continuous variables do not adapt well into this domain. Outside of simple coincidence detection, it requires the representation of time and spike history in memory the network must remember the times and places of past spikes. The output of the network is also an event spike or set of events, and therefore does not map well to a linear solution space. We have developed a biologically plausible network synthesis method in which these problems are addressed. The basic network consists of presynaptic spiking neurons which connect to a spiking output neuron, via synaptic connections to its dendritic branches, as illustrated in Figure 2. The synapses are initialized with random weights which do not change thereafter; this, together with a subsequent non-linearity, provides the projection to a higher dimension required for the improved separability. The dendritic branches sum the synaptic input currents. Some user-selected feature of the network—recurrent connections, axonal or dendritic delay, synaptic functions, or some combination of these—implements memory in the form of persistence of recent spikes; and there must be a non-linear response, which provides the non-linearity in projection necessary for improved separability. In the top schematic in Figure 2 we have renamed the hidden layer as synapses, to emphasize that these the hidden layer elements are not spiking neurons. Presynaptic neurons are connected to a postsynaptic neuron through randomly generated, fixed weighted synapses. Synapses are implemented as filter elements which produce a non-linear impulse response, in response to incoming spikes. The postsynaptic dendritic branch acts as a hidden layer element, and integrates the synaptic currents by means of a non-linear time-persistent filter. Memory may be implemented specifically as axonal or dendritic delays, or in terms of axonal functions. Dendritic signals are summed at the soma, and if they exceed a threshold, the axon hillock emits a spike. The outputs from the dendritic branches are summed in the soma of the output neuron. At this stage we are able to use a linear solution to calculate the correct weights for the connection between dendritic branches and soma; solution by pseudoinverse or backpropagation will both work. The linear solution solves the dendritic weights required to produce soma values which are below threshold for non-spike times and above threshold for spike times. The soma potential value for which the linear weights are calculated can be set to be one of two binary values, as in a classifier output; for example, it can be set to unity at spike output times, and zero when no spike is wanted. This may not be necessary in some applications where an analog soma potential would be a useful output. The final output stage of the neuron is a comparator with a threshold for the soma value, set at some level between the spike and no-spike output values. If the soma potential rises above the threshold, a spike is generated; and if it does not, there is no spike. This represents the generation of an action potential at the axon hillock. The reason that this network works is that it converts discrete input events into continuous-valued signals within the dendritic tree, complete with memory the synapses and dendritic branches may be thought of as infinite-impulse response filters; and at the same time this current and historic record of input signals is projected non-linearly into a higher-dimensional space. The spatio-temporal series of spikes are translated into instantaneous membrane potentials. We can then solve the linear relationship between the dendritic membrane potentials and the soma potential, as though it was a time-independent classification problem: The linear

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solution is then fed to the comparator to generate an event at the axon of the output neuron. One issue is that when output spikes are sparse which is a common situation there is little impetus for the network to learn non-zero outputs. We have increased the quality of learning by adding non-zero weight to the target sequences, by increasing either the target output spike amplitude, or width, or both. In most cases it is more appropriate to increase the width as in the example network of section 3. The inputs to this method do not necessarily need to be spikes. The method will work to respond to any spatio-temporal signals which fall within an appropriate range of magnitude. However, given that the target for this work is synthesis of spatio-temporal spike pattern processing systems, we analyze the system for spiking inputs. The axon signals are weighted and transmitted to the dendritic branch, which sums inputs from several axons. The axon signals are non-linearly transformed.

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## 3: Dendrite - Wikipedia

*Electrical Dynamics of the Dendritic Space by Sergiy Mikhailovich Korogod, , available at Book Depository with free delivery worldwide.*

A single level in the hierarchy possibly contains several regions. Higher hierarchy levels often have fewer regions. Higher hierarchy levels can reuse patterns learned at the lower levels by combining them to memorize more complex patterns. Each HTM region has the same basic functionality. In learning and inference modes, sensory data  $e$ . In generation mode, the bottom level regions output the generated pattern of a given category. The top level usually has a single region that stores the most general categories concepts which determine, or are determined by, smaller concepts in the lower levels which are more restricted in time and space[ clarification needed ]. When set in inference mode, a region in each level interprets information coming in from its child regions in the lower level as probabilities of the categories it has in memory. Each HTM region learns by identifying and memorizing spatial patterns, which are combinations of input bits that often occur at the same time. It then identifies temporal sequences of spatial patterns that are likely to occur one after another. The new findings on the neocortex are thus progressively incorporated into the HTM model, which can thus change over time. The new findings do not necessarily invalidate the previous ones, so ideas from one generation are not necessarily excluded in its successive one. Because of this evolving nature of the theory, there have been several generations of HTM algorithms [5] , which are briefly described below.

**Training[ edit ]** During training, a node or region receives a temporal sequence of spatial patterns as its input. The learning process consists of two stages: The spatial pooling identifies in the input frequently observed patterns and memorizes them as "coincidences". Patterns that are significantly similar to each other are treated as the same coincidence. A large number of possible input patterns are reduced to a manageable number of known coincidences. The temporal pooling partitions coincidences that are likely to follow each other in the training sequence into temporal groups. Each group of patterns represents a "cause" of the input pattern or "name" in On Intelligence. The concepts of spatial pooling and temporal pooling are still quite important in the current HTM theory. Temporal pooling is not yet well understood, and its meaning has changed over time as the HTM theory evolved.

**Inference[ edit ]** During inference, the node calculates the set of probabilities that a pattern belongs to each known coincidence. Then it calculates the probabilities that the input represents each temporal group. This belief is the result of the inference that is passed to one or more "parent" nodes in the next higher level of the hierarchy. If sequences of patterns are similar to the training sequences, then the assigned probabilities to the groups will not change as often as patterns are received. The output of the node will not change as much, and a resolution in time[ clarification needed ] is lost. The higher-level node combines this output with the output from other child nodes thus forming its own input pattern. Since resolution in space and time is lost in each node as described above, beliefs formed by higher-level nodes represent an even larger range of space and time. This is meant to reflect the organization of the physical world as it is perceived by human brain. Jeff Hawkins postulates that brains evolved this type of hierarchy to match, predict, and affect the organization of the external world. It relies on a data structure called sparse distributed representations that is, a data structure whose elements are binary, 1 or 0, and whose number of 1 bits is small compared to the number of 0 bits to represent the brain activity and a more biologically-realistic neuron model often also referred to as cell, in the context of the HTM theory. In this new generation, the layers and minicolumns of the cerebral cortex are addressed and partially modeled. An HTM layer creates a sparse distributed representation from its input, so that a fixed percentage of minicolumns are active at any one time[ clarification needed ]. A minicolumn is understood as a group of cells that have the same receptive field. Each minicolumn has a number of cells that are able to remember several previous states. A cell can be in one of three states: Spatial pooling[ edit ] The receptive field of each minicolumn is a fixed number of inputs that are randomly selected from a much larger number of node inputs. Based on the specific input pattern, some

minicolumns will be more or less associated with the active input values. Spatial pooling selects a relatively constant number of the most active minicolumns and inactivates inhibits other minicolumns in the vicinity of the active ones. Similar input patterns tend to activate a stable set of minicolumns. The amount of memory used by each layer can be increased to learn more complex spatial patterns or decreased to learn simpler patterns. Active, inactive and predictive cells[ edit ] As mentioned above, a cell or a neuron of a minicolumn, at any point in time, can be in an active, inactive or predictive state. Initially, cells are inactive. How do cells become active? If none of the cells in the active minicolumn are in the predictive state which happens during the initial time step or when the activation of this minicolumn was not expected , all cells are made active. How do cells become predictive? Thus a cell learns to recognize a known sequence by checking whether the connected cells are active. If a large number of connected cells are active, this cell switches to the predictive state in anticipation of one of the few next inputs of the sequence. The output of a minicolumn[ edit ] The output of a layer includes minicolumns in both active and predictive states. Thus minicolumns are active over longer periods of time, which leads to greater temporal stability seen by the parent layer. Inference and online learning[ edit ] Cortical learning algorithms are able to learn continuously from each new input pattern, therefore no separate inference mode is necessary. During inference, HTM tries to match the stream of inputs to fragments of previously learned sequences. This allows each HTM layer to be constantly predicting the likely continuation of the recognized sequences. The index of the predicted sequence is the output of the layer. Since predictions tend to change less frequently than the input patterns, this leads to increasing temporal stability of the output in higher hierarchy levels. Prediction also helps to fill in missing patterns in the sequence and to interpret ambiguous data by biasing the system to infer what it predicted. The validity of the CLAs[ edit ] The following question was posed to Jeff Hawkins September with regard to cortical learning algorithms: In the neuroscience realm there are many predictions that we can make, and those can be tested. In our case that remains to be seen. To the extent you can solve a problem that no one was able to solve before, people will take notice.

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## 4: - NLM Catalog Result

*Contents: Definition of the neuron -- 3D geometry of dendritic arborizations -- Basics in bioelectricity -- Cable theory and dendrites -- Voltage transfer over dendrites -- Current transfer over dendrites -- Electrical structure of an artificial dendritic path -- Electrical structure of a bifurcation -- Geography of the dendritic space.*

Definition of the neuron; 2. Basics in bioelectricity; 4. The cable theory and the dendrites; 5. Voltage transfer over the dendrites; 6. Current transfer over dendrites; 7. Electrical structure of an artificial dendritic path; 8. Electrical structure of a bifurcation; 9. Geography of the dendritic space; Electrical structures of biological dendrites; Electrical structure of the whole arborization; Electrical structures in the 3D dendritic space; Dendritic space as coder of the temporal output patterns; Their complexity and diversity lends a majesty and beauty to the task of understanding the brain. But are they more than just random protrusions? Could their very complexity and diversity be important for the computational properties of the brain? I am sure that readers of this book will also be convinced. The book progresses through careful treatment of the electrical properties of dendrites to how the geometry interacts with synaptic input to produce rich repertoires of firing output. It is an important book for experts and students of dendrites alike as well as an eye-opener for neuroscientists in every field. Serge Korogod and Suzanne Tyc-Dumont characterize the dendrites as an immense unknown. They have been pioneers in exploring this frontier. In this book they have distilled lifetimes of work by themselves and colleagues in France and the Ukraine to formulate new rules for how the electrical states of dendritic arborizations represent space and time in generating the neural code. In clear language they show how the interactions between these passive and active properties and dendritic geometry create different scales of dynamical dendritic space. New insights are provided into the significance of the dendrites of motoneurons, cerebellar Purkinje cells, and cortical pyramidal neurons. Their models available online give dramatic evidence for these insights. This is a key book for all those interested in dendrites and in the neural basis of cognition and behavior. Shepherd, Yale University School of Medicine.

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## 5: Electrical Dynamics of the Dendritic Space - PDF Free Download

*ELECTRICAL DYNAMICS OF THE DENDRITIC SPACE* The authors explain how the whole dendritic arborization contributes to the.

This will be a very peculiar space: It is mysterious and practically unexplored like the outer space we glimpse at in the sky. Curiously, we can further extend this analogy: This was performed in the pioneering work by Paul Gogan and co-workers using a modified astronomical camera to image the microstructure of the dendritic membrane during the excitation of single live neurons in culture see references in Chapter The explorers of the dendritic space still have to invent the appropriate spacecrafts and technologies. As in cosmology, experimentation is limited, and mathematical and computer models are the only way of gaining insight into the nature of the dendritic space. The itinerary of our travel relies on these tools. We start with a brief historical background to the dendritic problem and describe the origin of the structural data used for further morphometric and computer simulation studies of the dendritic arborizations Chapters 1 and 2. Chapter 3 describes basic bioelectricity with emphasis on space. We show how charge carriers are separated in space and thus electric fields and currents are created across the neuronal membrane. An important generalization is that, despite multiplicity and diversity of channel types, the number of different types of current-voltage relations is restricted to three. Chapter 4 recapitulates the cable theory of the dendritic transfer properties with special focus on the terms of the cable equation which determine the electrical communication across the membrane and along the dendritic membrane. This issue is further developed in Chapters 5 and 6, specifying the voltage and current transfer along the dendrites. We highlight that the transfer maps provide an informative representation of the dendritic electrical structure. Chapters 7 and 8 explain how the electrical structures of an artificial dendritic path and of a branch bifurcation are built and how they indicate electrical relations in different dimensions of the dendritic space that are the proximal-to-distal and the path-to-path relations. Next the critical role of metrical asymmetry of the dendritic branches becomes obvious. Chapter 9 navigates in the dendritic space of biological neurons and introduces our library of reconstructed cells providing specific examples of metrical asymmetry of complex dendritic arborizations. Chapter 10 explores the electrical structures of single biological dendrites as the basic elements for constructing the whole arborization. Here electrical features related to elementary structural heterogeneities present in random combinations in the biological dendrites are noticeable. The electrical structures of the whole reconstructed dendritic arborizations of different types of neurons are analyzed and classified in Chapters 11 and Relations of the electrical structures related to size, complexity and asymmetry of the arborizations are explored. Finally, Chapter 13 considers the consequences of morphological and electrical structures of the dendritic arborizations for the generation of output discharge patterns. These spatial-temporal patterns indicate some new emerging rules by which the dendrites govern the whole cell activity. This book results from more than 15 years of cooperation between French and Ukrainian laboratories: It originated in the form of seminars, lectures, published papers and notes for students. We have benefited from innumerable discussions with students and colleagues. To acknowledge all of them personally is impossible but we wish to thank first our collaborators who have co-authored our published articles and who were directly involved in various aspects of our work at different periods between and This book would have never happened without them. In the French team, we are specially grateful to Dr. Cesira Batini and Dr. We should like to pay tribute to Paul Gogan who initiated the quantification of dendritic geometry. His vision was far in advance of the impact of computer science in biology. He had foreseen what could be done by introducing high computational technology in our neurobiological laboratory. His knowledge of electrophysiology, his wide scientific background and his generous participation in our work make him an essential person to thank. We would also like to thank the technicians, secretaries, programmers and photographers of our laboratories for their generous assistance and invaluable help. In the Ukrainian team, Yuri Ivanov, Irina Kopysova and Vladimir Sarana valuably

participated at earlier stages of our joint work on the dendritic processing. We especially acknowledge the contribution of Dr. Iryna Kulagina, who is the coauthor of most of the results presented in this book, some of which have already Preface xi been published, as well as unpublished data in Chapter Her thorough and creative work provided novel dynamic electrical maps of the dendritic space which look sunny and bear clear landmarks of the determinative role of geometry in spatial-temporal electrical phenomena in the dendrites. We appreciate the creative contribution by Valery Kukushka who developed the NeuronViewer, a tool for interactively displaying spatial-temporal dendritic activity described in Chapter Scientific cooperation between our teams was efficiently supported by the French Embassy in Ukraine and we are deeply grateful for that. We want to thank our friends and colleagues Dr. Gerta Vrbova for reading some parts of the manuscript and for their comments, criticisms and encouragement. Finally and importantly, we regret that we can only provide an incomplete picture of dendritic spatial processing, but we are happy to open this space for younger generations of researchers. This long period of trial and error and of vigorous opposition by the adherents of the reticularism is simply explained by the great difficulty of recognizing a nerve cell on histological preparations Figure 1. All becomes clear in our minds. Why do dendritic arborizations exist, why are they so varied, so abundant, so extensive? Simply to enable the cell to receive, and to transmit to its cylinder-axis, the greatest possible variety of signals, from as many different sources as possible; put simply, to make of the cell a microcosm whose connections to the interior and exterior worlds are as numerous and complex as possible. He called the nervous tissue the most intricate structure known in the living world. He observed a great number of neurons stained with the Golgi method in a variety of species. It was in the darwinism context of the time and tuned with the comparative phylogenetic approach. During evolution, the structural complexity of the dendritic arborization is greatly increased and he also illustrated the idea that the ontogenetic history of a neuron replicates its phylogenetic history Figure 1. The evolutionary aspects of the shapes of cellular structures were also studied in the Moscow Brain Institute, where the concept that the higher we ascend the 1 2 Definition of the neuron Figure 1. The dendrites become increasingly important and complex. Growth of the the dendritic arborization of a pyramidal cell observed at different stages of development of the human embryo. A definitive nervous system first appears unequivocally in the coelenterates including hydroids, jellyfish, sea anemones and comb jellies some million years ago. The nerve cell types evolve from unipolar to bipolar, multipolar and heteropolar types Figure 1. The most primitive left send axons into a superficial plexus. In animals with central nervous systems the commonest type is a similar bipolar cell in the epithelium with short, simple or slightly elaborated arthropod distal process and an axon entering the central nervous system and generally bifurcating into ascending and descending branches. A presumably more derived form is that with a deep-lying cell body and long branching distal process with free nerve endings. In vertebrates such cells secondarily become unipolar and grouped into the dorsal root ganglia. Isopolar, bipolar and multipolar neurons in the nerve net of medusa. These may be either or both interneurons and motoneurons: Unipolar neurons representative of the dominant type in all higher invertebrates. Both interneurons and motoneurons have this form. The upper four are examples of interneurons and lower two of motoneurons. Dendrites may be elaborated but are not readily distinguished from branching axonal terminals. The number and exact disposition of these two forms of endings and of major branches and collaterals are highly variable. These are the dominant types in the central nervous system of vertebrates. The upper two represent interneurons and the lower a motoneuron. Adapted from Bullock and Horridge, The shape hypothesis is a concept within other principles operating in evolution. The evolution of progressively more complex functions has been made possible by the evolution of more complex structural patterns, hence more complex connectivity and greater differences between individual neurons. From lower to higher animals there is a scale of increasing complexity in connectivity patterns that is made possible by greater structural specificity and resolution in the morphogenetic mechanisms by which neurons become a highly complex system. How neurons grow into the fantastic patterns of connections that bring about their properties, which make in turn their richness of behaviours, remains unknown. We know that the driving forces of evolution have created the conditions for an

enormous increase in the number of elements, in particular those in between receptors and motor neurons, the number and profusion of their branching processes together with the differentiation of shapes and connections. This structural complexity is the background that provides for complex manipulations of signals representing internal and external worlds. An important contemporary concept of the neuron doctrine is that the neuron is made of several regions of different functional capacity facultatively interacting in complex ways, which will be discussed in later chapters. Some of the functionally diverse regions correspond to the anatomically distinct parts of the cell. The axon is a process specialized to distribute or conduct nerve impulses generally over great distances. It is smooth and only sends off branches at long intervals, if at all. It is commonly surrounded by a barrier of nonnervous cells called neuroglia inside the central nervous system and Schwann cells outside. The dendrites are processes specialized for collecting information from other neurons, glial cells, circulating hormones and extracellular signals. Vertebrate dendrites are commonly highly branched, irregular in thickness, thorny and filled with cytoplasm more like that of the soma than that of the axon. No other cells can compete with neurons and their dendritic arborizations for sheer complexity of form and the extraordinary range of sizes that they display Van der Loos, Figure 1. The membrane that surrounds every living cell is essentially such a lipid sheet formed into a bubble. The lipids are the primary component of cell membranes. Particularly abundant are the phospholipids, a class of lipids that consist of a sugar molecule glycerol linked to two fatty acids and to a polar alcohol molecule via a phosphodiester 1. Purkinje cell adult human ; B: These molecules are amphiphilic, containing both polar and non-polar domains. Phospholipids form sheets by lining up with non-polar domains inward and polar domains outward. Channels are macromolecular pores lodged in the lipid bi-layer that make up the cell membrane and are positioned in a transmembrane orientation such that one end is in contact with the environment and the other end is located in the cellular interior. Integral membrane proteins consist of one or several transmembrane TM regions connected by extra-membrane segments. TM regions are 15-20 amino acids in length; just enough to span the lipid bilayer. They mediate the transport of ions and small molecules across the cell membrane along their chemical potential gradient. The other membrane components are carriers, which bind to a solute and move it across the membrane and protein pumps, which transport ion species against the chemical potential gradient expending energy in the process. Most channels in contemporary cells are highly selective to only one type of ion: The selectivity is encoded in the amino acid sequence. The ligand-gated superfamily of channels is activated in response to specific interactions with small molecules.

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