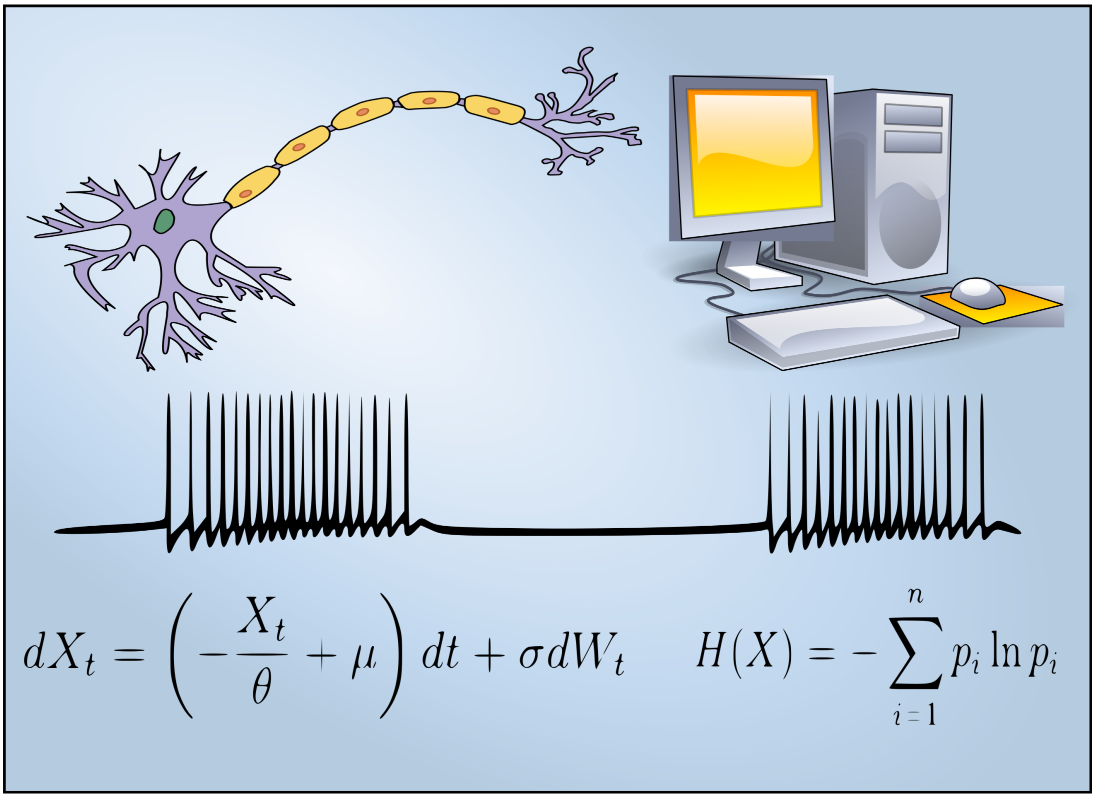
Neural Coding: Information beyond Shannon



Programme and Abstracts

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Institute of Physiology
Academy of Sciences
of the Czech Republic

Celebrating the 60th anniversary of its foundation

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Foreword

A Random Walk through Computational Neuroscience and Sixty Years of the Institute of Physiology, Prague

"A *neuron* is an electrically excitable cell that processes and transmits information ..." is the opening of the Wikipedia article if inquiring about neuron. This fact automatically implies an everlasting close relationship between neuroscience and information theory. Because of the celebration of *the sixtieth anniversary of the Institute of Physiology* we wish to remind the participants of this workshop that our Institute has always been active in this close interdisciplinary interaction, only the labels have changed over the decades. Of course, without claiming completeness and precedences, we wish to mention some names close to us and their roles in the history of the Institute and in the history of the field in general.

The concept of randomness is crucial to information theory, and its application came later, after the famous formalizations made in neuroscience by McCulloch-Pitts and Hodgkin-Huxley. George Gerstein published a paper called "Mathematical models for all-or-none activity of some neurons" in the journal *IRA* (now *IEEE*) *Transactions on Information Theory*. Simultaneously many other papers aiming to find how information is coded by neurons opened the golden era in this direction of research. Personally, the sixties were great in so many respects so why should not theoretical neuroscience also be included. In this decade, papers on the topic of stochastic neuronal activity started to appear in large numbers being published in the most prestigious journals.

Two immensely important meetings were organized during that period. Eduardo Caianiello attracted prominent researchers to Ravello to attend a *School on Neural Networks* in June, 1967. The beauty of the Amalfi coast surely stimulated the participants and the contributions of Luigi Ricciardi, Peter Johanesma or Michael Arbib's. Some ideas on information processing in the cerebellum, should be mentioned. In the following year, January, 1968, and at the almost as beautiful location as Ravello, in San Diego, the workshop on *Neural Coding* was organized by Donald Perkel and Theodore Bullock. Such a long time after the event, it is difficult to speculate why no Europeans, except Donald McKay from UK, who also attended the Ravello meeting, were invited to San Diego. Among the participants were – Jack Cowan, George Gerstein, Vernon Mountcastle, Wilfried Rall, Jose (Pepe) Segundo, Richard Stein and others, several of whom also attended the meeting in Ravello. No one from Prague participated in these meetings, nevertheless, what was going on here was at least part of the general trend.

George Gerstein spent his sabbatical here at the Institute and it was a few years after publication of his seminal article, coauthored by Benoit Mandelbrot, on Random walk models for spike activity of a single neuron. At the same time two young researchers Jan Bures and Tomas Radil arranged that a LINC-8 was purchased and used in recording and analyzing the spiking activity of neurons. (The LINC-8 was built as a laboratory computer. It was small enough to fit in a laboratory environment and included hardware capabilities necessary to monitor and control experiments.) Even younger fellows Ivan Krekule, Jan Skvaril and Josef Syka did both experimental and theoretical research in that direction. The end of the sixties was so turbulent in Prague that this so promising effort did not last very long. At least, the paper in *Kybernetika* (that time computational neuroscience was usually labeled as Cybernetics) on Spontanous discharge patterns of mesencephalic neurons was published in 1971.

After this period, history started to move much faster, as I personally recall. However, the hope in cracking the neural code decreased. In the seventies, we had several visitors. George Moore came to visit Ivan Krekule and gave a seminar at the Institute. Renato Capocelli, a student of Luigi Ricciardi brought us a new book by his teacher on stochastic diffusion processes. Later on, Henry Tuckwell shortly visited Jan Bures, the former one being the spreading depression modeler, the latter an expert on its experimental studies. The time changed into the eighties and at this point the third meeting has to be mentioned. Luigi Ricciardi organized it in May of 1987. The opening was held in Palazzo Cassano in Napoli and the meeting at hotel Caesar Augustus on the island of Capri. The beauty of the location probably surmounted the previous meetings and the impulse for future research was at least equally important. Among many participants were Sun-ichi Amari, Arun Holden and John Rinzel together with others who had already attended Ravello twenty years earlier. At the same time, the label "computational" became fashionable. Actually, the honour of first using this term is claimed by Eric Schwartz who, at the invitation of Charles Smith and Carl York, organized a meeting and later edited a book called *Computational Neuroscience*. However, simultaneously Neuroinformatics as a field which stands at the intersection of neuroscience and information science was established. So, we have several labels suitable for this workshop but the labels are not as important as the content.

The end of the eighties brought enormous changes in our personal lives. Suddenly we became a real part of events. This period is so recent that it is hard to recall it in a proper perspective. In the autumn of 1995 we organized the Neural Coding workshop and from that time every second year the event has moved all around the world coming back to Prague a year ago. Pepe Segundo is always with us and it ensures the continuity with the workshop organized in San Diego fifty-five years ago. Pepe is a permanent attender but the other legendary figures, at least occasionally, join these workshops. George Gerstein was with us in Tainan, John Rinzel in Plymouth, Luigi Ricciardi in Prague and Versailles, a session remembering the work of Donald Perkel was organized in Montevideo, Sun-ichi Amari and Henry Tuckwell come more frequently. Many, many other old and new friends attend but to mention all of them would make the list too long for this short Foreword. However, those who extended their contacts into a long lasting cooperation deserve to be acknowledged – Jean-Pierre Rospars, Susanne Ditlevsen, Laura Sacerdote, Roger Rodrigues, Charlie Smith, Henry Tuckwell, Cindy Greenwood and recently two young colleagues – Ryota Kobayashi and Massimilliano Tamborrino.

Now we meet on a new occasion and we hope that the location and the interaction among the participants will again remain in your hearts and minds for a long time.

Petr Lansky

Workshop Information

Main Topics

One of the primary, and still largely unresolved, goals of computational neuroscience is to understand *how neurons process and convey information*. Since the early studies, the challenges of understanding the principles of *neuronal coding* have attracted increasing number of scientists from different fields. Among the main themes of the workshop is:

- What can information theory tell us about information processing in neurons?
- Influence of environmental statistics on information coding in sensory neurons.
- Noise and its role in neuronal coding.

The main impact of the workshop lies in the distribution of ideas and approaches that, although applied to different systems, share the common language of information theory. In particular, we believe that the computational neuroscience community has not yet fully benefited from the richness and generality of information theory as originally proposed by Shannon himself. Consequentially, workshops of this kind have the potential to change the perception of certain topics and perhaps, hopefully, provide solutions to some of the long-lasting questions in neuronal information processing.

Conference Venue and Organizers

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Programme

Wednesday, July 3		
Opening		
9:00– 9:20	Welcoming by the Director of the Institute of Physiology AS CR *Lucie Kubinova*	
9:20– 9:30	*Break*	
Session I		
9:30– 9:55	Stochastic Neuronal Models and Information Transfer in Neurons *Petr Lansky*	p. 13
9:55–10:20	Non-parametric Estimation of Mutual Information of *d*-dimensional Vectors *Laura Sacerdote*	p. 19
10:20–11:00	*Coffee Break*	
Keynote Lecture		
11:00–12:00	Mathematical and Neuroscientific Arguments for Generalized Inverse Gaussian ISI Durations of Cortical Neurons *Toby Berger*	p. 8
Session II		
12:00–12:25	On the Functional and Structural Characterization of Hubs in Protein-protein Interaction Networks *Concettina Guerra*	p. 9
12:25–14:30	*Lunch*	
Session III		
14:30–14:55	*(Topic to be specified later)* *Daniel Suta*	p. 20
14:55–15:20	A Simple Model That Can Accurately Predict Spike Timings Generated by Various Kinds of Neurons *Ryota Kobayashi*	p. 10

15:20–15:55	Adaptation Improves Information Transfer in Hodgkin-Huxley Neurons *Lubomir Kostal*	p. 11
15:55–16:30	*Coffee Break*	

Session IV

16:30–16:55	Computing Surprise *Alberto Apostolico*	p. 7
16:55–17:20	Information Filtering by Spiking Neurons as a Simple Form of Information Processing *Benjamin Lindner*	p. 15
17:20–17:55	The t-Transform and Its Inverse in Modeling Neural Encoding and Decoding *Aurel Lazar*	p. 14
18:30–19:00	*Registration*	
19:00–22:00	*Dinner*	

Thursday, July 4

Session V

9:00– 9:25	On the Calculation of Fisher Information and Entropy by Penalized ML Density Estimation *Ondrej Pokora*	p. 17
9:25– 9:50	Beyond Shannon Information in Quantum Communication *Vladyslav Usenko*	p. 21
9:50–10:15	Maximizing Information Divergence from Exponential Families *Frantisek Matus*	p. 16
10:15–11:15	*Coffee Break*	

Session VI

11:15–11:40	The Effect of Interspike Interval Statistics on the Information Gain under the Rate Coding Hypothesis *Shinsuke Koyama*	p. 12
11:40–12:05	Information from Molecules: a Pluridisciplinary Approach to the Sense of Smell *Jean-Pierre Rospars*	p. 18
12:10–12:50	**Discussion**	
13:00–14:30	*Lunch*	

Computing Surprise

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Classical information theory equates information to surprise. This talk examines the algorithmic aspects of finding surprising regularities in sequences of biological and other diverse nature. The germane challenges of computing sequence similarity and classification, based on some implicit notion of mutual compressibility, will be also briefly discussed.

Mathematical and Neuroscientific Arguments for Generalized Inverse Gaussian ISI Durations of Cortical Neurons

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The Generalized Inverse Gaussian (GIG) family of neuron models subsumes the Schrodinger/Gerstein-Mandelbrot IG model and the gamma models studied by Berger-Levy and by others. We analyze doubly matched (i.e., joint source-channel encoded) GIG neurons that maximize the Shannon average mutual information between the afferent excitation and the efferent spike train per Joule of expected energy expenditure. Mathematical and neuroscientific arguments in support of adopting GIG models for primary cortical neurons also are presented.

On the Functional and Structural Characterization of Hubs in Protein-protein Interaction Networks

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A number of interesting issues have been addressed on biological networks about their global and local properties. The connection between the topological properties of proteins in Protein-Protein Interaction (PPI) networks and their biological relevance has been investigated focusing on hubs, i.e. proteins with a large number of interacting partners. In this talk, I will address the following questions: Do hub proteins have special biological properties? Do they tend to be more essential than non-hub proteins? Are they more evolutionarily conserved? Do they play a central role in modular organization of the protein interaction network? Are there structural properties that characterize hub proteins?

A Simple Model That Can Accurately Predict Spike Timings Generated by Various Kinds of Neurons

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Information is transmitted in the brain through various kinds of neurons that respond differently to the same input signal. Hodgkin-Huxley model has been revised by including diverse ionic currents to account for the response properties of neurons. However, the revised models require the high computational cost, which hinders systematic analyses on information processing in a neuron. Here, we develop a simple neuron model that is capable of accurately predicting spike responses recorded from electrophysiological experiments (Kobayashi, Tsubo & Shinomoto, *Frontiers in Computational Neuroscience*, 2009). The key features of the proposed model are a non-resetting leaky integrator and an adaptive threshold equipped with fast (10 ms) and slow (200 ms) time constants. This model can easily be tailored to a variety of neurons, i.e., regular spiking, intrinsic bursting, and fast spiking neurons, by adjusting three parameters only. Both the high flexibility and the low computational cost would help to model the brain faithfully and to study computational properties in single neurons.

Adaptation Improves Information Transfer in Hodgkin-Huxley Neurons

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The problem of information processing and transfer in single neurons, and neuronal networks, is an intensively studied topic in computational neuroscience.

In this contribution we employ the extended Hodgkin-Huxley neuronal model, and we address the effect of adaptation on different aspects of information transmission. We analyze both the asymptotic limits on reliable information transfer (information capacity) and the bounds on non-asymptotic performance. Metabolic cost of neuronal activity and complexity of decoding operations are taken into account, thus influencing the optimal "balance" between information, cost and possible complexity of neuronal information transmission.

The Effect of Interspike Interval Statistics on the Information Gain under the Rate Coding Hypothesis

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The question, how much information can be theoretically gained from variable neuronal firing rate with respect to constant average firing rate is investigated. We employ the statistical concept of information based on the Kullback-Leibler divergence. We show that if the firing rate variation is sufficiently small and slow (with respect to the mean interspike interval), the information gain can be expressed by the Fisher information. Furthermore, under certain assumptions, the smallest possible information gain is provided by gamma-distributed interspike intervals. The methodology is illustrated and discussed on several different statistical models of neuronal activity.

Stochastic Neuronal Models and Information Transfer in Neurons

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Neural spike trains present a challenge for researchers for more than a half century. Experimental techniques are supported by modelling aiming to answer questions like – what is the code, what is the role of randomness in the neuronal firing and others. The basic types of spiking models will be mentioned and a few examples of their applications will be given. Opinions whether the models can help in cracking the neural code will be appreciated.

The t-Transform and Its Inverse in Modeling Neural Encoding and Decoding

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The t-transform is a key tool for characterizing the encoding of stimuli with spiking neural circuits. Formally, the t-transform maps an analog signal into a time sequence. For single-input multi-output neural circuits consisting of a set of receptive fields and a population of integrate-and-fire, threshold-and-fire and/or Hodgkin-Huxley neurons, the analysis of the inverse t-transform has revealed some deep connections between faithful decoding and the bandwidth of the encoded stimuli [1]. In the noiseless case, a Nyquist-type rate condition guarantees invertibility with perfect stimulus recovery [2]. In the noisy case, a standard regularization framework provides optimum stimulus recovery [3]. In addition, the decoding algorithms are tractable for stimuli encoded with massively parallel neural circuits [6]. More recently, we generalized these circuits to encode 3D color visual information for models of stereoscopic vision, to integrate sensory information of different modalities and dimensions, and to handle nonlinear dendritic signal processing [5]. These results set the stage for the first rigorous results in spike processing [4].

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Information Filtering by Spiking Neurons as a Simple Form of Information Processing

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Neural systems do not only transmit but also process sensory stimuli. A simple form of such processing, observed also experimentally, is that information about certain frequency bands of a time-dependent stimulus is discarded. In my talk I review mechanisms at the cellular and at the network level that lead to such a frequency-dependent reduction of information.

Maximizing Information Divergence from Exponential Families

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Motivated by Linsker infomax priciple, N. Ay formulated the problem of maximization of the information divergence from exponential families. This mathematical problem exposes a mechanism for implementation of the infomax in neural networks and elsewhere. Recent results and connections to statistics and cryptography will be reviewed.

On the Calculation of Fisher Information and Entropy by Penalized ML Density Estimation

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The idea of the penalized ML estimation of the density (Good, 1980, and later) and its application for the estimation of the Fisher information and the differential entropy from a sample data set will be presented. Recent experience, the benefits and the drawbacks will be discussed.

Information from Molecules: a Pluridisciplinary Approach to the Sense of Smell

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In animals the sense of smell is the most ancient and most essential of senses because it is involved in behaviours indispensable for survival such as finding and identifying food and mate. Nonetheless it has been for long the most neglected in scientific studies. Being the most primitive of senses, it was considered less interesting than the "noble" ones, hearing and seeing, on which conscious human communications are based. The situation changed in 1991 when Linda Buck and Richard Axel, who received the Nobel prize for that, discovered "a new gene family" whose function is to code for olfactory receptors. Whereas only a few tens of different receptor proteins were expected, they found a thousand ones, so 3 % of genes serve to code for olfactory receptors only, a quite large proportion for a sense deemed of secondary importance. This discovery turned an obscure field of science into a promising one, attracting a host of researchers from various disciplines.

In this talk I will present the current status of our understanding of olfaction, the nature of odorants and the long chain of events involved in their perception. The molecular mechanisms by which volatile molecules are detected at extremely low concentrations, as well as the cerebral neural networks converting the raw signals into meaningful messages, will be described. The richness of information that can be retrieved from odour plumes and the principles by which olfactory information is coded and processed in the brain will be presented. Examples taken from both invertebrates and vertebrates will illustrate how qualitative, intensitive and temporal aspects of odour signals are discriminated, and actually utilized by animals in various behaviours. The psychological, evolutionary and technological significance of these advances will also be outlined to offer a concise but comprehensive introduction to information processing in olfactory systems.

Non-parametric Estimation of Mutual Information of d-dimensional Vectors

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We demonstrate that the estimation of the mutual information is equivalent to the estimation of the entropy of a suitable random vector and this result is used to propose a non-parametric estimator for the mutual information of a d-dimensional random vector.

The equivalence result is obtained by demonstrating an equation which links the mutual information with the entropy of a suitable random vector with uniform marginal distributions. When $d = 2$, our result coincides with the findings by Jenison and Reale [1] on the connection between the mutual information and the entropy of the copula associated to the original random vector. In addition, the multivariate case requests the introduction of the so called "Linkage Functions" proposed by Li, Shaked and Scarsini [2] in a different context.

Furthermore, we present a set of examples to compare the properties of the new estimator compared with those previously described. The lack of influence of the dimensions of the considered vectors on the complexity of the system, represent, with its simplicity, the main advantages of the proposed estimator.

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(Topic to be specified later)

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Beyond Shannon Information in Quantum Communication

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We consider the task of secure quantum communication, where a substitution of Shannon information by a more general quantum Holevo information is necessary to access security. Holevo information is considered as principal upper bound on information leakage from the quantum communication channel, which can be used by an eavesdropper. We show that by properly choosing the encoding alphabet and using the quantum nature of the signal states we can effectively eliminate the information leakage. Releasing our assumptions on the power of an eavesdropper and returning to the Shannon information description, we are able to access nontrivial types of classical correlations between the communicating parties and eavesdropper. The result demonstrates an inspiring influence of quantum approach on the classical information theory.

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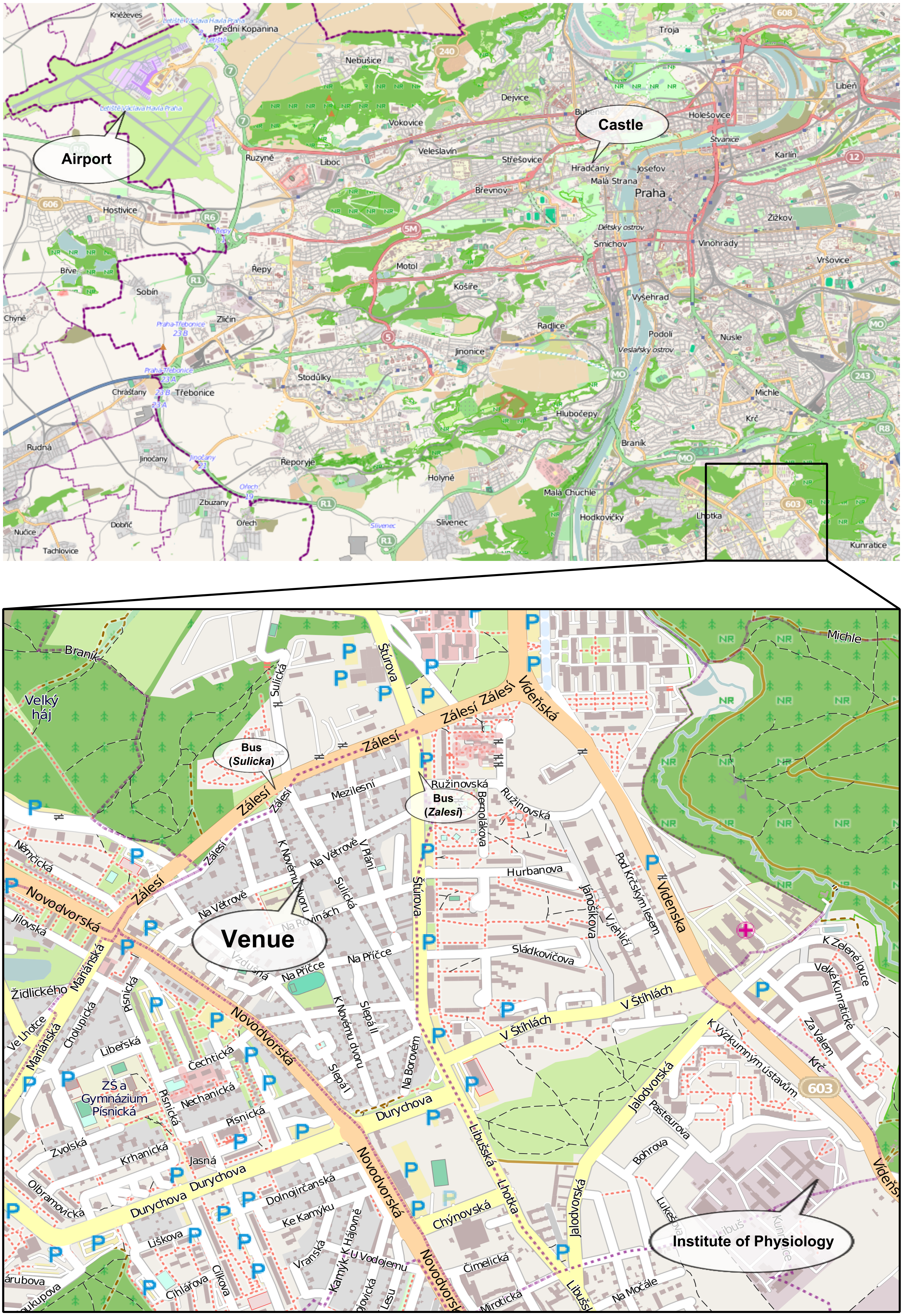
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