Final report of OTKA K 127909

We have concluded a very successful project:

Number of referred, international journal publications in the course of the project: **19**, from these:

Number of D1 journal publications: **5**

Number of Q1 journal publications: **9**

Cumulative impact factor of our journal publications in project K 127909: **59.989**

Details:

The Budapest Reference Connectome Server of ours (http://connectome.pitgroup.org) produces the consensus connectome from more than 400 braingraphs, with numerous selectable parameters. By using this server, our former PhD student, Csaba Kerepesi, has discovered the phenomenon of the Consensus Connectome Dynamics (CCD), visualized on an animation, based on real data: https://youtu.be/yxlyudPaVUE . We hypothesize that the CCD describes the development of the connections of the human brain.

Before this work, no high-definition directed braingraphs were published, because the tractography methods in use are not capable of assigning directions to the neural tracts discovered. Previous work on the functional connectomes applied low-resolution functional MRI-detected statistical causality for the assignment of directions of connectomes of typically several dozens of vertices. By using CCD, we were able to assign directions of the edges in the MRI-based human braingraphs, first in the literature.

Balázs Szalkai, Csaba Kerepesi, Bálint Varga, Vince Grolmusz: High-Resolution Directed Human Connectomes and the Consensus Connectome Dynamics, **PLOS ONE**, Vol. 14 No. 4,: e0215473 (2019) https://doi.org/10.1371/journal.pone.0215473) **[Q1 publication]**

We have mapped the frequently appearing human braingraphs in our publication, first in the literature:

Máté Fellner, Bálint Varga, Vince Grolmusz: The Frequent Subgraphs of the Connectome of the Human Brain, **Cognitive Neurodynamics** Vol. 13, No. 5, pp. 453-460 (2019) https://doi.org/10.1007/s11571-019-09535-y https://rdcu.be/bAHoe

In mapping the human structural connectome, we are in a very fortunate situation: one can compute and compare graphs, describing the cerebral connections between the very same, anatomically identified small regions of the gray matter among hundreds of human subjects. The comparison of these graphs has led to numerous recent results, as the (1) discovery that women's connectomes have deeper and richer connectivity-related graph parameters like those of men, or (2) the description of more and less conservatively connected lobes and cerebral regions, and (3) the discovery of the phenomenon of the consensus connectome dynamics. Today one of the greatest challenges of brain science is the

description and modeling of the circuitry of the human brain. For this goal, we need to identify sub-circuits that are present in almost all human subjects and those, which are much less frequent: the former sub-circuits most probably have functions with general importance, the latter sub-circuits are probably related to the individual variability of the brain structure and function.

In the work above, the frequent connected subgraphs of at most six edges are described in the human brain. We analyze these frequent graphs, and also examine sex differences in these graphs: we demonstrated numerous connected subgraphs that are more frequent in female or male connectomes. While there is no difference in the number of k edge subgraphs in males or females for k=1, and for k=2 males have slightly more frequent subgraphs, for k=6 there is a very strong advantage in the case of female braingraphs.

We have mapped the frequent complete subgraphs of the human connectome, first in the literature, in:

Fellner Máté, Varga Bálint, Grolmusz Vince: ***The Frequent Complete Subgraphs in the Human Connectome***, PLOS ONE 15(8): e0236883 (2020), 2020 **[Q1 publication]**

In the frequent complete subgraphs of the human brain networks every pair of vertices is connected by an edge. We also examined sex differences in the results. The mapping of the frequent subgraphs gives robust substructures in the graph: if a subgraph is present in the 80% of the graphs, then, most probably, it could not be an artifact of the measurement or the data processing workflow. We have listed the frequent complete subgraphs of the human braingraphs of 413 subjects (238 women and 175 men), each with 463 nodes, with a frequency threshold of 80%, and identify 812 complete subgraphs, which are more frequent in male and 224 complete subgraphs, which are more frequent in female connectomes.

We have introduced the frequent neighborhood mapping method, first time in the literature, and applied it in two works, as follows.

In the first one, we have studied the frequent neighbor sets of the most deeply investigated brain area, the hippocampus. By applying the Frequent Network Neighborhood mapping method, we identified frequent neighbor-sets of the hippocampus, which may influence numerous psychological parameters, including intelligence-related ones. We have found “Good Neighbor” sets, which correlate with better test results and also “Bad Neighbor” sets, which correlate with worse test results.

Fellner Máté, Varga Bálint, Grolmusz Vince: ***Good neighbors, bad neighbors: the frequent network neighborhood mapping of the hippocampus enlightens several structural factors of the human intelligence***, SCIENTIFIC REPORTS 10: (1) 11967, 2020 https://doi.org/10.1038/s41598-020-68914-2 **[D1 publication]**

In the second one, we have used the new method of the Frequent Network Neighborhood Mapping, which serves as a robust identification of the neighborhoods of given vertices of special interest in the graph of the human brain. We have applied the novel method for mapping the neighborhoods of the human hippocampus and discovered strong statistical asymmetries between the connectomes of the sexes, computed from the Human Connectome Project. We analyzed 413 braingraphs, each with 463 nodes. We have shown that the hippocampi of men have much more significantly frequent neighbor sets

than women; therefore, in a sense, the connections of the hippocampi are more regularly distributed in men and more varied in women. Our results are in contrast to the volumetric studies of the human hippocampus, where it was shown that the relative volume of the hippocampus is the same in men and women.

Fellner Máté, Varga Bálint, Grolmusz Vince: ***The Frequent Network Neighborhood Mapping of the human hippocampus shows much more frequent neighbor sets in males than in females***, PLOS ONE 15: (1) e0227910, 2020 https://doi.org/10.1371/journal.pone.0227910 **[Q1 publication]**

While numerous connectomical results were published enlightening the relation between the braingraph and certain biological, medical, and psychological properties, it is still a great challenge to identify a small number of brain connections closely related to those conditions. In the work, by applying the 1200 Subjects Release of the Human Connectome Project (HCP) and Support Vector Machines, we have identified just 102 connections out of the total number of 1950 connections in the 83-vertex graphs of 1064 subjects, which—by a simple linear test—precisely, without any error determine the sex of the subject. Next, we re-scaled the weights of the edges—corresponding to the discovered fibers—to be between 0 and 1, and, very surprisingly, we were able to identify two graph edges out of these 102, such that, if their weights are both 1, then the connectome always belongs to a female subject, independently of the other edges. Similarly, we have identified 3 edges from these 102, whose weights, if two of them are 1 and one is 0, imply that the graph belongs to a male subject—again, independently of the other edges. We call the former 2 edges superfeminine and the first two of the 3 edges supermasculine edges of the human connectome. Even more interestingly, the edge, connecting the right Pars Triangularis and the right Superior Parietal areas, is one of the 2 superfeminine edges, and it is also the third edge, accompanying the two supermasculine connections if its weight is 0; therefore, it is also a "switching" edge. Identifying such edge-sets of distinction is the unprecedented result of this work.

László Keresztes, Evelin Szögi, Bálint Varga, Vince Grolmusz: Identifying Super-Feminine, Super-Masculine and Sex-Defining Connections in the Human Braingraph, **Cognitive Neurodynamics**, Vol. 15. No. 6. pp. 949-959 (2021) https://doi.org/10.1007/s11571-021-09687-w [impact factor: 3.925]

In the work

"Bálint Varga, Vince Grolmusz: The braingraph.org Database with more than 1000 Robust Human Structural Connectomes in Five Resolutions, **Cognitive Neurodynamics** Vol. 15 No. 5**,** pp. 915-919, (2021) https://doi.org/10.1007/s11571-021-09670-5 [impact factor: 3.925]"

we have introduced a robust error-correcting method for the construction of human braingraphs. The method uses probabilistic tractography, filtering the extremal edge-weights, and an intelligent averaging strategy. We have detailed and discussed the specific choice of the repetition- and averaging parameters. The resulting, probably most robust dataset of human connectomes, is available at https://braingraph.org .

In the article

Balázs Szalkai, Bálint Varga, Vince Grolmusz: The Graph of our Mind; **Brain Sciences,** Vol. 11, No. 3. 342 (2021) https://doi.org/10.3390/brainsci11030342 [impact factor 3.332]

we have examined the sex differences in the male and female connectomes on a large dataset. We have found that in numerous graph-theoretical parameters women have better braingraphs than men: the female braingraphs are better expanders, have more edges, larger bipartition widths, and larger vertex cover than the braingraphs of the male subjects. These parameters are closely related to the quality measures of highly parallel computer interconnection networks: the better expanding property, the large bipartition width, and the large vertex cover characterize high-quality interconnection networks.

In the work

Kristóf Takács, Vince Grolmusz: The multiple alignments of very short sequences, **FASEB BioAdvances,** 2021;3:523-530, https://doi.org/10.1096/fba.2020-00118

we have studied the multiple alignments of very short sequences. Multiple alignments play a pivotal role in gene and gene motif identification, but the study of short sequences in this context was an unknown area.

In the work

László Keresztes, Evelin Szögi, Bálint Varga, Viktor Farkas, András Perczel and Vince Grolmusz: The Budapest Amyloid Predictor and its Applications, **Biomolecules**, 11(4) 500, (2021) https://doi.org/10.3390/biom11040500 [impact factor: 4.082]

we have introduced the Budapest Amyloid Predictor tool for hexapeptides at the address https://pitgroup.org/bap . The amyloid state of proteins is widely studied with relevance to neurology, biochemistry, and biotechnology. In contrast with nearly amorphous aggregation, the amyloid state has a well-defined structure, consisting of parallel and antiparallel β-sheets in a periodically repeated formation. The understanding of the amyloid state is growing with the development of novel molecular imaging tools, like cryogenic electron microscopy. Sequence-based amyloid predictors were developed, mainly using artificial neural networks (ANNs) as the underlying computational technique. From a good neural-network-based predictor, it is a very difficult task to identify the attributes of the input amino acid sequence, which imply the decision of the network. Here, we present a linear Support Vector Machine (SVM)-based predictor for hexapeptides with correctness higher than 84%, i.e., it is at least as good as the best published ANN-based tools. Unlike artificial neural networks, the decisions of the linear SVMs are much easier to analyze and, from a good predictor, we can infer rich biochemical knowledge. In the Budapest Amyloid Predictor webserver the user needs to input a hexapeptide, and the server outputs a prediction for the input plus the $6 \times 19 = 114$ distance-1 neighbors of the input hexapeptide.

One of the unprecedented result of the Budapest Amyloid Predictor is the site-specific amyloidogenecity order of the 20 amino acids (Table 2 in the publication above).

In the publication

Kristóf Takács, Vince Grolmusz: On the Border of the Amyloidogenic Sequences: Prefix Analysis of the Parallel Beta Sheets in the PDB_Amyloid Collection, **Journal of Integrative Bioinformatics,** Vol. 19, No. 1., (2022) pp. 20200043, https://doi.org/10.1515/jib-2020-0043 [**SCOPUS D1 publication**]

we have analyzed the prefixes of the sequences of our previously developed & published PDB_Amyloid dataset (available at https://pitgroup.org/amyloid/), and found interesting coincidences with less-known amyloid-forming proteins from the PDB.

Our contribution in the following publication includes the application of the Budapest Amyloid Predictor in evaluating the *C. elegans* proteome:

Muntasir Kamal, Levon Tokmakjian, Jessica Knox, Peter Mastrangelo, Jingxiu Ji, Hao Cai, Jakub Wojciechowski, Micael P. Hughes, Kristof Takacs, Xiaoquan Chu, Jianfeng Pei, Vince Grolmusz, Malgorzata Kotulska, Julie Deborah Forman-Kay, Peter J. Roy: A Spatiotemporal Reconstruction of the C. elegans Pharyngeal Cuticle Reveals a Structure Rich in Phase-Separating Proteins, **eLife**, https://doi.org/10.7554/eLife.79396 (2022) [impact factor: 8.713}, **[D1 publication]**

Determining important vertices in large graphs (e.g., Google's PageRank in the case of the graph of the World Wide Web) facilitated the construction of excellent web search engines, returning the most important hits corresponding to the submitted user queries. Interestingly, finding important edges -- instead of vertices -- in large graphs has received much less attention until now. Here we examine the human structural braingraph (or connectome), identified by diffusion magnetic resonance imaging (dMRI) methods, with edges connecting cortical and subcortical gray matter areas and weighted by fiber strengths, measured by the number of the discovered fiber tracts along the edge. We identify several ``single'' important edges in these braingraphs, whose high or low weights imply the sex or the age of the subject observed. We call these edges implicator edges since solely from their weight, one can infer the sex of the subject with more than 67 % accuracy or their age group with more than 62 % accuracy. We argue that these brain connections are the most important ones characterizing the sex or the age of the subjects. Surprisingly, the edges implying the male sex are mostly located in the anterior parts of the brain, while those implying the female sex are mostly in the posterior regions. Additionally, most of the inter-hemispheric implicator edges are male ones, while the intra-hemispheric ones are predominantly female edges. Our pioneering method for finding the sex- or age implicator edges can also be applied for characterizing other biological and medical properties, including neurodegenerative- and psychiatric diseases besides the sex or the age of the subject, if large and high-quality neuroimaging datasets become available.

We emphasize that our contribution below identifies statistically valid single brain connections related to the sex and the age of the subjects in a large and robust dataset. To our knowledge, our results are unprecedented in this aspect.

László Keresztes, Evelin Szögi, Bálint Varga, Vince Grolmusz: Discovering Sex and Age Implicator Edges in the Human Connectome, **Neuroscience Letters** Vol. 791, 136913 (2022) https://doi.org/10.1016/j.neulet.2022.136913 [impact factor 3.197]

The primary structure of the proteins is characterized by their amino acid sequence. While the primary structure determines the spatial folding of the proteins and, consequently, all chemical and biological properties of the given protein, inferring those properties from the amino acid sequence is a very difficult task. Here we consider the amyloid predictors: tools, which tell us if a given amino acid sequence has or has not the propensity to become amyloid.

Amyloids are misfolded protein aggregates, which -- in contrast with the unstructured aggregates -- have a well-defined structure, comprising parallel beta-sheets. Amyloids are present in numerous organisms in biology and in several human neurodegenerative diseases (e.g., Alzheimer's, Parkinson's, Huntington's diseases.

Sequence-based amyloid predictors would help the understanding of the amyloid state of the proteins: instead of the difficult, costly, and slow wet-laboratory tests, one can use the predictor on thousands or millions of inputs for enlightening the amyloidogenecity of the proteins. In the last several years, the six amino acid long peptides (the hexapeptides) have become a standard model of studying amyloid formation in dozens of publications.

We have constructed a linear Support Vector Machine (SVM) predictor for hexapeptides, with better accuracy (84%) than most of the neural network-based tools. The main advantage of our new predictor, compared with other amyloid-predictors, is the easy applicability for inferring location-dependent amyloidogenic properties of amino acids, as we describe below. We note that linear SVMs have a clear advantage here: for example, neural network-based predictors are neither simple nor easy-to-apply, and inferring the causality of their classifications is a very difficult task. In the case of SVMs, especially for linear SVMs, the causality is much more transparent.

One of the greatest advantages of linear SVM predictions is that we can easily see the reasons behind the decision of the model. If our model is accurate enough, then from the coefficients of the normal vector of the separating hyperplane, the weight-differences of the distinct variables can be derived. We apply this observation below.

Perhaps the best demonstration of the patterns, discoverable by AI predicting tools, is the amyloidogenecity patterns found by the Budapest Amyloid Predictor tool of ours. These patterns give a concise, well-defined set of rules of amyloidogenecity properties of hexapeptides: since there are 20 amino acids, one can consider 64 million = 20^6 hexapeptides, these rules are well-applicable in gaining chemical insight in the amyloid formation. We note that the correctness of the Budapest Amyloid Predictor is not 100%, but only 84%. The patterns or rules, which we describe here, do not imply the actual amyloidogenecity of the hexapeptides, but only the prediction, given by the Budapest Amyloid Predictor.

Some of the discovered patterns are demonstrated in here. The capital letters are the standard codes for the twenty amino acids, while to the positions, denoted by ``x'' one can place any amino acid (independently of the placements of other x's). For example, the pattern xxDxEx describes 20^4= 160,000 hexapeptides, all of which are predicted as non-amyloids. Similarly, the pattern CxFLWx describes 20^2=400 hexapeptides, such that all of them are predicted as amyloids.

László Keresztes, Evelin Szögi, Bálint Varga, Viktor Farkas, András Perczel, Vince Grolmusz: Succinct Amyloid and Non-Amyloid Patterns in Hexapeptides, **ACS Omega** (2022), https://doi.org/10.1021/acsomega.2c02513 [impact factor: 4.132] [**Q1 publication]**

In chemoinformatics and bioinformatics, most frequently, we do not have large enough data sets for training artificial intelligence tools for given applications: we have too many variables or too little well-labeled data. In image processing, for example, the Gaussian blurring is used for a long time for artificially enlarging the training sets in numerous applications. We have identified the need for similar methods in biological and chemical data and introduced the new Newtonian blurring in our article below. The novel method of Newtonian blurring does not introduce any artifacts or noise, just relaxes an error-correcting method: In our original method, we have applied an averaging strategy as follows: the computation was repeated 10-times, and the results were averaged for these 10 runs. In the new Newtonian blurring method, we also used a 10-times repetition and choose 7 repetitions in every possible 120 ways from the 10, and average for each the 7 runs. This way, we will multiply the dataset-size by 120 times.

László Keresztes, Evelin Szögi, Bálint Varga, Vince Grolmusz: **Introducing and Applying Newtonian Blurring: An Augmented Dataset of 126,000 Human Connectomes at braingraph.org**, Scientific Reports, 12:3102 (2022), https://doi.org/10.1038/s41598-022-06697-4 [impact factor: 4.379], [**D1 publication]**.

The next publication describes the SCARF webserver, which is the web version of our SCARF program, published earlier:

Balázs Szalkai, Vince Grolmusz: SCARF: A Biomedical Association Rule Finding Webserver, Journal of Integrative Bioinformatics, Vol. 19, No. 1. pp. 20210035, (2022) (an invited paper), https://doi.org/10.1515/jib-2021-0035 . It is a **D1 publication** (by Scopus).

News coverage:

News coverage of our breakthrough results in Hungarian newspapers and news outlets, including prime, national outlets as origo.hu, index.hu hirado.hu, hvg.hu, infostart.hu and others:

Media reflections to our work "Discovering Sex and Age Implicator Edges in the Human Connectome"

Radio report, aired on November 11, 2022 on Radio Kossuth, on "Napközben".

- https://www.origo.hu/tudomany/20221025-az-elte-kutatoi-olyan-agyi-kapcsolatokat-talaltak-amelyekbol-a-nemre-kovetkeztethetunk.html or cached version
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Presentation on "Bioinformatics 2022" Conference by Vince Grolmusz on SVM-based AI methods in biology & chemistry

Long interview with Vince Grolmusz on brain & mathematics

Appeared in "Élet és Tudomány,: link.

Media coverage of our publication: Succinct Amyloid and Non-Amyloid Patterns in Hexapeptides

Online articles:

- https://www.origo.hu/tudomany/20221006-mesterseges-intelligenciaval-talaltak-amiloidokat-az-elte-kutatoi.html or cached version
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Media coverage of our publication: Introducing and Applying Newtonian Blurring: An Augmented Dataset of 126,000 Human Connectomes at braingraph.org

Online articles:

- https://www.origo.hu/tudomany/20220308-az-elte-kutatoi-az-emberi-agy-kapcsolatainak-leirasat-hasznaltak-innovativ-gepi-tanulasi-modszerek.html or cached version
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Media coverage of our publication: The Frequent Complete Subgraphs in the Human Connectome

On the television:

On the Hungarian Television Channel M5 “Hiradó”, September 9, 2020:

On radio:

In the “Felfedező” on Hungarian Radio 1 Kossuth, September 17, 2020:

Online articles:

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Media coverage of our publication: Good Neighbors, Bad Neighbors: The Frequent Network Neighborhood Mapping of the Hippocampus Enlightens Several Structural Factors of the Human Intelligence

Television appearances:

On RTL Klub "Reggeli" show on August 5, 2020:

or here.

On the Hungarian Television Channel M5 "Hiradó" on August 5, 2020:

Online articles:

- https://www.origo.hu/tudomany/20200802-az-elte-kutatoi-bizonyitekot-talaltak-arra-mi-befolyasolja-az-intelligenciat.html or cached version
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