

MULTI-LEVEL EXPLANATIONS IN NEUROSCIENCE I: FROM GENES TO SUBJECTIVE EXPERIENCES*

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Brains are the most complex systems in the known Universe. Understanding brain dynamics, control of behavior and mental processes is the ultimate challenge for science. It requires multi-level explanations, starting from evolutionary pressures, genes, proteins, cells, networks of neurons, psychophysics, subjective experiences at the mental level, and social interactions. Many branches of science contribute to this endeavor. Physics provides experimental and theoretical tools at the molecular and brain signal processing level, and mathematical tools at the level of neurodynamics. Inspirations from understanding brains are of great practical importance in many fields, including neuropsychiatry, neuropsychology and artificial intelligence. Neurodynamics provides the best language to link low-level molecular phenomena to high-level cognitive functions. Computational simulations help to understand molecular dynamics and analyze real brain signals. This is a very fruitful area of research that requires global, interdisciplinary effort of experts from many branches of science.

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1. Introduction

In the XXI century, science has finally reached the stage at which we can start to understand complex systems, including connections between brain, behavior and mind. Physics of mind should describe processes that govern mental events. This idea 20 years ago seemed to be so far-fetched that an article in *Computer Physics Communications* was accompanied with editor's remark: "We hope our readers will find inspiration in these more

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unusual contributions, such as that of Duch on *Computational Physics of the Mind* [1]. Two decades later *Physics of Life Reviews* has organized a special issue on the physics of mind. Recent article in *Nature Physics* calls for “unconventional collaborations with researchers” to build a “physics of society” [2].

New techniques to analyze genetic and cellular processes at molecular level measure brain signals and use computational tools to model brain processes, facilitating development of multi-level theories of brain functions. Physics is at the core of brain research, providing experimental techniques for people studying genomes and proteins, cells and their structures, but also developing new neuroimaging and electrophysiological techniques, and computational models of neural dynamics that help to understand mental processes.

I will present here an overview of attempts to use computational models of brain functions to develop new language for understanding mental processes. It will provide a path from *physis* to *psyche*. Pauli wrote in 1952 [3]: “It would be most satisfactory if *physis* and *psyche* could be seen as complementary aspects of the same reality”. We are slowly reaching this point. In recent years, a number of interdisciplinary research centers has been created in Poland, including our Center for Modern Interdisciplinary Research at the Nicolaus Copernicus University, with laboratories working on genomics, molecular biology, environmental chemistry, nanotechnologies. Our Neurocognitive Laboratory works on neuroimaging, brain neuroplasticity, theoretical approaches to brain signal analysis, computational modeling of neurodynamics, neuropsychology and developmental psychology. We see a great potential in interdisciplinary multi-level approach to brain research that should help to maximize human potential at all stages of life.

The next section reviews history and the current situation of brain/mind research, followed by the current state of multi-level phenomics addressing global brain initiative goals. In the fourth section, geometric model of mental spaces is introduced, followed by the section on neurodynamics in attractor networks. Trajectories of continuous dynamics may be visualized and after discretization provide an abstract model of individual mental processes. Such models may be implemented in software representing cognitive architectures. However, in contrast to psychological theories based on artificial constructs [4], they are grounded in physical processes in the brain that can be objectively measured [5].

2. Historical remarks

Psychophysics was an important part of physics for a long time. Understanding the relation of objective measurements to psychological sensations has motivated Newton to work on the model of spectral hues represented

by points on a circle. In the XIX century, Hermann von Helmholtz has worked less on electromagnetism than on the physiology of perception, color vision, theories of perception of space and sound or nerve physiology. Creation of good models to relate various features of sensory perception proved to be much more difficult than creation of models based on objective measurements of physical quantities. Methods of measuring the strength of psychological sensations in relation to the intensity of physical stimuli were developed by E.H. Weber (1834, 1846) and G.T. Fechner, whose classic book *Elements of Psychophysics* was published in 1860. This book had strong influence on Ernst Mach, who developed measurement theory and wrote that “a psychophysical measurement formula assigns numbers to sensations in the same way a thermometer assigns the temperature to a state of heat”. This has proved to be much more difficult than Mach has imagined, because sensations are the final step of a complex process converting sensory signals into subjective percepts.

In 1920, Schrödinger has published 3 papers in the *Annalen der Physik* [6] describing color vision using curved Riemannian manifolds. Psychological spaces for representation of pure tones, odors and tastes were also proposed. Unfortunately, physicists have lost their interest in psychophysics, with notable exception of acoustics and optics communities concerned with tone, speech and visual perception. The work by famous physicists at the beginning of XX century has been largely forgotten in the excitement brought by quantum physics. Development of new neuroimaging techniques and computational models helped to overcome difficulties of conducting experimental and theoretical brain research. Recently, it became clear that the way to understand the mind leads through modeling of neural processes at many levels, from biophysical to the systems level [7]. Brain research is very difficult because each brain is unique, influence of experiment on cognitive system is irreversible, therefore, stability, comparison of results, and attempts to generalize them are hard to manage. Recent replicability crisis in psychology and the difficulty of creating psychological constructs that correspond to brain processes has prompted some researchers [8] to claim that psychology cannot be an empirical science. However, tools that are developed now may provide models predicting functions of individual brains.

An attempt to base psychology on behaviorism, objective observations, was motivated by successes of physics. Kurt Lewin (born in Mogilno in 1890), one of the founders of social psychology, has published several influential books in 1936 [9], 1938 [10], and 1951 [11] describing psychological processes in topological spaces, focusing on conceptual representation of mental states and understanding their dynamics using psychological force field analysis. Unfortunately, these forces were based on subjective psychological constructs inferred from behavioral observations. Daniel Kahneman

in his Nobel Prize speech in economics (2002) said: “As a first-year student, I encountered the writings of the social psychologist Kurt Lewin and was deeply influenced by his maps of the life space, in which motivation was represented as a force field acting on the individual from the outside, pushing and pulling in various directions. Fifty years later, I still draw on Lewin’s analysis of how to induce changes in behavior . . .” [12].

Grand field theory project of Lewin has never been completed, but we are now in much better position to create such a theory. Dynamical theory of mental processes may be based on forces that operate on mental states represented by attractor dynamics describing events in psychological spaces. Psychological forces may be defined as the probability of transition from one cognitive state in the “valence field” (emotional states) to another state (Lewin’s impact is reviewed in [4]). In Lewin’s approach, cognitive dynamics of human behavior is represented as a movement in phenomenological (he has used the word “hodological”) space, “life space” or a “field” that includes person’s values, needs, goals, motives, moods, hopes, anxieties, and ideals. Forces in this field arise in social situations, driving cognitive movement toward or away from goals of the person. Lewin’s description of mental change includes 3 stages: unfreezing or escaping the inertia, transition without clear idea where it leads, and freezing or crystallizing new behaviors. He has used physical concepts in metaphorical way to describe psychological phenomena, but we can now link them to the dynamics of attractor neural networks, simulated as well as observed using electrophysiological or neuroimaging methods [13, 14].

Developments in the theory of complex systems give a chance to renew the interest in psychophysics and the neurodynamics of the brain. Computational physicists will undoubtedly play a major role in these modeling attempts. The final goal — understanding brains and building artificial minds — encompasses much more than the original goals of psychophysics. Computational tools allow chemists, physicists and biologists to solve problems that are too complex for human brains, for example, to build complex networks of molecular signaling pathways, genetic and metabolic processes in biological systems, with knowledge automatically extracted from tens of thousands of publications [15]. Building tools for psychology and developing autonomous mind-like systems may completely change the way science is done.

Psychophysics has another important aspect, even more difficult than quantification and description of psychological sensations. The problem of explaining relations between the mental and the physical world is known as the “psychophysical problem”, or the mind-body problem, and has been known since antiquity. Many scientists believe that it has not yet been fully resolved, as the review of the history of psychophysics shows [16]. Under-

standing means finding models that can be expressed either in a symbolic way, or by using mathematical equations and computational simulations. Questions “why” are answered by evolutionary biology, taking into account specific living conditions of various species. Questions “how” require elucidation of mechanisms. In contrast to common opinion, we have models of brain functions allowing for understanding of principles, but not all details, of the psychophysical problem.

Large international efforts are now undertaken to create “International Brain Initiatives” around the world. Global neuroscience should “align aspects of the various national brain research projects around the world” [17]. In 2013, United States “Brain Research through Advancing Innovative Neurotechnologies” (BRAIN) Initiative, and the European Brain Project were announced, leading to “Canberra Declaration” of International Brain Initiative, a global collaboration that includes now Australia, Canada, China, European Union, Japan BRAIN/MINDS project, Korea and United States, and involvement of international organizations, programs such as IEEE Brain initiative. These multi-billion dollar projects are aimed at acceleration of brain research, including basic research and neurocognitive technologies. Global initiatives represent opportunities for physicists to work with cognitive scientists on development of new experimental techniques, signal analysis methods, computational models and simulations. The BRAIN Initiative is supported by 5 USA federal agencies and over 20 private partners that formed the BRAIN Initiative Alliance [18]. The National Institute of Health BRAIN 2025 report [19] defined 7 highest priorities:

- Identify and provide experimental access to the different brain cell types to determine their roles in health and disease.
- Generate circuit diagrams that vary in resolution from synapses to the whole brain.
- Produce a dynamic picture of the functioning brain by developing and applying improved methods for large scale monitoring of neural activity.
- Link brain activity to behavior with precise interventional tools that change neural circuit dynamics.
- Produce conceptual foundations for understanding the biological basis of mental processes through development of new theoretical and data analysis tools.
- Develop innovative technologies to understand the human brain and treat its disorders, and create and support integrated human brain research networks.

- Integrate new technological and conceptual approaches produced in goals 1–6 to discover how dynamic patterns of neural activity are transformed into cognition, emotion, perception, and action in health and disease.

I will focus here on the last topic, relations between brain and mind. While this is a very broad topic, the states of the brain may be investigated from two broad perspectives: electrophysiological and neuroimaging, and computational simulations of neurodynamics linked to mental states described by psychological constructs.

3. Phenomics: understanding the brain at many levels

Phenomics is the branch of science concerned with identification and description of measurable physical, biochemical and psychological traits of organisms [20]. Many branches of phenomics have been created to describe processes and entities at molecular level: genomics, epigenomics, proteomics, metabolomics, interactomics, transcriptomics, exposomics, virusonomics, healthomics *etc.* Connectomics describes all kinds of connections between brain regions and types of neurons. Behavioronomics describes and classifies various types of behavior. As a result omics.org has a list of hundreds of various “omics”, analyzing functions and interactions in various -ome layers of biological entities [21].

Currently, characterization of full set of phenotypes of an individual is at rather low level, characterize genomes. A few best-known large scale phenomics projects include:

- Human Genome Project, since 1990;
- Human Phenome Project, since 2003;
- Human Epigenome Project, since 2003;
- Personal Genome Project, 2005;
- Human Connectome Project, since 2009;
- Developing Human Connectome Project, 2013.

These and several other large-scale phenomics projects try to create “genotype–phenotype” maps and link phenotypic characteristics to health, disease and evolutionary fitness. Consortium for Neuropsychiatric Phenomics [22] investigates phenotypes of people suffering from serious mental disorders at all possible levels since 2008. Can neurocognitive phenomics

be developed to understand general behavior of people, their mental states? Depending on the precise questions asked, brain processes at various temporal and spatial levels may be most relevant, from 10^{-10} m to 1 m, and even wider time scale, from picoseconds to years (Fig. 1). Full understanding of animal behavior requires analysis of many processes: formation of proteins based on information stored in genes and involvement of internal environment in post-translational processes, assembly of cell structures — membranes, receptors, ion channels, synapses — and emergence of biophysical properties of neurons, their interactions with other brain cells, formation of whole brain networks resulting from interactions with external environment, dynamical states that may arise in such networks, responsible for perception, control of movement, formation of cognitive phenotypes, explaining normal and abnormal behavior, including psychiatric syndromes. Different branches of science have contributed to the growing knowledge at each of these levels. Physics contributes not only providing experimental methods at every level, but also theoretical biophysical models for understanding and simulating neurodynamics at the system level.

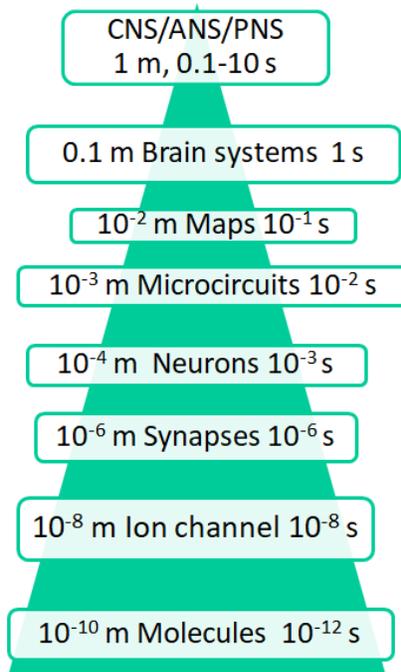


Fig. 1. Spatial and temporal resolution of processes influencing brain activity.

Understanding of human behavior has been based on observation and psychological theories that has been disconnected from the brain mechanisms responsible for behavior. Psychiatry has traditionally used psychological constructs to describe behavioral syndromes that shared some core characteristics. Manuals that are used for diagnosis of mental disorders list different symptoms and if some subset is observed in patient's behavior, assign them to broad categories such as autism spectrum disorders or schizophrenia. In recent years, psychiatrist understood that "...these categories, based upon presenting signs and symptoms, may not capture fundamental underlying mechanisms of dysfunction" [23]. Instead of classification of mental disease by symptoms, multi-level neuropsychiatric phenomics has been proposed to describe processes that regulate working of the large brain systems.

National Institute of Mental Health (NIMH) in the USA promotes analysis of major brain networks and their dynamics, regarding it as the best approach for understanding abnormal behavior. Five high-level brain systems have been distinguished, each composed of many subsystems that are labeled by psychological constructs. For example, Cognitive Systems are responsible for many processes, including several types of memory, attention, perception, language and cognitive control. Negative Valence Systems are primarily involved in responses to aversive situations or context, such as fear, anxiety, and loss. Positive Valence Systems enable reactions to positive motivational situations or contexts, such as reward seeking, consummatory behavior, and reward/habit learning. Social Processes Systems mediate responses in interpersonal settings of various types, including perception and interpretation of others' actions. Arousal/Regulatory Systems provide appropriate homeostatic regulation of such systems as energy balance and sleep, generating activation of neural systems appropriate in various contexts.

These large brain systems depend on the processes at genetic, molecular, cellular, circuit levels, and may also be characterized by physiological and behavioral changes, subjective mental reports. Collecting all this information in a big "Research Domain Criteria" (RDoC) matrix should help to fill the gaps of our knowledge. Many white spots still remain. This research should provide bridges between all levels, linking adjacent level, from environment to behavioral syndromes and subjective states. Neural network level allows for simulation of functions assigned to specific psychological constructs. By identifying biophysical parameters of neurons required for normal neural network functions, it is possible to modify these parameters and investigate abnormal network states. For example, creating models of working memory, or shifts of attention that depend on properties of individual neurons as well as the whole network may show the range of biophysical parameters that preserve normal functions. Going outside this range will break the system in various ways that can be related to known mental problems.

Following psychiatry similar approach should be actively pursued in psychology and learning sciences [24]. Examples of this strategy will be presented below. However, before doing that, some remarks on our ability to understand subjective mental states will be made.

4. Geometric model of mind

A few attempts to create description of mental events in psychological spaces have been made in the past. Kelly has created personal construct psychology (PCP), using geometry of psychological spaces as alternative to logic [25]. His ambitious project was aimed at complete theory of cognition, action, learning and intention. Psychological constructs were used to divide space into “repertory grid” to analyze schemas that are the basis of decision making and world views. This approach was used in psychotherapy to build models of patient’s behavior. PCP ideas are still developed by a community of psychologists who run *Journal of Constructivist Psychology*. There are many software packages for construction of repertory grids. However, PCP offers a very crude representation of mental models. Shepard [26, 27] tried to formulate universal laws of psychology in appropriate psychological spaces. His approach based on group theory was quite successful in psychophysics. Lewin, Kelly, Shepard and many other psychologists have dreamed about such geometrical model of mind for a long time (see [28] for brief history).

Subjective mental states seem to be outside the realm of physics. What we can aim at is to find isomorphism of brain states and transitions between these states, and corresponding mental states. Brain and mental states are like two sides of the same coin, brain states and behavior observed from outside, and mental states interpreted and expressed inside the system itself. Brain states are estimated from analysis of EEG, MEG, NIRS-OT, PET, fMRI and other signals. To link them with mental states, we need to extract quasi-stable microstates that are responsible for perception of objects, actions, thoughts and imagery. Projection of continuous brain signals on a set of semi-discrete attractor network states allows for recognition of intentions to act. This is the main approach to the brain-computer interfaces for mental control of computer programs or various devices for the disabled people.

Forward models of fMRI data in response to auditory or visual stimulations with pictures or video have been constructed [29]. These models may be used to reconstruct information about stimuli from fMRI data, including abstract semantic information, and even complex stimuli such as sentences. Reconstructions of mental representations are quite noisy, but show that some brain states may be categorized in a meaningful way describing them in a symbolic way. Distribution of brain activity measured by fMRI was determined for imagery of over 1700 objects [30, 31], creating brain atlas of

activations that have semantic interpretation. Generic decoding of brain activity for arbitrary seen and imagined objects has been demonstrated, using fMRI signals to predict visual features that are created by deep convolutional neural networks used for image recognition. A set of decoded features that contains some invariants emerging in hierarchical images processing may be used to identify seen/imagined object categories that have not been used for training [32]. This technique can also be used to decode images in dreams [33].

John Locke (1690) defined consciousness as “the perception of what passes in a man’s own mind”. Brain is very noisy and we are able to perceive only strong peaks of neural activity that can be identified and are sufficiently persistent to be categorized. Quasi-stable brain activity patterns are associated with phonological or motor representations and can be expressed either in a verbal way (speech or silent thought) or by motor actions. Conscious mental events are just shadows of deeper physical reality [34]. This metaphor may be compared to the famous allegory presented in the *Republic* of Plato: prisoners in a cave see only shadows of real things projected on the wall. The task of philosophers is to perceive the true form of things. Externally observable behavior and internal conscious states are results of drastically simplified neurodynamical states, the strongest activations that can be clearly distinguished from noise in neural system.

From the formal point of view, we are searching for mapping between mental states $S(M)$ and brain states $S(B)$. Words describing mental states are used for communication, serving as labels of internal microstates. From the point of view of causality, such a macroscale description may carry more information than microscopic description [35]. Spivey [36] in his book *The Continuity of Mind* proposed to view mental events as continuous trajectories in the state space based on activity of neural assemblies. Dimensionality of such a representation is too high for such a representation to be useful. This idea is also at the basis of Friston’s free energy principle [37]: brains have to maintain non-equilibrium steady-state (homeostasis) restricting the state of whole organism to a limited number of quasi-stable state, creating attractors that help to maintain dynamical equilibrium. Haken’s synergetics ideas [38] present a different approach to self-organized systems, focusing on emergence of macroscopic order from microscopic interactions and phase transitions between different states. Transitions between attractor states in brain networks have different character.

Dale and Spivey [39, 40] recommended symbolic dynamics analysis of the trajectories in the space of brain activations. Symbolic dynamics suffers from combinatorial explosion of the number of symbols in high-dimensional spaces and brain-based state space is not suitable for direct representation of subjective mental states. We are aware of very few processes that go on

in the brain. Useful representations of meaning, allowing for recognition of large number of concepts from fMRI signals, have surprisingly low dimensionality. In the pioneering paper by Mitchell *et al.* [29], concepts were characterized by just 25 attributes, while Binder *et al.* [41] in their brain-based framework for semantic representation have used 65 attributes. Such vectors have coefficients that estimate silence of properties that can be associated with a given concept based on sensory, motor, spatial, temporal, affective, social and cognitive experiences, derived from large text corpora. Vector representing word meaning have coefficients that estimate contributions of global brain activations for a combination of properties to the final activation characteristic for a given word, as seen in the semantic atlas [30]. Such vectors may be used to generate fMRI activations with good accuracy [29].

Representation of mental states in psychological spaces spanned by dimensions using brain-based attributes should reflect qualities of experience important for description of inner experience. Mental states, movement of thoughts could be presented as trajectories in psychological spaces. To find correspondence between brain and mental states, decomposition of brain states into components for each attribute should be performed. Some attributes may be approximately identified by activation of well-defined brain regions, for example sensory components such as color or smell. Other attributes, such as emotional states, social aspects or self, are related to activation of complex subnetworks. Nevertheless, it will be possible not only to label brain states using symbols, but to use brain states to create trajectories of mental states, creating geometrical model of mind. Such an approach could also solve the problem of the lack of good phenomenology of mental states [42] and show explicitly mind–brain–body relations, bridging the famous gap between subjective and objective worlds.

Artificial intelligence is a branch of science that tries to solve problems for which there are no effective algorithms but sufficient heuristic knowledge has been accumulated to find approximate solutions. Attempts to construct models of mental processes at the symbolic level have brought artificial intelligence close to cognitive science. In the functionalist tradition, Newell in *Unified Theories of Cognition* [43] defined mind as “a control system that determines behavior of organism interacting with complex environment”. Computer models of such control systems are called “cognitive architectures”. In particular, Brain-Inspired Cognitive Architectures (BICA) are based on functional divisions of software modules into perception, working memory, declarative memory and executive functions, as it is outlined in the recent proposal for *Standard Model of the Mind* [44]. Such architectures represent knowledge at symbolic level. They are quite useful in some applications but have not yet led to general human-level intelligence. Brains work using deeper representation based on perception, allowing for natural

associations and creative imagery. Only in recent years, deep machine learning techniques allowed to analyze visual, auditory and other types of inputs necessary for perception at the level similar to human. Many inspirations for computational intelligence have already been derived from neural systems, including machine learning algorithms [45] and models of creativity in artificial systems [46, 47]. A survey of AI and machine learning relations with neuroscience shows how current advances have been inspired by brain research, and how both fields may benefit from mutual interactions [48].

In the following section, I will show how geometric models of mental processes may be derived from computational models of biologically-inspired neural networks. Neurodynamics offers a new language that may explain normal and abnormal behavior that is hard to understand using psychological constructs.

5. Neurodynamics

Cognitive Computational Neuroscience (CCN) researchers created many software packages to simulate biologically inspired or even biologically plausible neural systems. Sophisticated compartmental models of single neurons (for example NEURON and GENESIS) include geometry of dendrites and specific ion channels, but are computationally very demanding for simulations of larger networks. The Brain Simulation Platform of the Human Brain Project [49] plans to scaffold models of molecular-level principal neurons and cellular-level reconstructions of cortical and sub-cortical regions, models for implementation in neuromorphic computing systems, and network-level models of the mouse brain. Such a simulator will be very complex. Experience with the Blue Brain project [50], detailed simulation of a single cortical column, shows that it may be difficult to use it for understanding of cognitive functions.

At the other end of the spectrum, we have population-based neural models that do not represent single neurons at all. A large number of excitatory and inhibitory groups of neurons is used to define mesoscopic dynamics of a network based on mean-field models. Such a simplification of neural activity allows for the whole brain modeling. Macroscopic phenomena, such as EEG or BOLD signals measured by fMRI can be reproduced and analyzed. The best example here is The Virtual Brain (TVB) simulator [51], enabling simulation of large-scale brain networks dynamics, realistic connectivity, use of tractographic data from Diffusion Tensor Imaging to generate connectivity matrices and build rough structures of cortical and subcortical brain networks. The connectivity matrix defines the connection strengths and time delays via signal transmission between all network nodes. The Virtual Brain simulates and generates the time courses of various forms of neural activity including Local Field Potentials (LFPs), EEG, MEG and

fMRI signals. TVB software is used to generate, manipulate and visualize connectivity and network dynamics, providing tools for classical time series analysis, analysis of structural and functional connectivity, exploration of network parameters, parallel simulations on computer clusters. Population-based models are used to simulate effects of neurological brain damage and neuropsychiatric disease.

Between these two extremes, detailed simulation at a single neuron level and population-based models, there are neural simulators based on simplified integrated and fire spiking neurons (ex. NEST and Open Source Brain [52]), and simpler models based on point neurons and rate coding, preserving key biological properties: excitatory and inhibitory connections with leak channels for spontaneous depolarization of neurons. The Neuroscience Gateway (NSG) [53] facilitates access of computational neuroscientists to computational models that may run on High Performance Computers (HPC) and offers cloud resources, sponsored by the National Science Foundation.

Emergent simulator is well-developed and offers minimal models that capture most important biological properties [54, 55]. The Hodgkin–Huxley point neurons in Emergent are based on a conductance-based models that aggregate values of ion concentration and trans-membrane ion flows, see Fig. 2. Networks of such neurons can be simulated with manageable computational costs. Five types of ion channels are included in Emergent [54]: excitatory input channels e and inhibitory channels i , the leak channel l for spontaneous depolarization, and two channels that control accommodation a and hysteresis effects h . Each trans-membrane ionic channel α is described by 3 parameters: E_{α} , g_{α}^t , and \bar{g}_{α} .

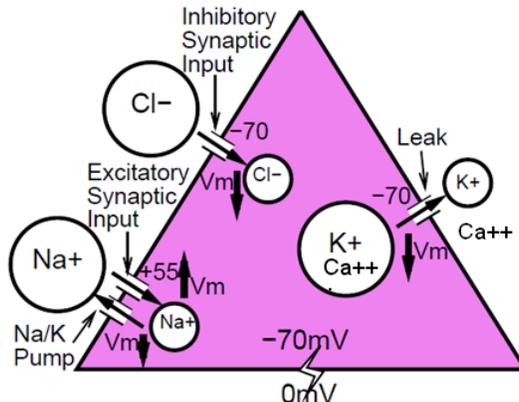


Fig. 2. Model neuron and its ionic channels, as used in Emergent simulator.

Parameter E_α is a static property of neurons, representing the reversal potential for ions flowing through channels α , *i.e.* the difference of electrical potential between the inside and the outside of the neuron in equilibrium state, when electric forces are equal to the trans-membrane diffusion force acting on ions. Parameter g_α^t represents the proportion of the total number of channels α that are open. Parameter \bar{g}_α indicates the total conductance for α when all of the channels for α are simultaneously open. The product $g_\alpha^t \bar{g}_\alpha$ consequently represents the conductance for channel α at time t .

The potential V_α^t for α at timestep t depends on the membrane potential at t (V_m^t) and on the equilibrium potential of α denoted E_α ; $V_\alpha^t = V_m^t - E_\alpha$. The current I is calculated using Ohm's law, as the conductance multiplied by the potential (1)

$$I_\alpha^t = g_\alpha^t \bar{g}_\alpha (V_m^t - E_\alpha) . \quad (1)$$

All five types of α channels have ionic currents that can be calculated in this way. In the "leaky bucket" model of neuron, ions are flowing in and out, controlled by these five types of channels:

$\alpha = e$: The *excitatory* input synaptic channels that let Na^+ ions to enter the cell. It opens when glutamate neurotransmitter is released by the presynaptic neuron and binds to the synaptic receptor. In this case, g_e^t is linearly dependent on the excitatory net input.

$\alpha = i$: The *inhibitory* channels let chloride ions Cl^- in, usually as a result of activation of GABA-sensitive receptors. This reduces membrane potential towards the resting potential of about -70 mV.

$\alpha = l$: The *leak* channels allow for flow across the membrane of potassium, calcium and sodium ions, controlling spontaneous depolarization of neurons.

$\alpha = a$: *Accommodation* is a mechanism that models neuronal fatigue, involving inhibitory currents (K^+ channels) that are sensitive to membrane potentials and open when calcium concentration is high. This is a longer term effect that helps to escape from attractor states.

$\alpha = h$: *Hysteresis* maintains for a short-time highly excited state of neurons in the absence of inputs, thanks to the voltage-dependent calcium and sodium channels that are open when membrane polarization is high.

For all channels, E_α and \bar{g}_α are constant in each simulation. The leak channels do not adjust their opening rate, so usually $g_l^t = 1$. For other channels, g_α^t is variable. The precise update equation depends on the α channel considered, as ionic channels are sensitive to the different factors described above.

Model neurons are organized in layers representing different brain areas, connected with each other in reciprocal way by projections (long axons), linking cortical regions. General principles of cortical connectivity may be summarized in a few points:

- afferent connections are accompanied by symmetrical efferent connections, effectively making networks recurrent [56];
- the structure of maps and intra-map connectivity follow similar principles all across the cortex;
- inhibitory competition dynamics regulates intra-layer activity levels;
- learning is implemented as a biologically-plausible mix of Hebbian learning and two-phases error propagation.

Detailed description of integrate-and-fire mechanism of neuron activation, network construction and equations used to calculate excitation and inhibition, is presented in the book *Computational Explorations in Cognitive Neuroscience: Understanding the Mind by Simulating the Brain* by O'Reilly and Munakata [54], and a short description of the models used below for illustration of brain dynamics in our paper [57].

Attractor dynamics is used here to illustrate working of bottom-up attention processes. Dwelling in each attractor basin gives sufficient time enabling reliable signal detection, object recognition or formulation of thoughts that act as verbal labels associated with attractor basins. Transitions between attractor states correspond to shifts of attention or stream of thoughts.

The connectivity of different layers follows general principles of layered cortical maps, and in the case of reading model used here includes two input layers: letter sequences in visual inputs, or phoneme sequences in auditory input layer. A larger semantic layer represents cortical areas of the brain. Various subnetworks in the brain compete for access to the highest level of control-consciousness. The winner-takes-most mechanism leaves only the activity of most coherent, strongest subnetworks, inhibiting other activations. This facilitates signal detection, creating stable attractor microstates that can be reliably distinguished from the noise in the brain and linked to phonological labels and motor actions. This mechanism allowed Huth *et al.* [30, 31] to create semantic map that shows unique cortical activations for over 1700 words. They are sufficiently similar in brains of different people to enable reliable categorization of brain states corresponding to semantic concepts.

Emergent is using Leabra model, Learning in an Error-driven and Associative, Biologically Realistic Algorithm [58]. This model has 6 important features: (1) it is based on integrate and fire point neurons; (2) only a small percentage of neurons are highly active at each time, *i.e.* sparse distributed representations are learned; (3) many layers of transformation are included in most models of cognitive functions; (4) inhibition is realized using k -winners-take-all (kWTA) mechanism; (5) a combination of Hebb correlation learning (neurons that are active at the same time develop stronger connections), and (6) error correction supervised task learning is used.

In the model of reading (based on standard 3-ways model [54], see Fig. 3), we shall assume that each neuron of the semantic layer represents a microfeature. In reality, such features are also encoded by distributed networks. This is the basis for “brain-based semantics”, proposed by Binder *et al.* [41]. The 3 layers between each input and semantic layer transform the signal from one representation to the other in both directions, *i.e.* the model may be trained by showing words in a written form, phonological form or distribution of active semantic microfeatures as input, and requiring appropriate distribution of activity in the two other layers. Showing the word “deer” we expect to activate phonological representation of spoken word and semantic representation of the concept of “deer”. After training on a set of words, the network prompted by an input shows attractor dynamics, converging on the

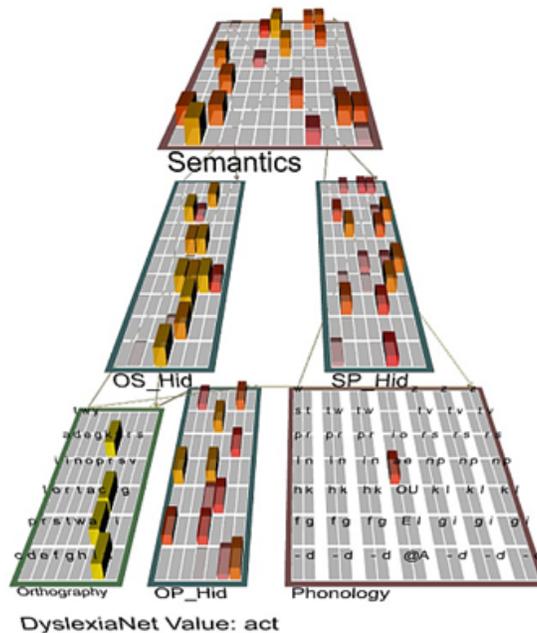


Fig. 3. Model of reading, with 140 units in semantic layer.

basin of attractor corresponding to the stimuli. If there is no clamping of input, after some time, spontaneous transition to associated attractor basins is made.

In the case of low-dimensional dynamical systems, symbolic dynamics (SD) may be used to analyze sequence of states. Phase space is partitioned into regions labeled with different symbols A_i . Every time the system trajectory is found in one of these regions, appropriate symbol is emitted. Sequence of symbols gives a coarse-grained description of dynamics that can be analyzed using statistical tools, ex.: $A_1, A_2, A_1, A_4, A_3 \dots$. Although discretization of continuous dynamical states loses the fluid nature of cognition, in some cases, symbolic dynamics may show interesting cognitive representations [36]. For example, distinguishing 4 microstates A, B, C, D in multichannel global field power EEG patterns of people with fronto-temporal dementia, schizophrenia and panic disorder, and analyzing frequency of transitions between these states allowed for reliable diagnosis based on transition profiles [59].

Symbolic Dynamics is a useful technique for low-dimensional dynamical systems. In high-dimensional cases, the number of symbols grows exponentially high, even if each dimension is divided into two regions for d -dimensions, there will be 2^d symbols. In the case of neurodynamics, we are mostly interested in high-dimensional dynamical systems, with $d > 100$. Trajectories of such a dynamical system representing changes in distribution of neural activities in the longer time scales may be visualized using recurrence plots (RP) [60], fuzzy symbolic dynamics [13, 14] or some other method of visualization of high-dimensional vector time series data.

Recurrence matrix \mathbf{R} is based on approximate equality of trajectory points [60]. Distances between trajectory vectors in time are calculated between each time point

$$\mathbf{R}(\mathbf{t}, \mathbf{t}') = \mathbf{R}(\mathbf{x}(\mathbf{t}), \mathbf{x}(\mathbf{t}')) = \|\mathbf{x}(\mathbf{t}) - \mathbf{x}(\mathbf{t}')\| ,$$

where the norm may exponentially rescale distances to emphasize small distances and convert them into a color code, as displayed in Fig. 4. Frequently, a binary matrix \mathbf{R}_{ij} is used with distances smaller than ε replaced by zero. Such recurrence plots are black-and-white [60]

$$\mathbf{R}(\mathbf{t}, \mathbf{t}'; \varepsilon) = \Theta(\varepsilon - \|\mathbf{x}(\mathbf{t}) - \mathbf{x}(\mathbf{t}')\|) .$$

Many measures of complexity and dynamical invariants may be derived from recurrence plot matrices: generalized entropies, correlation dimensions, mutual information, redundancies, trapping times, *etc.* Probability of recurrence may be computed from recurrence plots, or from clusterization of trajectory points that shows how strongly some basins of attractors capture neurodynamics, how large they are and for how long the trajectory

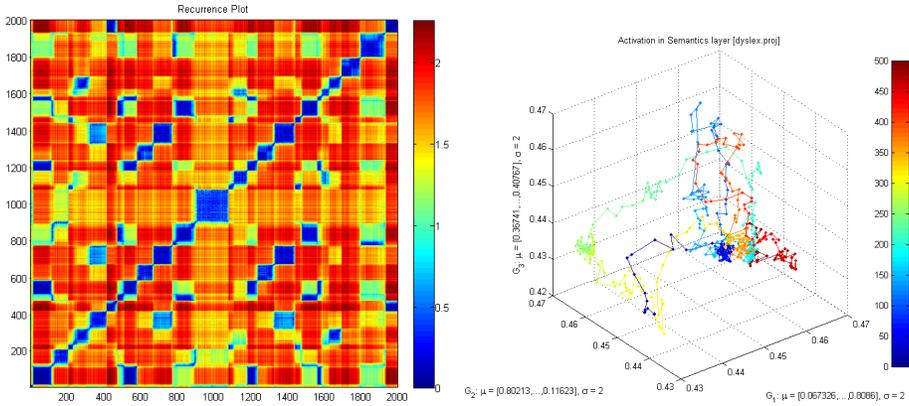


Fig. 4. Recurrence plots and fuzzy symbolic dynamic plots of trajectories based on 140 neural units.

stays in each basin. Recurrence quantification analysis (RQA) finds non-linear invariant measures of a time series and their physical interpretation, including sample entropy, detrended fluctuation analysis (DFA), measuring statistical self-affinity of trajectories, maximum line length (L_{max}), largest Lyapunov exponent mean line length (L_{mean}), mean prediction time of the signal recurrence rate (RR), probability of recurrence determinism (DET), repeating patterns in the system laminarity (LAM), frequency of transitions between states, trapping time in a given attractor state. Such an analysis has been successfully applied to many real signals, including diagnosis of autism spectrum disorder from EEG measurements at very early age [61]

$$S(\mathbf{x}(t), \mathbf{x}_0) = \Theta(\varepsilon - \|\mathbf{x}(t) - \mathbf{x}_0\|) \Rightarrow \exp(-\|\mathbf{x}(t) - \mathbf{x}_0\|) .$$

We have developed a Toolbox called Viser for various visualizations of trajectories [62]. Fuzzy symbolic dynamics is a natural way to generalize symbolic dynamics and recurrence plots. Instead of indicator functions that label distinct regions of the phase space, membership functions are used to indicate degree to which a point on the trajectory belongs to a fuzzy set. For two or three membership functions, one may directly plot values of these functions for each point on the trajectory. Recurrence plots measure distance of all previous trajectory points to each new point. FSD measures distances to several fixed points. Another useful visual representation, called Prototype Distance Plots (PDP) [63], is to place membership functions in all regions with high-density of trajectory points, defining prototypes in the centers of attractor basins. PDP matrix is similar to the recurrence plots, but it has lower number of rows, one for each prototype, with the number of columns equal to the number of trajectory points.

Such a visual representation of trajectories shows various aspects of dynamics that are difficult to discover looking at individual components, local trajectory clusters and their relations. FSD and PDP can be applied to raw signals, transformed signals (ex. ICA/PCA components), or to signals in the time-frequency domain. In general, 3 steps are required:

- Standardize original data in high-dimensional space;
- Find cluster centers (*e.g.* by k -means algorithm): $\mu_1, \mu_2, \dots, \mu_d$;
- Use non-linear mapping to reduce dimensionality.

Sharp indicator functions are used to define discrete symbols and use symbolic dynamics, replacing trajectories $\mathbf{x}(t)$ by strings of symbols. Soft functions characterize points on trajectories in lower-dimensional spaces, depending on the number of reference functions used. Despite drastic reduction of dimensionality, fuzzy symbolic dynamics in two- or three-dimensional spaces shows interesting features of trajectories $Y(t) = (y_1(t; W), y_2(t; W))$. Gaussian membership functions $y_k(t; W) = G(\mathbf{x}(t) - \mathbf{x}_k; \sigma_k)$ with large dispersion may be used, estimating probability of trajectory arriving at some distance from the reference points in the phase space

$$y_k(t; \mu_k, \Sigma_k) = \exp\left(-(\mathbf{x} - \mu_k)^T \Sigma_k^{-1} (\mathbf{x} - \mu_k)\right).$$

The key problem is to find good reference points for membership functions that will reveal structures of states and their relations [13]. It may also be useful to define first linear projections, combinations of signals from sources or electrodes that show significant coherence. Trajectories in such a space show switching between activity of subnetworks, and may also be presented using visualization. For example, the idea of “biologically meaningful dimensions” has been recently used to define tendency towards certain mental disorders [64], such as autism [65] or Obsessive–Compulsive Disorder [66]. Projections based on strength of joint activity of selected pairs of regions that are functionally connected define directions that show tendency to different mental disorders. Each individual case is a point in a cloud that may be diagnosed, but clouds for some disorders show significant overlaps with clouds for other disorders. For example, resting state fMRI analysis of functional connections for schizophrenia and autism spectrum disorder shows overlapping populations, with schizophrenia population showing increased liability on the ASD dimension, but not *vice versa* [67].

This may be a robust finding, but it is also possible that differences between these populations may be revealed if the number of dimensions is increased, or better correlation measures are employed. Temporal resolutions of fMRI is too low to show what is the character of underlying

dynamics: it could be an intermittent shift between different attractors or a fluctuation within a single broad attractor basin. Solution to such questions may have a great therapeutic significance, helping to define new forms of neurofeedback [68]. So far, resting state data have provided only averages over relatively long-time period (about 10 minutes), so we can only display a static picture.

Visualization of neurodynamics has not been yet a major area of research, so many questions are still open. There is no universal best way of looking at brain processes. Selection of relevant brain regions or connections between some regions, as dimensions in which trajectories are displayed depends on the task, as has been shown in the case of OCD, schizophrenia, and autism spectrum disorders. In practice, activity of a larger number of regions of interest (typical parcellation used in functional brain atlases defines 100–240 regions) is used, so visualization methods based on dimensionality reductions are necessary. One simple way to create meaningful trajectory visualizations is to find most frequent patterns of activation $A_i = A(D_i)$ for a given condition (such as disease type) D_i and place there reference FSD membership function $F_i(x) = F(\|x - A_i\|; \sigma_i)$. For example, using the power of event-related potentials computed from averaging EEG signals was used to label 4 distinct states. Symbolic dynamics used to analyze frequency of transitions between these states was sufficient to distinguish several mental disorders [59].

Supervised clustering techniques may determine typical patterns where centers of the FSD reference functions should be placed. Trajectory of neurodynamics will then lie close to one of the axis, *i.e.* for disease D_i , we may expect that $F_i > F_j, i \neq j$. The trajectory may switch between several patterns, showing tendency to several disorders that may be manifested in the dynamics of a single brain. An example of switching between two high-dimensional patterns visualized using FSD is shown in Fig. 5. Large fluctuations around two relatively stable patterns are observed, switching between them. A few additional attractor basins that are relatively similar to the major attractors are also seen. Moving the point of view by shifting reference functions to the center of these attractors helps to see more features that distinguished them from others.

We have developed optimization methods that calculate centers and dispersions of FSD reference functions in a way that increases average or minimal separation between adjacent attractor basins to show properties of high-dimensional trajectories in more details [63]. Using such tools, we may investigate various effects in complex dynamical networks. Neurodynamics may be characterized by various measures: position and size of basins of attractors, transition probabilities, types of oscillations around each attractor, fluctuations around centers of attractor basins. Some of these features

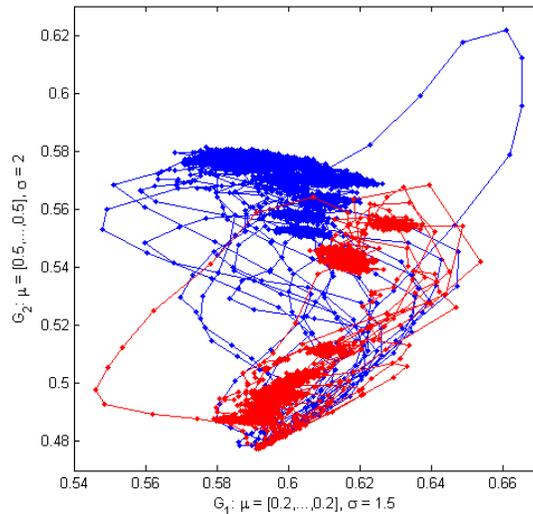


Fig. 5. Example of two large basins of attractors characterizing different forms of behavior.

may be computed using recurrence analysis. However, such features as the strength of the attractor are rather difficult to evaluate. Using artificial neural models, such as those implemented in Emergent simulator, the depth or strengths of attractors may be investigated by plotting the variance of the trajectory around mean value in the attractor basin (this estimates the size of the basin) as a function of noise (Emergent has many ways of adding noise, including membrane, synaptic or activation potential noise). Variance of distances measured from the center of the cluster of trajectory points grows with synaptic or membrane noise; for narrow and deep attractors, it grows slowly, but for wide attractor basins, it grows fast. At large noise levels, the basin of attractor is not able to trap the system dynamics. Mutual inhibition of all desynchronized neurons in such a noisy system destroys attractor basins. The threshold for this process gives an estimation of how hard it is to get out of the attractor [69].

In general, characterizing attractor basins in high dimensions is difficult: there may be many paths that lead to other attractor basins, the trapping (dwell) time is, therefore, a unique characteristics of the attractor state, and depends strongly on the noise level. Transitions between attractors cannot be easily predicted and depend on various neural mechanisms, including relative strength of all 5 types of ion channels. Spontaneous attention requires synchronization of neural activity around some pattern and is a result of multiple constraints satisfaction, inhibitory competition, neural fatigue, excitatory inputs, bidirectional interactive processing between associated attractors sharing some features. These effects can be seen in visualization of

activity of the semantic layer in the model of reading, in the 140-dimensional layer with semantic units, phonological and orthographic input layers, interacting with each other through hidden neuron layers.

We have performed many simulations to understand neurodynamics of such systems. Concepts that have similar meaning, such as hind-deer or cost-wage, have semantic layer patterns that are largely overlapping, their basins of attractors are close to each other. Training with more variance in phonological or written form of words may increase variance of attractor basins and improve generalization for distorted inputs. Without neuron accommodation, attractor basins are tight and narrow, leading to poor generalization and weak associations with other concepts. With accommodation, basins of attractors shrink and vanish after short time because neurons desynchronize due to the fatigue; this allows other neurons to synchronize, leading to activation of new concepts. Resulting trajectory visits many attractor basins, and may come back after some time to previous basins, simulating spontaneous stream of thoughts arising in the mind. Even if the system comes back close to previously visited states, it is modified, semantic activations are changed by the context provided by past trajectory. This is seen in the recurrence plot in Fig. 4, where some states have dark blocks to the left of the diagonal, signifying that trajectories come close to previous attractor basins.

To understand the long-term dynamics, one may label each quasi-stable state with the name of the nearest attractor basins that arises when the system is prompted with a given word. In this way, we can create symbolic dynamics based on a sequence of visited attractor basins. Some transitions are rare, so like in molecular dynamics, long-time simulations are needed to explore all potential transitions between attractor basins. They depend on priming (history of previous dynamics, or stimulation with new context) and stochastic dynamics driven by the noise in the system.

Averaging over 10 runs with 25 labeled states, a directed transition graph has been created using the reading model, as shown in Fig. 6 [70]. Boxes contain labels of attractor basins (words used in training), and directed edges have two numbers m/n , showing how many times each transition appeared, and how many transitions were made from a given box. For example, edge connecting *rope* and *post* is used 3 times out of 16 transitions from *rope*. In this way, we have non-linear sequence of transitions that carries information analogous to symbolic dynamics [71, 72]. Although many books on symbolic dynamics for simple dynamical systems and chaotic systems have been written so far, graphs of the type presented here have not been analyzed. Some measures developed in recurrence quantification analysis can also be used on symbolic dynamics directed graphs.

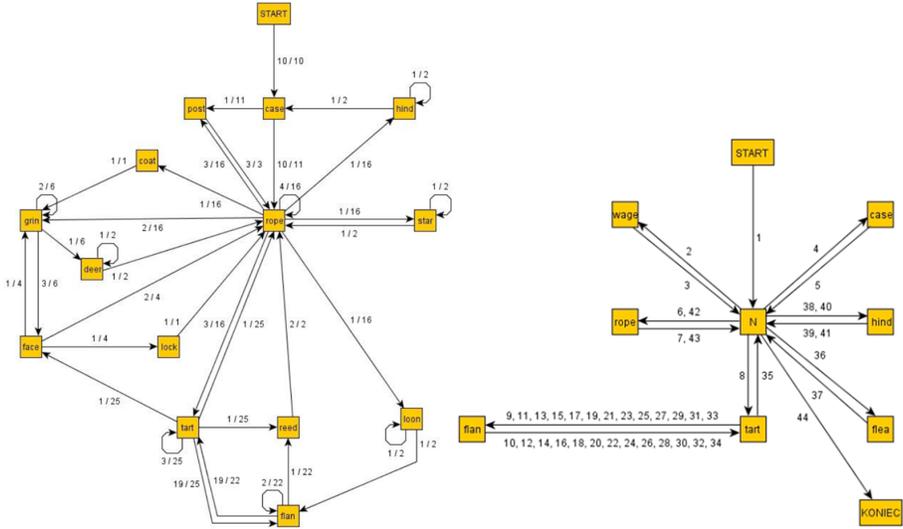


Fig. 6. Transitions between attractors in a trained network with stochastic dynamics and moderate noise level.

Sometimes neurodynamics cycles between several states are entering into a kind of obsessive loop, for example alternating between “tart” and “flan” (Fig. 6). Connected attractor basins share some microfeatures, some are deactivated by accommodation and inhibition processes. Visualization using recurrence plots or fuzzy symbolic dynamics does not show individual features of patterns. These patterns change rapidly during transitions from one state to the other. The landscape of actual and potentially accessible attractor states in the phase space changes in time. FSD plots make an impression that basins of attractors that have been explored in the past still exist, but they may not be accessible for some time, depending on the state of neurons encoding microfeatures in the semantic layer.

Real brain dynamics may be analyzed in similar way, looking for transitions between brain activations [31]. EEG oscillatory signals may be averaged to obtain global power in different frequency bands for each electrode, providing an analogue to microfeatures that are used in simulations. While this has been used with considerable success for early diagnosis of autism [61], the signals measured by the electrodes are mixtures coming from many sources. Reconstruction models should give more reliable equivalent of microfeatures. Most meaningful results allowing for understanding of brain processes in psychological terms should be based on decomposition into subnetwork activity. Brain-based semantics used in Natural Language Processing is a step on this way [41], but it has not yet been based on real brain activations.

FSD visualization and directed graphs showing neurodynamics in simplified form may be based on the resting state neuroimaging data and EEG analysis of such data may reveal interesting patterns in the rare cases of Multiple Personality Disorder, showing two or more distinct types of groups of patterns that characterize the behavior. The use of attractor dynamics to construct mental models is within our reach although a lot of work remains to be done.

6. Conclusions

Psychological constructs used in psychiatry do not have direct connections to physical reality and are thus not capable of capturing brain mechanisms responsible for behavior [23]. Neurodynamics provides a useful language that allows for deeper understanding of behavior and many properties of mental processes. It may be linked to parameters that characterize biophysical properties of neurons and their connections, and to the network level that controls behavior, attention, memory activations and actions. Computational models provide a test ground for analysis of dynamical systems, but they can also be applied to real brain signals. There are many interesting questions that can be formulated in the language of neurodynamics. For example, a few questions related to dynamical models of neural systems are listed below:

- How to visualize and characterize different types of attractors arising in long-term dynamics of biologically inspired neural systems?
- How does depth/strength and size of basins of attractors depend on neural properties and on neural connectivity, and what is a good way to describe such properties?
- How does accessibility of attractor basins depend on properties of ion channels, neuron accommodation, inhibition strength, local excitations, long-distance synchronization and various types of noise?
- How stable are different neural models, how strongly trajectories depend on precise values of parameters?
- Are statistical features derived from recurrence quantification stable or do they suffer from numerical artifacts?
- Symbolic dynamics based on directed graphs derived from analysis of multiple runs generating long trajectories carries a lot of information but methods to analyze it yet to be developed. Some ideas may be adopted from network science [73].

- Transition probabilities between attractor basins may be used as a measure of distance to present dynamics in spaces with psychologically meaningful dimensions; such distances are not symmetric, but Finsler spaces may be used to define such representations.

Application to real brain signals leads to more questions:

- How to decompose real brain signals into components that represent microfeatures defining brain-based semantics [41]?
- EEG analysis in the source space should be more useful than in the signal (electrode) space, but it requires precise information about electrodes and anatomical MRI scans, that are rarely available. Yet, recurrence quantification analysis performed by Bosl *et al.* [61] in signal space gave excellent results for very early diagnosis of ASD, showing clearly age-dependent changes in brain activity. How non-linear analysis of neurodynamics differs when analyzed at the source and the signal level?
- Can selection of functional fMRI connections that allowed for definition of biologically meaningful markers distinguishing ASD, OCD, schizophrenia and major depression tendencies [64, 66, 68] be also found by analyzing coherence or other measures applied to the EEG signals in the source space?
- Trajectories of neurodynamics presented in large-scale subnetworks activation space may reveal information about normal and abnormal mental processes, providing unique map of mental space. Is there a unique decomposition of the whole brain activity into a combination of large scale networks that involve partially overlapping regions?
- fMRI signals have temporal resolution that may be not sufficient for analysis of switching between large-scale networks; localized well-trained activity may be washed out by averaging over regions of interest. Co-registration of fMRI and EEG signals is difficult but seems to be necessary for gaining precise information about brain dynamics [74, 75].

Characterizing influence of genetic and molecular processes on potential network states leads to many questions:

- What are precise relations of ion channels, proteins that build them and genes that code for these proteins? In the case of some disease such as autism, large number (about 1000) genes are weakly correlated

with symptoms of the disorder. Many deficits at molecular level may lead to similar dysfunctions at the network and behavior levels, how can we characterize them?

- Mental disorders in childhood are the end result of specific developmental pathway. Precise diagnostics requires understanding how behavioral symptoms differ depending on abnormal structures of specific types of neurons in different brain areas?
- Neural models of mental functions may replicate results of simple psychological experiments [54]. Changing network connectivity or changing properties of individual neurons gives estimates of the range of parameters that preserve normal neurodynamics. In this way, tendencies towards different mental diseases may be linked with molecular and genetic level. How detailed should the models be to allow for realistic conclusions?
- How are neural properties influenced by pharmacological interventions? This requires detailed models of ion channels.
- Our model of the effects of influence of calcium channelopathy on neuronal dynamics [57] explains some detailed properties of emergent reflex attention. It is the first computational model of calcium channelopathy theory of autism outlined in [76]. It may be applied to other disease, providing mechanistic explanation of higher levels of cognition that is linked to genetic and molecular level.

Finally, mapping between neural and mental spaces may also be addressed:

- It is now possible to decode images from the brain [31]; similar techniques could be used to project brain signals into a space of meaningful psychological dimensions that reflect inner experience. Trajectories that fall into attractor basins can then be treated as representations of certain mental states, viewing “mind as a shadow of neurodynamics” [28, 34].
- Spontaneous thoughts and effects of bottom-up attention are simulated by transitions between attractor basins. The speed of such transitions is a natural measure of how quickly the brain will resynchronize when a new thought or stimulus comes. It should be correlated with psychological measures of the ability of switching between mental processes, multitasking and flexibility of thinking [77].

- The speed of mental calculations and memory processes depends on neural noise [78] and can be simulated using neural models.
- Formation of new basins of attractors depends on the learning procedures, existing associations, conceptual framework that already exist. This should allow for investigation of various memory distortion, formation of strong beliefs, polarization of opinions and conspiracy theories [79].
- Dyslexia and other disorders may be studied using neural models of information flow between different brain regions. Neural models may provide some suggestions how to optimize this information flow, what type of stimuli may change properties of attractor basins and how the speed of new stimuli presentation may affect comprehension.

Neurodynamics leads to emergent processes that cannot be explained using psychological constructs and verbal descriptions. It provides a new language, fruitful novel approach that will certainly deepen our understanding of the brain.

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